

Scales and costs of habitat selection in heterogeneous landscapes

DOUGLAS W. MORRIS

Centre for Northern Studies, Department of Biology, and School of Forestry, Lakehead University, Thunder Bay, Ontario, Canada P7B 5E1

Summary

Two scales of habitat selection are likely to influence patterns of animal density in heterogeneous landscapes. At one scale, habitat selection is determined by the differential use of foraging locations within a home range. At a larger scale, habitat selection is determined by dispersal and the ability to relocate the home range. The limits of both scales must be known for accurate assessments of habitat selection and its role in effecting spatial patterns in abundance. Isodars, which specify the relationships between population density in two habitats such that the expected reproductive success of an individual is the same in both, allow us to distinguish the two scales of habitat selection because each scale has different costs. In a two-habitat environment, the cost of rejecting one of the habitats within a home range can be expressed as a devaluation of the other, because, for example, fine-grained foragers must travel through both. At the dispersal scale, the cost of accepting a new home range in a different habitat has the opposite effect of inflating the value of the original habitat to compensate for lost evolutionary potential associated with relocating the home range. These costs produce isodars at the foraging scale with a lower intercept and slope than those at the dispersal scale.

Empirical data on deer mice occupying prairie and badland habitats in southern Alberta confirm the ability of isodar analysis to differentiate between foraging and dispersal scales. The data suggest a foraging range of approximately 60 m, and an effective dispersal distance near 140 m. The relatively short dispersal distance implies that recent theories may have over-emphasized the role of habitat selection on local population dynamics. But the exchange of individuals between habitats sharing irregular borders may be substantial. Dispersal distance may thus give a false impression of the inability of habitat selection to help regulate population density.

Keywords: costs of habitat selection; dispersal; habitat selection; landscape ecology; patch choice; small mammals; spatial scale

Introduction

Density-dependent habitat selection has been invoked as a potentially potent force influencing population dynamics and community organization (Rosenzweig, 1974, 1981, 1985; Morris, 1988; Pulliam, 1988; Oksanen, 1990; Danielson, 1991; Pulliam and Danielson, 1991). The strength of this force is likely to be influenced by individual foraging ranges, and by how far individuals can successfully disperse, relative to the size, shape, and distribution of habitats in the landscape. The development and application of landscape models of habitat selection depend upon our ability to (1), successfully measure the spatial extents of foraging and dispersal, and (2), to interpret their effects on population dynamics.

I will consider two influential scales of habitat selection. I will call the scale related to foraging decisions within home ranges the foraging scale. I will call the scale related to the relocation of

home ranges the dispersal scale. I assess the effects and implications of both scales on habitat selection by explicitly analysing the contrasting influences of foraging range and dispersal distance on a free-ranging population of small mammals. First, I evaluate the contrasting effects of foraging and dispersal at a boundary between two habitat patches. I then modify habitat selection theory to develop explicit predictions about the influence of spatial scale on patterns of population density. I follow this with descriptions of field and analytical protocols that detect and quantify different scales of habitat selection. I apply both the theory and the protocols to the scale of habitat selection by deer mice (*Peromyscus maniculatus*) occurring in two habitats in heterogeneous prairie landscapes in Alberta. I conclude by discussing the ecological and evolutionary implications of habitat selection in spatially heterogeneous landscapes.

A model of habitat selection at patch boundaries

Consider a simple landscape composed of two homogeneous habitats on opposite sides of a sharp gradient (Fig. 1). Assume that both habitats are occupied by a single species, and that individuals of that species select habitat in a way that maximizes their lifetime reproductive success. At some small scale near the habitat boundary individuals will be incapable of differentiating between patches, and the two habitats function as one. The size of this scale will depend upon the differences between the habitats, the ability of individuals to discriminate between habitats, and the distinctness of the habitat boundary.

At a somewhat larger scale, individual foragers whose home ranges span the boundary can choose whether to forage in one or both habitats (Fig. 1). At this fine-grained (MacArthur and Levins, 1964) foraging scale, the decision to be selective or opportunistic in habitat use depends upon the costs of travelling through or around one type of patch in favour of finding and exploiting the other, *versus* the benefit of exploiting both (Rosenzweig, 1974, 1981).

At yet a larger scale, habitat choice during foraging will be constrained by the location of the home range. The relatively coarse-grained decision of where to locate the home range depends, primarily, upon three factors. (1) The costs associated with the amount of time lost from reproduction that is used to locate and establish a home range. (2) The survival and reproductive risks associated with both activities. (3) The expected survival and reproductive benefits of alternative home range locations (Morris, 1987a). Costs at this scale are likely to depend upon the distance travelled in search of a home range.

When the location of an individual within a habitat is such that the distance to another habitat is greater than the dispersal scale, individuals living in one habitat have no choice of an alternative. Only individuals that live along habitat boundaries can expect to encounter more than a single habitat during their lifetime. As a consequence, there will exist a still larger spatial scale where the population dynamics in each habitat will tend to be relatively insensitive to either the foraging or dispersal scales of habitat selection (Fig. 1).

Figure 1 should sound an alarm to all ecologists who hope to assess either habitat selection, or the density-dependent 'qualities' of alternative habitats. Studies that contrast habitat patches along their common border may assess a different process of habitat selection than do studies that contrast habitat patches, or study plots, that are not in close proximity to one another. Indeed, if the scale of the latter studies is greater than that of dispersal, such studies may be incapable of assessing habitat selection at all!

The relative importance of the processes in Fig. 1 to a population occupying different habitats will depend upon the size and configuration of habitat patches, and also upon density-dependent differences in reproductive success among habitats. It should thus be possible to use density-dependent habitat selection theory to examine the effects of each scale on population dynamics.

The Scales of Habitat Selection

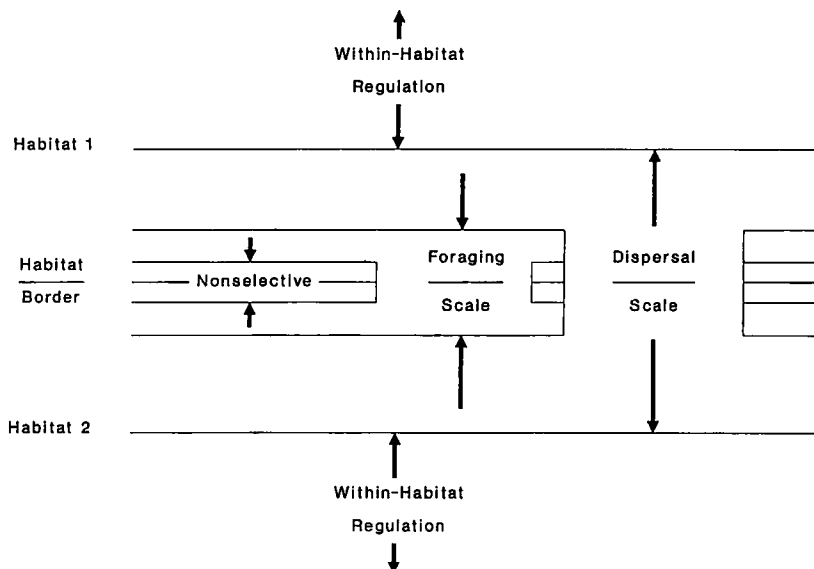


Figure 1. The scales applicable to density-dependent habitat selection between two homogeneous habitats sharing a common border. The non-selective scale corresponds to small-scale perception such that individuals are unable to differentiate between habitats (e.g. the minimum sized foraging patch). The foraging scale is that scale where fine-grained foragers optimize among alternative patches of the two habitats. The coarse-grained dispersal scale constrains habitat choice by the location of an individual's home range. Beyond the dispersal scale, individuals living in one habitat are unable to disperse to the other and population regulation will be influenced primarily by within-habitat effects. The maximum size of these effects corresponds to the maximum dispersal distance of a single individual (i.e. it does not include multi-generation migration). Similar processes also operate within single habitats.

