Optimally Foraging Deer Mice in Prairie Mosaics: A Test of Habitat Theory and Absence of Landscape Effects
Author(s): Douglas W. Morris
Source: *Oikos,* Vol. 80, No. 1, (Oct., 1997), pp. 31-42
Published by: Blackwell Publishing on behalf of Nordic Society Oikos
Stable URL: http://www.jstor.org/stable/3546513
Accessed: 06/08/2008 09:11

Optimally foraging deer mice in prairie mosaics: a test of habitat theory and absence of landscape effects

Douglas W. Morris

Morris, D. W. 1997. Optimally foraging deer mice in prairie mosaics: a test of habitat theory and absence of landscape effects – Oikos 80: 31–42.

The foraging behavior of individuals, as well as the patterns of abundance that it helps create, is likely to depend on habitat and its associated landscape context. I tested this idea by measuring deer-mouse abundance and quitting-harvest rates (giving-up densities of resources in artificial foraging patches) along transects crossing badland boundaries between small and very large patches of prairie habitat in western Canada. Giving-up densities declined with increased population density among replicated census transects, they were independent of density at the foraging scale spanning habitats within transects. Giving-up densities were higher in prairie than in adjacent badland, deer mouse densities were opposite. Population density in the badland declined toward the border with prairie, presumably because individual foraging ranges near the boundary include an increasing proportion of the less rewarding prairie habitat. The pattern in density is consistent with the assumptions that habitat selection depends on the optimal behavior of individual foragers, and that it tends to equalize expected fitness between habitats. Predation risks, assessed from foraging in sheltered vs unsheltered patches, appeared higher in prairie than in badland. Landscape had no influence on predation risk, on patterns of foraging behavior, or on population density across habitat boundaries. Whereas landscape no doubt influences regional population size, and thereby influences probabilities of extinction and colonization, it may play an insignificant role in determining patterns of abundance across boundaries at the scale where optimally foraging individuals attempt to maximize their fitness.

D. W. Morris, Dept of Biology and Faculty of Forestry, Lakehead Univ., Thunder Bay, ON, Canada P7B 5E1 (douglas.morris@lakeheadu.ca).

Ideal habitat selectors should adjust their density to match spatial variation in habitat quality (e.g., Fretwell and Lucas 1970, Pulliam and Caraco 1984, Fagen 1987, 1988, Recer et al. 1987, Morris 1994). They can do so at both foraging and dispersal scales, each of which create distinctive spatial signatures in density (Morris 1987, 1992, 1995). But we know very little about patterns of actual density variation at both small and large scales. One might expect, for example, that patterns of density across habitat boundaries may depend on the size and landscape mosaic of the habitat patches (e.g., Pulliam 1988, Oksanen 1990, Pulliam and Danielson 1991, Oksanen et al. 1992). At one extreme, population size and spatial patterns in population density may simply reflect the relative composition of habitats in the landscape (the random sample hypothesis, Connor and McCoy 1979, Andrén 1996). At another extreme, patterns of density could depend on a variety of landscape features including the size, composition, distribution, connectivity, contrast and spatial context of habitats (and their interactions, Wiens et al. 1993) as they influence crucial processes such as dispersal, colonization and extinction.

Between the extremes, a variety of 'landscape effects' may modify local and regional population density. 'Surplus' foragers may frequently spillover from rich to

poor patches and inflate local density (Pulliam 1988, Pulliam and Danielson 1991). Small patches of poor habitat embedded in a rich landscape may have higher density, or a different pattern of density, than much larger patches of the same kind. If the landscape is composed predominantly of rich patches, the spillover can dramatically increase local density in poor patches (Pulliam and Danielson 1991, Pulliam 1996). The spillover effect should be smaller when the proportion of rich to poor patches is reduced.

The differences in density created by landscape composition should also modify local resource abundance and the exploitation of resources by individuals. Landscape effects on forager density and behavior can similarly emerge if landscape modifies community composition. Asymmetries between predator and prey in body size, mobility and population densities may, for example, often cause predators to respond to a larger spatial scale than do their prey. Predator species composition and density may be more prone to vary with the degree of landscape fragmentation than that of prey, but nevertheless create an indirect effect of fragmentation on the density and behavior of prey. The effects of landscape composition and fragmentation on the persistence and conservation of species are thus linked directly to processes that influence individuals. It should be possible to connect the behavior of individuals and the dynamics of their populations to (1) develop explicit theories for landscape ecology, and (2) to test for the possible effects of landscape on population and community dynamics.