It should also be possible to use the theory to develop protocols suitable for identifying the spatial limits of each process.

Density-dependent habitat selection at different spatial scales

A fundamental assumption of density-dependent habitat selection theory is that the expected reproductive success of individuals occupying a habitat should decline with increased population density,

$$W_i = f(N_i) \quad (1)$$

where W_i is the average reproductive success of individuals occupying habitat i (e.g. *per capita* population growth rate), and N is the density of individuals. The simplest form of Equation 1 occurs when fitness is a negative linear function of population density, i.e.

$$W_i = A_i - b_i N_i \quad (2)$$

where A_i is the maximum reproductive success possible in habitat i at low density, and b represents the *per capita* decline in reproductive success (Fig. 2, left).

Density-Dependent Habitat Selection

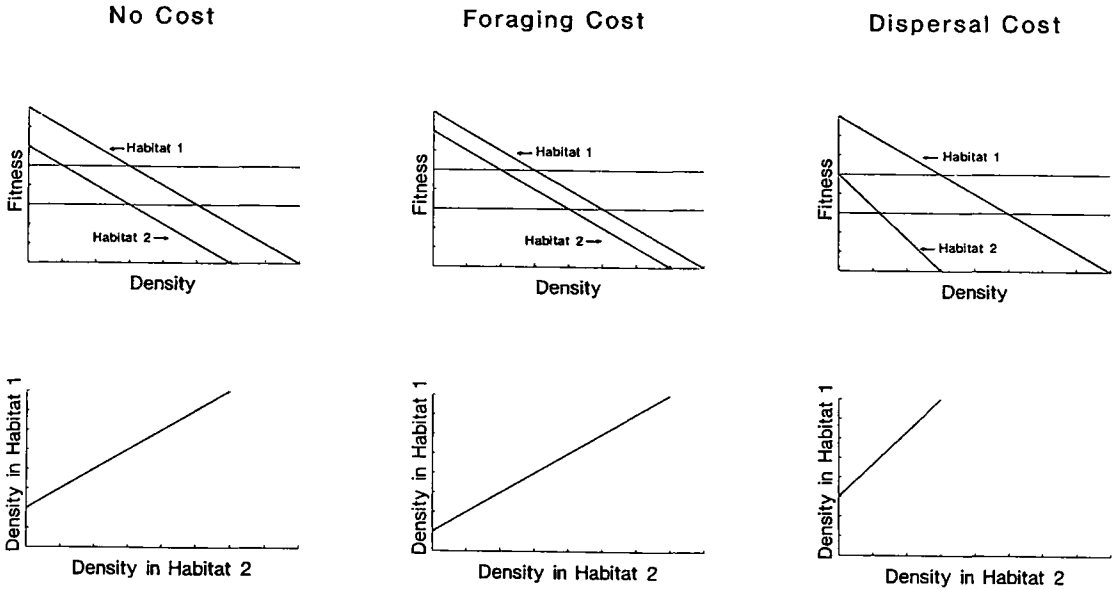


Figure 2. The effect of foraging and dispersal costs on density-dependent habitat selection. Figures on the top are plots of fitness in two habitats as a function of population density. Figures on the bottom replot the fitness-density functions as isodars. Foraging cost inflates the value of the low-quality habitat and results in non-selective habitat use at a smaller fitness differential than otherwise (the isodar intercept is reduced). Dispersal cost devalues alternative home ranges, and the cost itself is likely to be density-dependent. The resulting isodar has a higher intercept and a greater slope than the cost-free alternative.

If habitat selection obeys an ideal free distribution (Fretwell and Lucas, 1970), individuals will adjust their densities in each habitat so that

$$W_1 = W_2$$

that is,

$$A_1 - b_1 N_1 = A_2 - b_2 N_2 \quad (3a)$$

Solving for N in the habitat with the greater density (assumed to be habitat 1):

$$N_1 = [(A_1 - A_2)/b_1] + (b_2/b_1)N_2 \quad (3b)$$

Equation 3b is the cost-free isodar of habitat selection between habitats 1 and 2 (Morris, 1988, 1989, 1990). It specifies the set of population densities in the two habitats such that the expected reproductive success of an individual is the same in both. The intercept $[(A_1 - A_2)/b_1]$ is proportional to the basic differences in average fitness between the two habitats at low density (e.g. differences in productivity). The isodar slope (b_2/b_1) is equal to the ratio of the slopes of the fitness-density functions (e.g. Equation 2).

To build an isodar, consider the pair of graphs on the left of Fig. 2. The upper graph is a plot of the decline in fitness with increasing density for habitats 1 and 2. Horizontal lines represent ideal distributions where reproductive success is equal in both habitats. An isodar (lower graph) is a

plot of the set of densities in habitat 1 *versus* those in habitat 2 such that reproductive success is equal in both (the densities corresponding to the intercepts with the entire set of horizontal lines). When the fitness-density curves are parallel to one another, the isodar slope is unity (Morris, 1988). An isodar for two identical habitats has a zero intercept and a slope of 1 (the fitness-density curves are congruent).

The assumption of linearity in Fig. 2 is not crucial. A non-linear fitness model can be analysed similarly on log-transformed density estimates (Appendix A).

With cost, a fine-grained forager should become nonselective in habitat even though its average fitness in its better habitat exceeds that in the alternative (Rosenzweig, 1974, 1981; Brown and Rosenzweig, 1986). That is, an individual foraging only in habitat 1 should abandon habitat selection and use both habitats whenever

$$W_1 \leq W_2 + C_F \quad (4)$$

where C_F is the density-independent fine-grained foraging cost. C_F is the cost associated with rejecting habitat 2 in favour of exploiting only habitat 1. This foraging cost can, under some conditions, be estimated by the fitness in the lower-quality patch weighted by the ratio of search and exploitation times for good patches (Rosenzweig, 1974, 1981; explained in Appendix B).

The effect of foraging cost on density-dependent habitat selection can be approximated by substituting the general cost of Inequality 4 into Equation 3a and solving as an isodar for the density in habitat 1,

$$N_1 = \{ [A_1 - (A_2 + C_F)]/b_1 \} + \{ (b_2/b_1)N_2 \} \quad (5)$$

Note that the isodar intercept is *less* with foraging cost than it is without (Equation 3b, Fig. 2, centre). Exploitation of the high-density, 'high-quality' habitat subsidizes the low-density, 'low-quality' habitat. This inflates the low-quality habitat's value relative to a forager's expected rewards in that habitat if it was the only one being exploited (i.e. if the high-quality habitat was unavailable). The isodar intercept will likely be reduced even further if the cost of fine-grained habitat selection is itself density-dependent (Appendix b).

We can now contrast Equation 5 with the costs associated with coarse-grained dispersal. An individual should move its home range from one habitat to another only when the expected fitness in the new habitat compensates for the lost time and risk associated with dispersal. That is, an individual should move from habitat 1 to habitat 2 whenever

$$W_2 \geq W_1 + C_{1 \rightarrow 2} \quad (6a)$$

where $C_{1 \rightarrow 2}$ is the cost of dispersal, amortized over the lifetime of the individual, associated with relocating the home range from habitat 1 to habitat 2 (Morris, 1982, 1987a). The effect of dispersal cost represented in the general Inequality 6a can be approximated by an isodar in terms of N_1 by

$$N_1 = \{ [A_1 - A_2 + C_{1 \rightarrow 2}]/b_1 \} + \{ (b_2/b_1)N_2 \} \quad (7a)$$

Note that here, in contrast to Equation 5, the isodar intercept is *greater* with dispersal cost than it is without (Fig. 2, right).

Should the isodar slope also vary with dispersal cost? Yes, if the cost is density-dependent. Increased crowding may result in reduced growth rate, smaller body size, reduced energy reserves, and increased susceptibility to disease, predators, or stress. Let $1-s$ ($0 < s < 1$) represent the probability of mortality during dispersal that is caused by intraspecific crowding (s equals the corresponding probability of survival). An individual should move its home range from one habitat to another only when

$$W_2 s \geq W_1 + C_{1 \rightarrow 2} \quad (6b)$$

where $W_2 s$ decreases with increased density. Including this survival risk of dispersal, the fitness in habitat 2 can be modelled by

$$W_2 = A_2 - (b_2/s) N_2 \quad (8)$$

and Equation 7a rewritten as

$$N_1 = [(A_1 - A_2 + C_{1 \rightarrow 2})/b_1] + [(b_2/(s b_1))N_2] \quad (7b)$$

Intraspecific crowding that increases the risks of dispersal reduces the *per capita* value of the lower-quality habitat, and produces a *steeper* isodar slope (Fig. 2, right). A similar effect would occur if crowding reduced post-dispersal fecundity. The 'crowding syndrome' no doubt influences foraging behaviour as well, but it is difficult to predict how it might apply differentially to exploitation *versus* search activities (see Appendix C for a discussion of the implicit assumptions of the dispersal models).

To summarize:

- (1) Habitat selection theories apply to both foraging and dispersal scales.
- (2) The costs associated with each of these activities are different.
- (3) Costs can be detected by the intercepts and slopes of isodars.
- (4) Foraging costs in coarse-grained environments reduce the intercepts of isodars relative to the cost-free alternative.
- (5) Dispersal costs increase both the intercept and the slope of isodars.

The final two points appear to provide the basis for a test to empirically distinguish between foraging and dispersal scales of habitat selection.

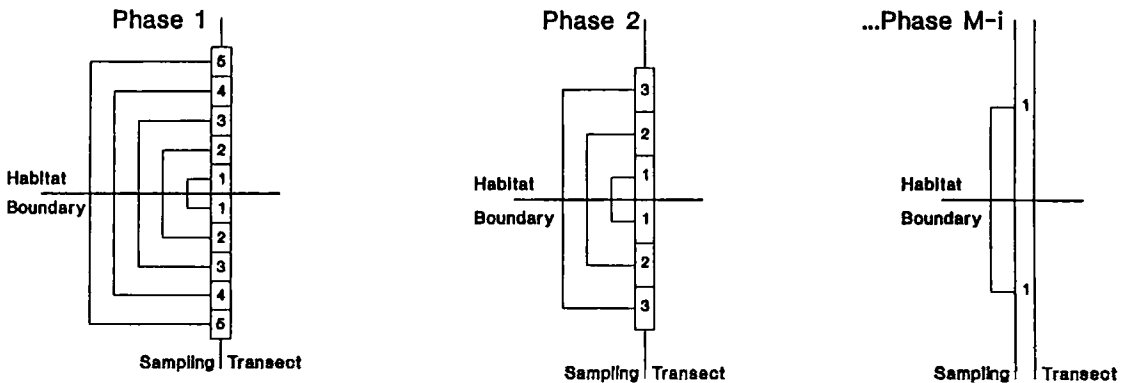


Figure 3. A field and analytical protocol to assess the scale of habitat selection. Each of the M-i phases is composed of a series of regression analyses comparing pairwise estimates of population density for different segments (rectangles) of the transect. These are represented by the 'connecting lines' in each phase. In phase 1, the analysis contrasts pairs of density estimates at the smallest reliable scale (segment length). In each subsequent phase the segment size is increased by the addition of a single sample point (assumed here to equal half the initial segment length). If the transect is symmetrical, the analysis can proceed until the segment size is equal to one half the transect length.

A field and analytical protocol to reveal the scales of habitat use

The differential effects on isodars of the costs of foraging and dispersal suggest a sequential field and analytical protocol to detect the spatial limits of each activity (Fig. 3). The following protocol details a sampling regime and a multi-phase isodar analysis capable of revealing each scale of habitat selection.

- (1) Identify the location of a sharp discontinuity in habitat.
- (2) Establish replicated, symmetrical, sample line or belt transects (depending upon what is appropriate for the species being censused) perpendicular to, and crossing, the gradient. Each transect should be composed of M sampling points with $M/2$ on each side of the habitat boundary.
- (3) Obtain estimates of population density at different points along each transect. The analysis is simplified if these points are located at constant intervals from the border.
- (4) Determine initial 'segment length' i as the minimum number of sampling points required to obtain a reliable estimate of density.
- (5) Number segments sequentially from the boundary to each end of the transect (Fig. 3).
- (6) Use the value from Step 4 in the first phase of the isodar analysis. Plot the density of individuals in the distal ($[M/2][1/i]$) segment on one side of the habitat boundary against the density of individuals in the corresponding distal segment on the other side of the boundary.
- (7) Calculate the density relationship in Step 6 by model 2 regression.
- (8) Repeat Steps 6 and 7 for all paired segments of length i (see Fig. 3).
- (9) Increase segment length to $i+1$ and repeat Steps 6–8 for phase 2 of the analysis.
- (10) Continue increasing segment length by 1 sampling point at a time, reanalysing as before until the largest scale of habitat use is revealed (see below) or until the segment length equals $M/2$.
- (11) Calculate the statistical significance of each regression equation.
- (12) Evaluate the proportion of variation accounted for by each equation.
- (13) Use step 12 to confirm differential scales of habitat selection. If the transect encompasses a region where population regulation is occurring more or less independently within each habitat, regressions of density from segments at opposite ends of the transect should account for substantially less variation in density than should regressions comparing adjacent segments on opposite sides of the habitat boundary.
- (14) Evaluate for differences in foraging and dispersal scales by contrasting the slopes and intercepts of significant regression equations among segments at the habitat boundary.
- (15) Use the intercepts and slopes of statistically significant isodars to evaluate quantitative and qualitative differences between habitats.
- (16) If competing species are expected to influence the isodar analysis, remove their effects by regression (Multiple species isodar analysis, see Morris, 1989), and repeat the protocol beginning at Step 6.

Study area and methods

Remnants of native mixed-grass prairie grade abruptly into steep, highly eroded postglacial badlands along several river systems in southern Alberta. Badland formation is extensive and spectacular along the Red Deer River (Dinosaur Provincial Park) and Milk River (Milk River Canyon) valleys. The contrast between badland and prairie habitats is dramatic, and the boundary is often discrete and unambiguous (Step 1 of the protocol).

Prairie habitats at each site are flat with more or less homogeneous mixed-grass prairie growing on aeolian sands and silts. The prairie is dominated by grasses (*Stipa comata*, *Bouteloua gracilis*,

Koeleria cristata) with numerous inconspicuous species and ephemeral forbs (e.g. *Selaginella densa*, *Phlox hoodii*, *Astragalus drummondii*, *Oxytropis splendens*, *Solidago missouriensis*) and interspersed 'shrubs' (*Artemisia frigida*, *Opuntia polyacantha*, *Mammillaria vivipara*).