At smaller scales, one might also expect that patterns of density across boundaries can be modified by local variation in habitat quality. A smooth and gradual transition between habitats is likely to produce a continuous and symmetrical pattern in abundance. But what pattern do we expect when the boundary is abrupt and when the habitats differ dramatically in quality? Should density vary continuously and symmetrically across the boundary, or should it mimic underlying asymmetries in quality?

Irrespective as to what the patterns are they should, at each scale, reflect the rewards obtained by individuals exploiting local variation in habitat quality. It should often be possible to measure these rewards through the decisions made by individual foragers. Point estimates of habitat quality, for example, can be obtained from the quitting-harvest rates of individual animals. The rates can be estimated from the giving-up density (GUD) of resources in otherwise identical and depletable foraging patches (e.g., Brown 1988, 1989, 1992, Brown et al. 1992a, Kotler et al. 1993, Ziv et al. 1995).

Optimally foraging individuals should exploit resources in any patch as long as the benefits exceed the combined costs of foraging, including costs associated with predatory risk and with missed opportunities of not foraging in other resource patches, or engaging in other activities (Brown 1988). When a single individual can exploit habitats on both sides of a common boundary the difference in GUDs between the habitats reflects differences in foraging costs. The forager reaps more value from patches located in the habitat with the lower GUD (habitat quality is inversely related to the quitting-harvest rate, Ziv et al. 1995). Thus, if one obtains simultaneous estimates of density and GUDs across habitat boundaries in different landscapes, or in areas with differing degrees of landscape heterogeneity, it is possible (1) to test habitat selection theory, (2) to determine the density-dependent response to local variation in habitat quality, and (3) to evaluate the influence of landscape heterogeneity on both habitat quality and its associated density.

I apply all three approaches to habitat selection by deer mice occupying heterogeneous prairie landscapes. I begin by developing a priori expectations for both density and giving-up density across habitat boundaries, then test the predictions with field data. The tests allow me to distinguish differences in quality between habitats, to determine the role of predatory risk in causing those differences, to reveal the spatial patterns of both GUDs and density, as well as their interactions, and to evaluate the potential effects of landscape heterogeneity on predatory risks, GUDs, and density.

Patterns across habitat boundaries

Imagine that individuals of a single species occupy two large habitats, 1 and 2, that share a sharp boundary. Imagine further that, at very low density, the value of 1 per unit area is greater than that of 2. What pattern of density should emerge across the boundary?

Assume that animals adjust population density across habitats 1 and 2 in a way that equalizes fitness between the two habitats (Fretwell and Lucas 1970) and that fitness declines with increased density and is determined by the energetic return from foraging. At low density, fitness will be greater in habitat 1 than in 2, all individuals should occupy 1 only and necessarily be coarse-grained (MacArthur and Levins 1964) in habitat use. As density increases, the fitness in 1 will decline to a value where individuals can reap the same fitness benefit in habitat 2. Both habitats should be occupied. Some individuals will continue to be coarse-grained, using only one habitat or the other, but those near the boundary will likely exploit both, harvesting patches in each to a level where benefits balance costs. The better habitat will, on average, contain a higher population density.

A simple example may help to make this clear. Assume that fitness, W_i, in each habitat is a negative and linear function of population density (N_i),

$$W_1 = A_1 - b_1 N_1 \qquad (1a)$$

and

$$W_2 = A_2 - b_2 N_2 \qquad (1b)$$

where we know from above that the maximum fitness in habitat 1 exceeds that in habitat 2 ($A_1 > A_2$). If there is no cost to habitat selection, and if habitat selection obeys an ideal free distribution (Fretwell and Lucas 1970), individuals should adjust their densities in each habitat such that

$$W_1 = W_2. \qquad (2)$$

Substituting the values from eqs 1 and solving for N, an ideal-free distribution will occur when