Badland habitats, by comparison, are characteristically heterogeneous with frequent changes in substrate, slope, aspect, and plant cover. Eroding sandstones and claystones in the badlands lack dense vegetation except in small 'pockets' of prairie or shrubs in suitable microclimates and occasional lush vegetation on north-facing slopes. Sparse drought-resistant shrubs (e.g. *Sarcobatus vermiculatus*, *Artemisia cana*, *Chrysothamnus nauseosus*) occur throughout.

In contrast to badlands elsewhere in southern Alberta, badland development at Dinosaur Provincial Park occurred in a series of erosional phases (Bryan *et al.*, 1987). Rapid drainage of ice-impounded lakes scoured a broad postglacial spillway which was further incised by residual melt waters. The result is that prairie habitats (mesas and terraces) occur within the Red Deer River badlands. The transition between these isolated prairie habitats and eroded badlands is often as abrupt as that at the prairie rim.

In the spring (13 April–10 June) of 1989, 21 live-trap transects (20 m trap spacing, 20 stations per transect) on a north-south axis and centred on prairie-badland boundaries were located within Dinosaur Provincial Park (Red Deer River), along the Milk River Canyon (Milk River), and along the Lost River valley (a tributary of the Milk) (steps 2 and 3 of the protocol). In autumn (11–19 September) 1990, a further six transects were located in each of Dinosaur Provincial Park and along the Milk River Canyon. The mean distance between transects located within a single river valley was greater than transect length.

All transects in the Milk and Lost River valleys included upland mixed-grass prairie, and descended into badland habitats. Four transects (two in each of 1989 and 1990) at Dinosaur Provincial Park also descended from the upland prairie into eroded badlands. The remainder (8) were composed of prairie-badland transitions located within the badland 'formation'. The isodar analyses reported here exclude these latter transects, and concentrate exclusively on upland/badland transitions.

Vegetation and substrate cover of each station were calculated from ten systematically located points along a randomly directed 10 m transect centred on each trap station. These data were summarized by three cover classes ('rock' (includes gravel), 'soil' (sand, soil, clay), and 'vegetation' (grasses, forbs, *Salaginella*)). Slope and elevation (converted to z-scores standardized to the mean elevation of each transect) were also used to characterize each station. Correlations among variables were used to define the gradient from prairie to badland habitats by Principal Components Analysis (SPSS PC+, Norusis, 1988). Principal component scores were generated for each station and entered into a Discriminant Function Analysis (SPSS PC+, Norusis 1988) to confirm distinctions between the two habitats. Classification probabilities were calculated for each station to evaluate the effectiveness of the analysis at discriminating between prairie and badland habitats.

Deer mice (*Peromyscus maniculatus*) were common in both habitats (880 of 886 captures). Other small mammals were rare and infrequently captured (*Lagurus curtatus*, *Perognathus fasciatus* – one capture each; *Onychomys leucogaster* – four captures). Thus, the small mammal community was composed almost entirely of a single species, and the potential effects of species interactions among them can be ignored in this study (Step 16).

Estimates of deer mouse density were obtained by live-trapping each transect for 2–3 consecutive nights (two-night sequences occurred when we avoided spring thunderstorms that create extreme hazards for large bipedal mammals in the badlands). With a maximum of three consecutive nights of live-trapping, point estimates of density may be misleading. I therefore set the minimum segment 'length' for the density estimates to pairs of stations (Step 4 of the

protocol). Density was estimated as the mean number of different individuals captured per station in each segment (i.e. the number of different individuals captured in each segment of two stations divided by two). Individuals captured in more than one segment contributed to the density estimate in each. Segments were numbered sequentially (Step 5). Isodar analysis and interpretation followed steps 6–15 of the protocol.

Results and interpretation

Deer mouse density

Estimates of mean deer mouse density per station ranged from zero in upland prairie (no deer mice were captured in 7 of 33 prairie transects) to 2.3 in badlands (Dinosaur Provincial Park, autumn 1990). The high 1990 densities at Dinosaur Provincial Park may have been an underestimate of true densities because there were more rodents available for capture than there were traps to hold them. The 1990 'Dinosaur' data were excluded from the isodar analysis.

The habitat gradient

The first principal component accounted for 56.7% of the common variation among the five habitat variables. PC 1 revealed a pronounced gradient between grass and herb-covered, flat, upland prairie and barren, steep, and exposed badlands (Table 1). The second principal component accounted for only 20.2% of the variation among variables and it and all subsequent components were discarded from further analysis.

Two-group discriminant function analysis contrasting principal component scores between upland and badland trap stations (23 transects) was highly significant ($\chi^2 = 695.5$, $df = 1$, $p < 0.0001$, 460 stations). Only three of the 230 prairie stations were misclassified by the analysis. Classification of badland stations was slightly less efficient (23 of 230 stations misclassified) reflecting small prairie 'pockets' within the badland habitat. The discrimination between prairie uplands and badlands along the prairie/badland gradient is an impressive confirmation of the discrete and unambiguous boundary between them.

The scale of habitat use

The first phase of the isodar analysis began by contrasting the paired segments (40 m linear distance) from opposite ends of each transect (stations 9–10 on each side of the boundary, Fig. 4). The regression was non-significant ($F = 2.61$, $df = 1, 21$, $p = 0.12$). Further regressions (Step 8) on two-trap segments were similarly non-significant until paired segments from 40–80 m (stations 3–4) on each side of the habitat boundary were contrasted (regression Equation 1: deer

Table 1. Correlations (standardized regression coefficients) between five habitat variables and the first principal component describing their common variation along a prairie upland/badland gradient (analysis based on 660 samples).

Variable	Description	Correlation to PC 1
VEGETATION	Vegetation cover	-0.95
SLOPE	Slope at the trap station	0.83
SOIL	Soil 'cover'	0.70
ROCK	Rock and gravel 'cover'	0.62
ZELEV	Z score of elevation	-0.61

mouse density in badland = $0.35 + 1.9$ deer mouse density in prairie, $F = 7.39$, $df = 1, 21$, $p = 0.01$, Fig. 5). Adjacent segments (stations 1–2) on opposite sides of the boundary produced an even tighter regression line (regression Equation 2: deer mouse density in badland = $0.23 + 1.1$ deer mouse density in prairie, $F = 11.78$, $df = 1, 21$, $p = 0.003$, Fig. 5).

Regression Equations 1 and 2 are consistent with active habitat selection by deer mice living along the border between badland and prairie habitats. Yet passive diffusion of individuals from high-density badlands to low-density prairie would also produce an increasing density gradient as one travels from prairie to badland habitat. Regressions of density in the two habitats, calculated from estimates adjacent to their common border, should produce less residual scatter than similar regressions calculated from estimates taken at a greater distance from the border. A reduction in scatter alone, is thereby insufficient to infer active habitat selection. But passive diffusion lacks, by definition, the costs that modify active habitat choice at the foraging and dispersal scales. Given the two alternatives between passive and active habitat selection, significant differences in isodar slopes between adjacent and more distant estimates of density can parsimoniously be explained only by active density-dependent habitat selection.

Despite considerable variation in segment 2, the slope of the regression equations for pairs of trap stations is greater for the more distal comparison (segment 2) than it is for the more proximal one (segment 1) (Fig. 5, geometric mean regression slope of regression Equation 1 = 1.90, 95% confidence interval = 1.16–2.64, geometric mean regression slope of regression Equation 2 = 1.12, 95% confidence interval = 0.71–1.5, Fig. 5). This pattern is consistent with foraging costs operating at a scale on the order of 40–80 m (stations 1 and 2 were located at respective distances of 10 and 30 m on each side of the habitat boundary). The lack of significant regression equations for any of the remaining two-trap segments suggests that the dispersal scale occurs on the order of only 120–160 m (stations 3 and 4 were located at 50 and 70 m on each side of the boundary). If the dispersal scale was larger than this, the regressions contrasting more distal segments (stations 5 and 6) should also have been significant (but with a slope and intercept not significantly different from regression Equation 1). Density-dependent habitat selection, as revealed by two-trap segments, is limited to within 80 m of the boundary between prairie and badland habitats.