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

Eq. 3 is the cost-free isodar specifying the set of densities in the two habitats such that the expected fitness of an individual is the same in both (Morris 1988, 1992). But habitat selection will frequently entail a cost (Rosenzweig 1974, 1981). An individual habitat selector whose home range spans the habitat boundary must compensate for the cost of rejecting the poor habitat in favor of exploiting only the better one (Rosenzweig 1974, 1981). Thus, an individual foraging only in habitat 1 should abandon habitat selection whenever

$$W_1 \leq W_2 + C \qquad (4)$$

where C is the density-independent foraging cost (Morris 1992). Substituting from eqs 1 into inequality 4 and solving for N as we did for eq. 2,

$$N_1 = ([A_1 - \{A_2 + C\}]/b_1) + (b_2/b_1)N_2, \qquad (5)$$

we note from the first right-hand term that the initial density difference between habitats with cost is less than the cost-free alternative. The value of C, and thus the density difference between habitats, depends on how much of the foraging range lies in habitat 2. Foraging cost is small for those individuals whose center of activity is located well away from the boundary in habitat 1. There will be a small reduction in density relative to a location where no foraging ranges include habitat 2 (compare eq. 3 with 5). If we census closer to the boundary, we are likely to encounter a higher proportion of animals whose home ranges include substantial portions of habitat 2, with correspondingly high costs of habitat selection. The density will be reduced further (Fig. 1). Note, as long as the difference in basic quality between the two habitats ($A_1 - A_2$) exceeds the maximum foraging cost, that the density, at any distance from the boundary, will be greater in habitat 1 than in habitat 2.

Should the pattern in GUDs vary similarly? The answer to this question likely depends on the scale one uses to measure habitat quality. Consider the case where the analysis is restricted to a distance of slightly less than one foraging range either side of the boundary. Any given individual will exploit both habitats and harvest patches in each to the point where the quitting-harvest rate (H) equals the combined costs of foraging,

$$\dot{H} = E + P + MOC \qquad (6)$$

where E represents the energetic costs of foraging, P equals predatory risks associated with foraging, and MOC corresponds to a composite of missed opportunities while foraging (Brown 1988, 1992). Each "cost" in Brown's seductively simple eq. represents a composite variable scaled by the marginal fitness of energy (Brown 1988). The GUD will differ between habitats if the costs (and thereby the value) of foraging in the habitats differ. There should be no difference in GUDs with distance from the boundary unless foraging costs also vary with distance (as they might if predatory risk increases with distance from the boundary [Brown et al. 1992b]).

Predictions may be more ambiguous if one measures habitat quality at a larger spatial scale where many animals are coarse-grained in habitat use. The main difficulty is that animals restricted to one habitat or the other may be in a different state than individuals that forage in both. An animal's state will influence its perception of foraging costs, and thereby its GUD (Brown 1988).

At the boundary, all individuals can be assumed to forage in both habitats and to be in a similar state compared to animals that forage in only one or the

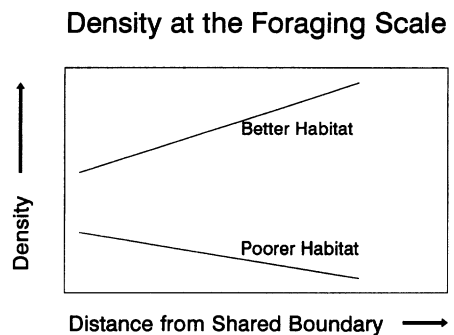## Density at the Foraging Scale

Fig. 1. An example of how the density of an optimally foraging species may vary away from a habitat boundary at the foraging scale. Fine-grained foraging costs increase with increasing area of the home range located in the poor habitat. The increased costs devalue the rich habitat and reduce density toward the boundary. The opposite occurs in the poor habitat. The divergence in density at the boundary reflects differences in basic quality between the two habitats. The pattern in density may vary if costs also vary with distance from the habitat boundary.

other. This assumption becomes increasingly distorted as one moves away from the boundary (the foraging ranges of a decreasing number of animals cross the boundary). I attempt to minimize this potential problem by restricting my analyses to a spatial scale where at least some individuals can legitimately be assumed to forage on both sides of the habitat boundary.

One can also use Brown's (1988) model to evaluate the density dependence in harvest rates. Increased density should often depress the per capita availability and renewal of resources. Foragers will place increased value on attaining energy for survival (increases the marginal value of energy thereby reducing foraging costs) and quitting-harvest rates (as well as GUDs) should decline. Density dependence in harvest rate will also depend on spatial scale. Animals that forage on both sides of a habitat border should attain similar profits on each side even though density varies. Harvest rates may differ among habitats (reflecting differences in foraging costs) but they should not vary with density at the foraging scale of density-dependent habitat selection (this prediction will hold only if the costs are not positively or negatively density dependent at the same scale).