Note, also, that the intercept of Equation 2 is less (but not significantly so) than the intercept of Equation 1 (Fig. 1). Recall that a reduction in the intercept is predicted with foraging cost. This bolsters the interpretation that the foraging scale of habitat use by deer mice exploiting prairie and badland habitats in southern Alberta is on the order of only 30 m (location of station 2) on each side of the habitat boundary. This is a remarkably close fit to reported home-range sizes on the order of 0.3 ha in grassland habitat (Stickel, 1968; Table 1).

It seems likely, in any case, that the dispersal scale has been adequately identified, and that the analysis could profitably be curtailed at phase 1. Yet further increases in segment lengths (Step 9) may reveal additional detail about geographical variation in deer mouse density, especially if segment 3 (stations 5 and 6) included both dispersal and independent habitat effects. The regression equation on the most distal three-trap segments (stations 7–9 on each side of the boundary) was highly significant (regression Equation 3: deer mouse density in badland = $0.48 + 1.5$ deer mouse density in prairie, $F = 8.47$, $df = 1, 21$, $p = 0.008$). The next three-station segment (stations 4–6 on each side of the boundary) produced a non-significant regression ($F = 2.03$, $df = 1, 21$, $p = 0.17$), whereas the comparison of adjacent segments (stations 1–3 on each side of the boundary) again produced a highly significant regression (regression Equation 4: deer mouse density in badland = $0.18 + 1.5$ deer mouse density in prairie, $F = 22.36$, $df = 1, 21$, $p < 0.001$, Figs 6 and 7).

I view the three-station regressions as support for my interpretations of foraging and dispersal

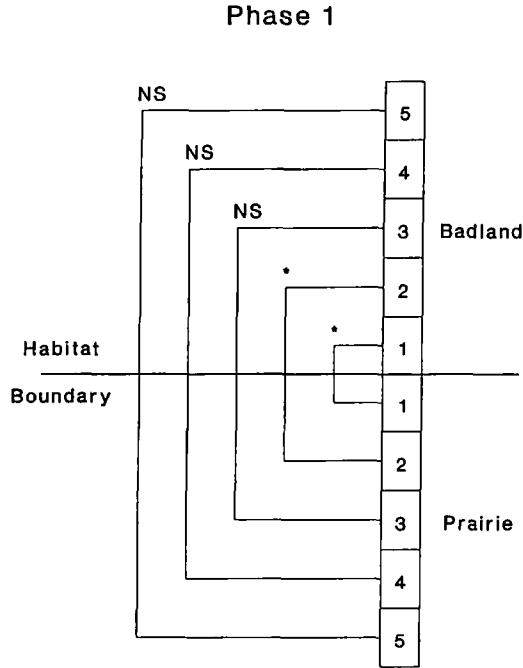


Figure 4. Phase one of the isodar analysis documenting foraging and dispersal scales of habitat selection in deer mice occupying prairie and badland habitats in southern Alberta. This phase contrasts the density of pairs of two-trap segments along 23 transects at prairie upland/badland habitat transitions. Only those comparisons marked with asterisks are statistically significant. The density of deer mice at one end of the transect cannot be predicted by the density at the other end.

Phase 1

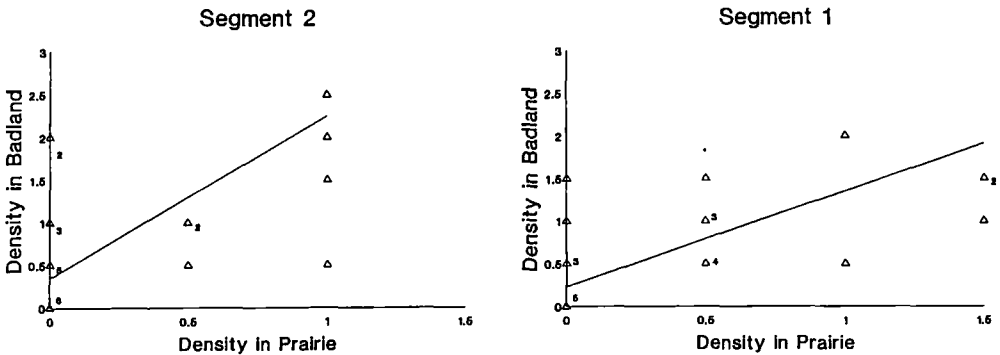


Figure 5. Statistically significant isodars from the first phase of the spatial analysis contrasting deer mouse density along 23 transects perpendicular to a boundary between badland and prairie habitats. The regression corresponding to segment 1 compares pairs of trap stations adjacent to the habitat boundary. The regression corresponding to segment 2 contrasts pairs of trap stations located at 50 and 70 m beyond the boundary. Numbers indicate the number of samples with identical values. Densities are the mean number of different individuals captured per station.

Phase 2

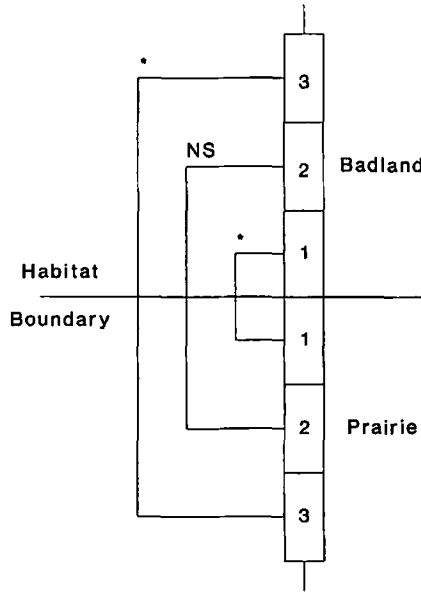


Figure 6. Phase two of the isodar scale analysis. This phase contrasts deer mouse density among pairs of three-trap segments along 23 transects at prairie upland/badland habitat transitions. Comparisons marked with asterisks are statistically significant.

Phase 2

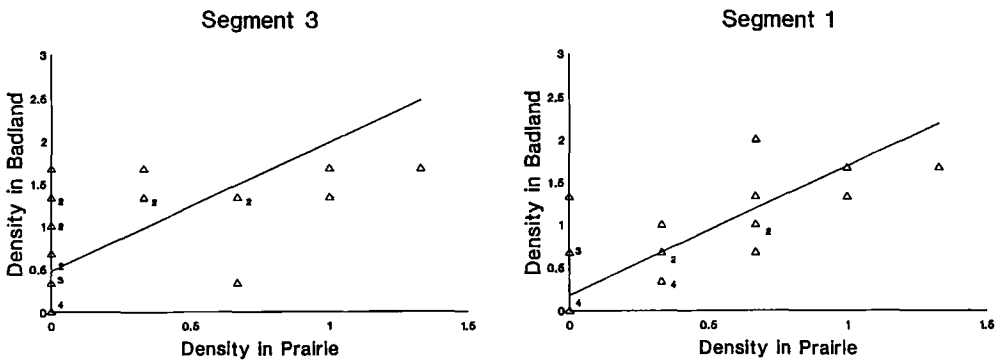


Figure 7. Statistically significant isodars from the second phase of the spatial analysis. The regression corresponding to segment 1 compares the three trap stations adjacent to the habitat boundary. The regression corresponding to segment 3 contrasts the triplet of trap stations located between 130 and 170 m beyond the boundary. Densities and symbols as in Fig. 5.