Methods

Study area and basic design

I live-trapped deer mice and measured their GUDs across prairie-badland boundaries along the Red Deer River valley in Dinosaur Provincial Park in southern Alberta, Canada. Badland development along the valley is extensive and spectacular. The margin of the river valley forms a sharp and obvious boundary between highly eroded badlands and native upland prairie. Pockets of prairie vegetation varying in area, shape, and configuration are found throughout the badland mosaic. Most of these occur on mesas and terraces with equally sharp boundaries between prairie and badland habitats. The deer mouse occupies both habitats and is the only common species of small mammal at this location (comprising more than 95% of all captures, Morris 1992).

In July 1995, my assistants and I established 18 live-trap transects. Nine of these crossed the boundary between upland prairie and the badland habitats along the margin of the river valley. The scale of each habitat would be measured in tens or hundreds of square kilometers. The distance between transects always exceeded transect length (95 m), usually by hundreds of meters. Nine others crossed the boundary between small patches of prairie (<0.5 km²) and the badland matrix within the valley itself. Each 'interior' transect was associated with a different patch of prairie, and again, distances between transects always exceeded transect length.

Each transect consisted of 20 consecutive live-trap stations, ten in each habitat, with a 5-m trap spacing. Live-traps were set on three randomly chosen transects in each of the two sets of transects for three consecutive days. This procedure was repeated until all transects had been censused. Traps were checked at first light and individually marked rodents were released at the point of capture. I estimated the number of animals available to forage between trap stations as the total number of different deer mice captured in adjacent pairs of live traps. The number of mice is a minimum estimate of density at this scale, but one that should be unbiased among transects unless some were prone to significant trap competition (unlikely in this study; there were always 11 or more empty traps on each 20-trap transect).

I selected a transect length that slightly exceeded estimates of foraging ranges of deer mice in prairie-badland landscapes in southern Alberta (approximately 30 m either side of the habitat boundary, Morris 1992). I used a 45-m rather than 30-m segment in each habitat to increase the distance available for detecting asymmetries in the density response between habitats. The 45-m segment is less than the average diameter of deer mouse home ranges in grassland habitat (e.g., Stickel 1968).

Foraging experiments

At the completion of a trapping round ten foraging sites per transect (five in each habitat) were located midway between alternating pairs of even- and odd-numbered trap stations (10-m interval between sites). Two foraging stations were located at each site. Foraging stations consisted of opaque 2.5 gallon (US, 30 cm × 25.5 cm × 15 cm) plastic bottles with a single 3.4-cm opening, each containing 4 ml of unhusked and pre-screened (>2-mm diameter) millet seeds thoroughly mixed in a matrix of 1.5 l of screened (70 grain) silica sand. The stations were readily exploited by foraging deer mice. The millet-sand mixture has been extensively used to assess GUDs of seed-eating rodents in the 15–100-g body mass range (e.g., Brown 1988, 1989, Kotler and Brown 1990, Kotler et al. 1993, Ziv et al. 1995). My use of bottles in place of foraging trays (e.g., Brown 1989) eliminated complications associated with rain, wind, and diurnally foraging birds.

Spatial heterogeneity in predatory risk can be assessed with GUDs if paired foraging stations are located in risky vs safe microsites (typically shrub and open sites for rodents inhabiting arid ecosystems, Brown 1989, Brown et al. 1992b, Ziv et al. 1995; shrub cover reduces the risk from avian predators [Brown et al. 1988, Kotler et al. 1991, Kotler and Blaustein 1995]). Shrub distribution was inadequate for this purpose at my research site. I created safe sites by manufacturing

artificial shrubs from an expanded-aluminum frame (82 cm × 40 cm) overlain by camouflage netting. Aluminum rods lying on the ground, and connecting the ends of the frame, transformed it into a semicircular 'quonset' shape and allowed the 'shrub' to be held in place by the weight of the foraging bottle. Artificial shrubs extended approximately 10 cm on all sides of the foraging bottles. Bottles were arranged in pairs (one sheltered and one unsheltered bottle) within 2 m of each foraging station. The openings of all bottles were oriented in an easterly direction and sheltered versus unsheltered treatments were randomized across opposite sides of each transect.

Bottles were checked daily for five consecutive days. The sand in foraged bottles was sifted to remove remaining seeds and debris, recharged with 4 g of millet, and the bottle returned to the exact spot from which it was removed. The sieved sample was cleaned in the field, placed in labeled plastic bags, returned to the lab, cleaned of any remaining sand particles, and the uneaten millet weighed to the nearest 0.01 g. Following completion of the fifth foraging round, bottles and shelters were relocated at the next set of six transects. To ensure that animals had adequate time to discover all bottles, and to adjust their behavior accordingly, I used only the data from the fifth day of foraging. All data were collected in an interval of 17 d (11 − 27 July).

Tests of assumptions

I tested the foraging-tray assumptions that quitting-harvest rates vary among patch types with pilot studies in two different locations within the badlands in August 1994. In one experiment I established pairs of foraging trays at the vertices of an equilateral triangle (20-m spacing). Each pair comprised one bottle with 1 l of sifted silica sand (50 grain), and a second within 2 m with 1.5 l of sand. Pairs were randomly assigned to contain either 2, 4, or 8 g of millet in both bottles. In a second experiment, I set out pairs of 1-l cardboard milk cartons (20-m spacing). Each pair comprised of a carton with 0.25 l of sand and one with 0.5 l of sand. These pairs were randomly assigned to contain either 2 or 4 g of millet in both cartons. Both experiments had two replicates (minimum of 100-m separation) in each badland location. GUDs were obtained from each experiment for eight consecutive d. The first three d were used to habituate animals to the experiment and are not analyzed. Millet was removed from the bottle containing 1 l of sand on day five.

The experiments would confirm the assumption that quitting-harvest rates are a function of patch type (Brown 1988) if animals harvest seeds to a lower giving-up density in a smaller volume of sand. If the GUDs are similar when the initial density of seeds varies, they would confirm three additional assumptions, 1, that my

initial mass of 4 g millet is appropriate for the assessment of the quitting-harvest rate, 2, that the rodents do not become satiated when given 4 g of millet, and 3, that the rodents' patch-leaving rule is governed by quitting-harvest rates rather than by either a fixed-amount or fixed-time harvesting rule (Brown 1989, Brown and Mitchell 1989, Valone and Brown 1989, similarity in GUDS may be too restrictive of a test for a patch-leaving rule based on quitting-harvest rates that is implied whenever the ratio of GUDS is more similar than the ratio of initial resource densities).

I did not test the assumption of diminishing returns in a foraging patch directly. The design of the foraging trays virtually guarantees diminishing returns unless animals systematically search through the sand for its randomly distributed larder of seeds. Systematic search is highly unlikely in the artificial foraging trays because animals must excavate sand to find buried seeds. The resulting quarries increase sand depth in the rest of the patch and reduce the harvest rate obtained from additional excavations. Desert rodents harvest similar patches with diminishing returns (Kotler and Brown 1990, Ziv et al. 1995) as do white-footed mice (unpubl.) and deer mice elsewhere in their geographic range (Douglas Davidson unpubl.).

All bottles and milk cartons in the pilot study were heavily foraged at one location, but some were unexploited at the other. I restrict analyses of these preliminary data to the exploited site. All analyses are based on paired t-tests in a completely balanced design. I could not combine data for analysis of variance because they were not truly independent (the same sites were foraged repeatedly throughout the experiment).

I tested for possible sex and age biases of foragers between habitats and landscapes with multiway contingency analyses (Sokal and Rohlf 1981). I restricted the analysis of sex ratios to adult animals because there were surprising inconsistencies among observers in their ability to determine the sex of juvenile mice.

The habitat selection and patch-use models I apply here implicitly assume that the frequency with which individuals cross habitat boundaries is comparable to the frequency with which they move a similar distance within a single habitat (fine-grained). I tested this assumption by searching for a difference in movements among the four trap stations located within 20 m on either side of the habitat boundary. I created two classes represented by the two stations most distant from the boundary (12.5 m and 17.5 m from the boundary, one on each side of the foraging sites located at 15 m) and the two stations closest to the boundary (2.5 m and 7.5 m, one on each side of the 5-m foraging sites). If movements across the habitat boundary are different from those within a single habitat, the number of animals captured only in the distant stations divided by the number of animals captured in both sets of stations in a single habitat should be dissimilar to the

number of animals captured only in the stations close to the boundary in a single habitat divided by the number of animals captured in both habitats at the sets of stations closest to the habitat boundary. I tested for differences in the ratios by 2×2 contingency analyses.