Phase 3

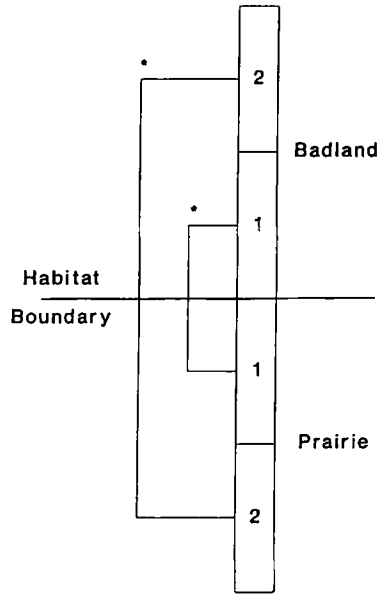


Figure 8. Phase three of the isodar scale analysis. Comparisons are regressions of density among pairs of five-trap transects along 23 20-station transects at prairie upland/badland transitions in southern Alberta. Both regression equations were statistically significant.

Phase 3

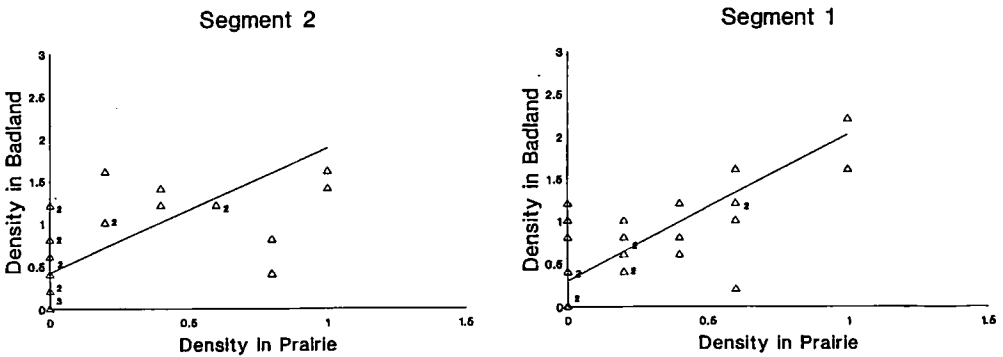


Figure 9. Statistically significant isodars from the third phase of the spatial analysis. The regression corresponding to segment 1 compares the first five stations proximal to the habitat boundary. The regression corresponding to segment 2 contrasts the five stations distal to the boundary. Densities and symbols as in Fig. 5.

scales in deer mice. The regression of adjacent densities (regression Equation 4) documents strong density-dependent habitat selection in the region of the habitat boundary. The slope of regression Equation 4 is intermediate between that of regression Equations 1 and 2, suggesting that it bisects the foraging and dispersal scales of habitat selection. The failure of the next segment (stations 4–6) to reveal density-dependent habitat selection can be accounted for if those density estimates are generally beyond the dispersal range of deer mice, or if they mix dispersal and independent habitat effects. But if so, why should the most distal comparison (stations 7–9) again yield a significant regression? The most likely explanation is that three-trap segments are of a critical size where they can occasionally detect local (transect to transect) variation in population density. This is precisely what we would expect if the foraging scale is on the order of two-trap segments.

I did not calculate regression equations for groups of four trap stations because such groupings would produce only two different regression equations (ten stations on each side of the boundary, eight would be in the analysis), the same number produced with more information from groups of five stations (all ten stations in each habitat included in the analysis). Both of these latter regressions were statistically significant (Fig. 8). The distal comparison (stations 6–10 on each side of the boundary, regression Equation 5: deer mouse density in badland = $0.42 + 1.5$ deer mouse density in prairie, $F = 7.66$, $df = 1, 21$, $p = 0.01$) again had a smaller F-ratio than the proximal one (stations 1–5, regression Equation 6: deer mouse density in badland = $0.30 + 1.7$ deer mouse density in prairie, $F = 18.57$, $df = 1, 21$, $p < 0.001$, Fig. 9). None of the coefficients were statistically different from one another.

The regressions in Fig. 5 are problematical in that each is based on a small range of possible densities. The small range of values limits our confidence that the 'boundary' between dispersal and foraging scales is found between the first and second census segments. If the change from foraging to dispersal scales does occur at about 30 m from the habitat boundary, increased segment length should produce a consistent increase in the slope of segments proximal to the habitat boundary (because the two scales are mixed). The data support this prediction (compare the slope of segment 1 among Figs 5, 7, and 9).

There is another consistent pattern in all three phases of the analysis. The correlation between densities tends to decrease with increased distance from the habitat boundary. This effect is most pronounced for the distal regressions (Figs 7 and 9) where deer mouse density in badland appears to be invariant across a wide range of prairie densities. The linear regressions are statistically significant, but the pattern of residuals is dramatically non-linear. I interpret this to mean that population dynamics at the distal ends of the transects occur more or less independently of one another. The significant distal regressions are likely caused, instead, by regional differences in abundance (transect to transect variation). The density of deer mice in the badland is tightly connected to that in the prairie near the habitat border, but is essentially disconnected beyond the effective dispersal range of about 140 m. This pattern is in agreement with the explanation that density-dependent foraging and dispersal link the dynamics on one side of the habitat boundary with those on the other.

Discussion

Implications of short-distance dispersal

It is apparent from all phases of the analysis, and at both the foraging and dispersal scales, that the population density of deer mice responds to habitat. Population density in badland habitat typically exceeds that of deer mice living in nearby prairie. Yet it is equally apparent that dispersal acts to regulate population density over a surprisingly small scale (140 m). The limited

spatial exchange of individuals caused by short-distance dispersal constrains the use of isodars. Isodars located at habitat boundaries are likely to yield different results than will isodars located farther away from the boundary.

Spatial constraints compromise one of the more desirable attributes of isodar analysis, its potential to reveal habitat differences (Morris, 1988). Quantitative differences (e.g. differences in productivity) produce isodars whose intercepts exceed zero, but whose slopes equal 1.0. Qualitative differences (e.g. differences in habitat structure or kinds of resource that influence foraging efficiency) produce isodars whose slopes are different from 1.0. Thus, isodar analysis, by interpreting the signals of differences in population density, allows the organisms themselves to 'tell' us how they perceive habitats. But if the isodars are dependent upon foraging and dispersal scales, our interpretations of habitat differences will depend upon the geographical scale of our density estimates.

Qualitative and quantitative differences in habitat have profound implications for population regulation. Quantitative differences alone imply that individuals are equally efficient in extracting resources and converting them into descendants in each habitat (otherwise the slope \neq 1.0). One habitat will consistently support a greater density than the other, but density-dependent feedback on reproductive success will be the same in both (parallel population regulation, Morris, 1988). Qualitative differences alone suggest that habitats differ in the influence of density-dependence on reproductive success. The proportion of the population in each habitat will remain constant (e.g. divergent population regulation, Morris, 1988). Which of these scenarios of habitat-dependent population regulation applies to deer mice living near the boundary between prairie and badland habitats?

Regressions of density estimates reflecting the foraging scale, (regression Equation 2), suggest that both habitats support the same average density of deer mice (positive intercept not significantly greater than zero, no quantitative difference), regardless of differences in absolute density (slope not significantly different from 1.0, no qualitative differences between habitats, congruent population regulation (Morris, 1988)). Regressions at the dispersal scale (regression Equation 1), however, suggest both quantitative and qualitative differences in habitat (positive intercept, isodar slope significantly $>$ 1.0, divergent regulation (Morris 1988)). The increases in the intercept and slope of the isodar, as we move away from the habitat boundary, confirm the spatial theory of habitat selection.

The differences between the isodars emphasize our concern that comparative estimates of habitat quality based upon density may be highly sensitive to the spatial context of the study. Studies that emphasize data collection only at ecotones may frequently evaluate a different scale of habitat use than studies that compare density estimates obtained in the 'centres' of more or less homogeneous, but functionally disconnected, patches. The ecotone study is likely to misinterpret habitat use because it is unclear whether it is evaluating foraging or dispersal scales. The disconnected patch study runs the risk of evaluating habitat use independent of habitat selection. Yet this latter design is probably effective if our objective is to evaluate the carrying capacity of different patches in terms of population density (e.g. regression Equation 5, quantitative and qualitative differences between badland and prairie habitats). It thus seems essential that habitat assessments incorporate a scale protocol, similar to that described here, in order to document the effective scale of any similarities and differences in habitat (see Appendix D for additional precautions).

The role of habitat selection in population regulation

From an ecological perspective, the small scale of dispersal in deer mice may appear to suggest that habitat selection by individuals plays a relatively insignificant role in determining local

population dynamics. If that is true, and if similar results are observed in other species, this would downgrade the potential of processes such as source-sink regulation in determining the dynamics of populations and the structure of ecological communities (e.g. Pulliam, 1988; Oksanen, 1990; Danielson, 1991; Pulliam and Danielson, 1991). A short dispersal distance in landscapes composed of large patches is also effective at reducing habitat sampling, thus reinforcing divergence among populations and the evolution of conservative niches (Holt and Gaines, 1992). As long as the mean linear dimension of patch size exceeds the dispersal scale, local population density is likely to be determined more by regulation acting within habitats than it is to be influenced by habitat selection. This assumes, of course, that changes in carrying capacity occur on a temporal scale of the same approximate duration as dispersal. Otherwise, gradual diffusion from areas of high to low density would tend to equalize individual expectations of reproductive success.

As noted above, a pattern of increased 'connectedness' in population density at habitat borders need not imply active habitat choice. Indeed, a process of purely passive migration can lead to evolutionarily stable strategies of habitat selection (Brown and Pavlovic, 1992). But passive migration suggests a diffusion process that, by itself, is unlikely to modify the slopes and intercepts of isodars at different distances from habitat boundaries. The same will not be true for species that exhibit both passive emigration and either habitat or density-dependent 'stopping rules' that modify dispersal distance. Such species, nevertheless, are clearly capable of habitat choice and lie somewhere between so-called active and passive habitat selectors. The protocol described here should be able to document species whose patterns of habitat use contain an active component. My data suggest that habitat selection, by deer mice living in prairie and badland habitats, is at least partially due to active density-dependent habitat choice.

Regardless of the evidence in favour of density-dependent habitat choice, density-dependent habitat selection may not appear to be a potent force influencing population regulation of deer mice exploiting prairie and badland habitats in southern Alberta. Native prairie, even with its currently reduced and fragmented extent, occurs on a scale that is conservatively three orders of magnitude greater than the apparent dispersal scale of deer mice. The same is true of badlands. Seasonal and annual fluctuations in deer mouse abundance are legend. Local changes in carrying capacity probably occur, therefore, on a temporal scale similar to the duration of successful dispersal, thus limiting the effectiveness of long-range diffusion in modifying population density. But badlands are erosional features of the landscape occurring along major river valleys and their associated tributaries. The resulting sinuous, reticulate form magnifies contact with prairie, and may increase the role of density-dependent habitat selection in local population regulation. This means that the importance of habitat selection as a process determining local population density depends, not only upon dispersal distance, but also upon the relationship between edge and habitat area in the landscape (edge can be measured as the fractal dimension of the landscape, e.g. Sugihara and May, 1990).

Dispersal is generally thought to have a significant effect not only on population regulation, but also on population persistence (Fahrig and Paloheimo, 1988; Anderson, 1989). In extremely patchy environments, local populations existing within individual habitat patches may frequently run an extinction risk at low density (e.g. Goodman, 1987). Population persistence under such conditions would depend upon recolonization from adjacent or nearby patches (Fahrig and Paloheimo, 1988). Those populations that persist will presumably preserve genotypes predisposed to dispersal on a scale that reflects the average distances required to move between habitats in the landscape. Dispersal distance, then, is likely to be a product of the landscape within which it has evolved.

It is apparent that additional research on the magnitude of dispersal and foraging scales will

be necessary to reveal general patterns in the scale of habitat and patch use in natural populations. This work will need to do more than document the spatial patterns of animal and plant abundance. It will need to place those patterns into the context of the processes that have created them. Further studies on density-dependent habitat selection would appear to be a profitable beginning.

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Appendix A

Non-linear density-dependent decline in fitness

The isodars in this paper are modelled on a linear decline in fitness with increased population density (Equation 2). Each individual is assumed to have an equal and additive negative effect on average reproductive success (Morris, 1988). Whether the assumptions of this model are correct, or not, a linear fit is always a reasonable first approximation to a wider class of possible responses.

Other models, including those based on continuous input, assume, for example, that intake rate declines in proportion to the ratio of resource density to consumer density (Parker and Sutherland, 1986; Milinski and Parker, 1991; Kacelnik *et al.*, 1992). Under these conditions, resource encounter will be proportional to the density of individuals in the patch. That is,

$$W_i = R_i / (N_i \alpha_i)^m \quad (\text{A1})$$

where W_i is the expected fitness in habitat i , R is the availability of resources corrected by renewal rate, N is population density, α is the *per capita* demand on resources, and m is an interference coefficient that specifies the reduction in an individual's intake rate with increased intraspecific density (Hassell and Varley, 1969; Sutherland, 1983; Milinski and Parker, 1991). For an ideal free distribution of foragers exploiting two patches,

$$W_1 = W_2$$

and

$$R_1 / (N_1 \alpha_1)^m = R_2 / (N_2 \alpha_2)^m \quad (\text{A2})$$

The resulting cost-free isodar is given by

$$\log N_1 = (\log R_1 / m_1) - (\log R_2 / m_1) + [(m_2 / m_1) \log \alpha_2] - \log \alpha_1 + [(m_2 / m_1) \log N_2] \quad (\text{A3})$$

The applicability of linear or non-linear fitness functions can thus be assessed by a comparison of isodars calculated on arithmetic *versus* logarithmic scales.

Appendix B

Density-dependent foraging costs

Rosenzweig (1974, 1981) demonstrated that a fine-grained forager in a two-patch environment should abandon exclusive use of the better patch (B) in favour of using both only when

$$\ln W_B < \ln W_G (1 + t_m/t_B) \quad (\text{A4})$$

where $\ln W_B$ is defined in this appendix as the average net fitness to be gained by foraging in patch B, $\ln W_G$ is the same for patch G, t_B is time spent harvesting resources in patch B, and t_m is the time spent moving throughout the patches while not exploiting them. The ratio t_m/t_B in this model can be thought of as the density-independent cost of selecting patch B over patch G. The ratio t_m/t_B will be inversely related to the abundance of patch B in an individual's home range. Individuals will thus exploit patch B to a lower net gain ($\ln W_B$) in home ranges where B is common, than they will where patch B is a smaller proportion of the home range.

With increased density, additional foragers are likely to depress resources, and thereby reduce the fitness gains of the patches they exploit. But t_m and t_B are likely to also be affected by the resource depression. Assuming no changes in foraging behaviour, a reduction in resource density in patch B is almost certain to reduce the amount of time an individual spends foraging, and to simultaneously increase its travel time in that patch. Similar effects are likely to occur with increased density through intra-specific encounters. Density-dependent costs thereby erode the net fitness gain that could otherwise be achieved by habitat selection. Habitat selection will be abandoned at a lower density than would occur in the absence of density-dependent costs because poor quality habitats will be occupied at a lower population size. The net result of density-dependent foraging costs is, therefore, an *additional* reduction in the isodar intercept.

Empirical complications at the foraging scale

The use of Equations 3b and 5 to predict density responses at the foraging scale raises an interesting complication. Recall that there is some threshold density in the high-quality habitat beyond which individuals should choose to be non-selective in habitat use. Beyond this density, all individuals should exploit both habitats regardless of the *per capita* reduction of fitness within them. If all individuals exploit both habitats, a complete census would 'capture' each individual in each of the two patch types, and the density of animals would appear to be the same in both. Detailed estimates of population density at the foraging scale might therefore be expected to produce an isodar with a slope of 1.0. The chance of this actually happening appears to depend upon the scale and distribution of habitat patches.

Imagine a fine-grained environment in which patches of habitat are smaller than home-range size. Individuals can expect to encounter patches of each type. Nevertheless, some home ranges will contain a higher proportion of high-quality patches than will others, and home ranges with equal proportions of the two patches are likely to vary in habitat configuration. Both effects will modify the travel cost of fine-grained habitat selection.

Individuals occupying home ranges with low travel costs between patches of high-quality

habitat should harvest the high-quality patches to a lower reward before becoming non-selective in habitat than should individuals occupying home ranges with higher costs (Rosenzweig, 1974, 1981; Equation A5). Average reproductive success will be greater in those home ranges with the lowest costs. As animals attempt to maximize their reproductive success through the location of their home range, they will preferentially occupy home ranges with the lowest habitat selection costs. This will produce a negative correlation between population density and the costs of fine-grained habitat selection. The result is that both habitats will be exploited at a higher density in areas where costs are low than in areas where costs are high, but the densities in adjacent patches of the two habitats will tend to be the same. An isodar, carefully constructed between pairs of adjoining patches at this foraging scale, should produce a slope near 1.0.

Next, imagine a coarse-grained environment where the two habitats join along a common boundary (Fig. 1). Assume that population density is sampled at several paired points along both sides of the boundary and that the samples are used to construct an isodar. Individuals occupying home ranges spanning the boundary will share components of their home range with other individuals whose home range falls entirely within one or the other habitat. Individuals whose home ranges span the boundary between the two habitats subsidize their use of the low-quality habitat by exploiting the high-quality one. This process inflates the expected rewards of the low-quality habitat near the boundary while diluting the high-quality one. Home-range overlap will thus tend to be greater on the low-quality side of the boundary, and less on the high-quality side, than would occur if none of the home ranges encompassed both habitats. The densities will be more similar than otherwise, and the isodar intercept will be reduced (Equation 5).

Appendix C

Assumptions of the dispersal models

An implicit assumption of Equations 6–8 is that dispersal is unidirectional from the higher to the lower-quality habitat. Yet it is apparent, especially in fluctuating environments, that un- or under-occupied patches of high-quality habitat may be colonized from lower-quality ones. Individuals faced with such a decision will still incur a cost of dispersal which would devalue the perceived rewards of the high-quality patch rather than the low-quality one (Morris, 1987a, 1991). This would lead to isodar predictions opposite those of Fig. 2 (Morris, 1987a; Fig. 2d). Isodar predictions may be difficult, however, for a shifting mosaic of patches with dispersers moving both to and away from low-quality areas.

Complicated scenarios of patch use may be relatively uncommon. Once occupied, population production in high-quality habitats should quickly exceed that in low-quality ones. Even if average reproductive success is equal in both, the higher-quality habitat will produce more individuals per unit area because of its numerical advantage. If the decline in fitness with density is similar in the two habitats, ideal habitat selection should lead to directional dispersal toward the habitat with low density (Holt, 1985; Morris, 1987b; see Morris, 1987a, 1988 for discussion of isodars between pairs of habitats with more complicated relationships between fitness and population density).

A related process of rapid population growth in newly colonized habitats may act to counter-balance directional dispersal. This is because the descendants of dispersers may frequently be able to occupy their natal habitat without paying as great a dispersal cost as their parents (i.e. they are dispersing within, rather than between, habitats). The average net fitness of descendants would then be greater than that of their immigrant predecessors. The result is an increased *per capita* population growth rate that can quickly eliminate any advantage for directional migration (Morris 1987a). Tests of the spatial theory must, therefore, be conducted in systems where

dispersal is likely to be an ongoing process (e.g. in systems with an annual 'reset' of habitat quality by overwinter mortality).

Appendix D

Precautions and caveats

One of the challenges, and attractions, of a landscape perspective is the necessity that ecologists deal explicitly with spatially autocorrelated processes. A common approach to autocorrelated spatial data integrates exploratory analysis of the spatial structure with a subsequent interpretation of its influence on ecological patterns and processes (e.g. Legendre and Fortin, 1989). The approach I outline here suggests a powerful alternative. For some processes, such as density-dependent habitat selection, it may be possible to infer, *a priori*, what the spatial autocorrelation should look like, and how it may vary with spatial scale. I suspect that other evolutionary theories may be able to be integrated with landscape ecology in a similar way.

It is possible, nevertheless, to interpret my results as nothing more than a product of spatial autocorrelation. Autocorrelated densities in neighbouring segments will create isodars with zero intercepts and slopes near unity. Animals occupying home ranges in adjacent segments could, for example, be captured in both. Animals occupying non-overlapping home ranges between distant segments could not be captured in both. The isodar may change if the autocorrelation decays with increased distance. Isodars constructed from distant segments would have a different slope and intercept than adjacent ones if individuals recognize the habitats as being different. In my research, the slope of the isodar was steeper at the dispersal scale. Spatial autocorrelation should not produce this effect unless fitness declines more rapidly in prairie habitat than it does in the badlands (diverging fitness-density functions, e.g. Morris, 1988). It would thus be informative to test the theory experimentally by altering resources so that one can predict, in advance, the relative density-dependent rewards in each habitat.

Practitioners of isodar analysis should also be alert to potentially confounding effects caused by patches with different resource renewal rates. This is because the relative abundances of such patches can have major effects on the abundance of predators and their prey in heterogeneous landscapes (Oksanen *et al.*, this volume). One of the population consequences of the Oksanen model is that density-dependent habitat selection, as revealed by isodar analysis, may frequently depend upon the mix of habitats. If low-quality habitat is abundant, densities may be depressed in high-quality patches. The habitats would then appear more similar than in a landscape dominated by high-quality sites. This should not be a serious problem in my design where the two habitat types of interest are juxtaposed along a common border. But if the 'habitats' differ in the proportional composition of smaller-scale patches, the functional form of the isodar would be landscape dependent. This is easily incorporated into the isodar design by examining the pattern of residuals among the different landscapes. Landscapes with many low-quality patches should lie above the regression line (inflated densities in the high-quality areas) whereas landscapes with few low-quality patches should lie below it (depressed densities in high-quality areas). Nevertheless, landscape composition is bound to remain a serious concern in habitat assessment, and is likely to be resolved only by comparisons that contrast density relationships across many alternative landscapes.