Analysis

I used repeated measures multivariate analysis of variance (Norušis 1992) on the 1995 data to test for differences in both rodent density and GUDs. Repeated measures designs are most frequently used to analyze experiments where subjects are measured repeatedly through time (von Ende 1993, Morris 1996). Here, I treat each transect as a subject along which I obtain repeated measures in space. The value of this approach is that it reduces the error term in foraging behavior and habitat selection associated with transect-to-transect variation by testing for spatial differences in density and GUDs within transects. Controlling between-transect effects is important and appropriate because I want to evaluate the responses of individuals across habitat borders within transects. These important differences, caused by the behavior of individuals within a transect, could otherwise be obscured if the variance among transects is large. The MANOVA allowed me to partition both GUDs and density into additive components caused by landscape (a between-transect effect, recall that the design was replicated between valley margin and badland mosaic), habitat, predatory risk, distance from the habitat boundary, and their interactions (within-transect effects). I used polynomial contrasts to evaluate whether any significant differences with distance were linear or more complicated functions.

I included density as a covariate in the analyses of giving-up densities. If the mean habitat quality of a transect is less variable than forager density, transects with high densities of deer mice should have lower per capita resource availability, a higher marginal valuation of energy and lower GUDs than low-density transects. Within transects, however, GUDs at the foraging scale should not vary with density if density is adjusted to equalize expected fitness. I repeated the analyses without covariates to exclude those that were not significant (there was no change in the pattern of significant vs nonsignificant results). Lastly, I tested for asymmetries in density-dependence by regressing rodent density against distance from the boundary in each habitat.

Results

Quitting-harvest rates depended on patch type
Deer-mouse GUDs in pilot studies were lower in comparisons pairing adjacent bottles containing 1 vs 1.5 l of

Table 1. Analyses of giving-up densities (GUDs) obtained from pilot studies assessing assumptions associated with the use of GUDs to assess habitat quality. Bonferroni corrections used throughout.

Comparison	N	Paired T
1 l sand vs 1.5 l sand[a]	18	5.12**
0.25 l sand vs 0.5 l sand[a]	20	4.08**
2 g vs 4 g millet[b]	12	0.87 NS
2 g vs 8 g millet[b]	12	1.67 NS
4 g vs 8 g millet[b]	12	0.39 NS
2 g vs 4 g millet[c]	8	2.07 NS
2 g vs 8 g millet[c]	8	0.38 NS
4 g vs 8 g millet[c]	8	0.59 NS
2 g vs 4 g millet[d]	20	2.71*

[a] Comparisons paired by initial millet density; [b] both 1 l and 1.5 l of sand present, comparisons paired by sand volume; [c] 1.5 l of sand only; [d] comparisons paired by sand volume; * $P < 0.05$; ** $P < 0.01$; NS $P > 0.10$.

sand (means of 0.25 g and 0.52 g respectively, Table 1). Mean GUDs were also lower in 1 l milk cartons containing 0.25 l of sand (mean = 0.04 g) than in cartons containing 0.5 l of sand (mean = 0.12 g, Table 1). Quitting-harvest rates were lower when animals had less substrate in which to search for seeds.

The patch-leaving rule appeared to depend on quitting-harvest rates
Mean GUDs were similar between bottles that varied the initial mass of millet between 2 g (mean = 0.33 g) 4 g (mean = 0.40 g) and 8 g (mean = 0.42 g, Table 1). These results were repeated when experiments used only 1.5 l of sand (2 g mean = 0.26 g, 4 g mean = 0.19 g, 8 g mean = 0.23 g, Table 1). Mean GUDs obtained from milk cartons containing 2 g were higher than those containing 4 g of millet (means = 0.11 g and 0.05 g, respectively, Table 1). All of the results are consistent with the assumption that animals use harvest rates to assess patch quality. None of the results is consistent with alternatives based on fixed-amount or fixed-time (the milk carton experiment implies that deer mice may, when they forage in very small patches, base their patch-use strategy on average rather than instantaneous harvest rates [Valone and Brown 1989], but the sample size is too small for a definite answer).

Different transects supported different densities of deer mice but the sex and age ratios did not differ between landscapes or habitats
The number of different deer mice captured on a transect varied by a factor of four (between three and 14 animals, both extremes were found in transects crossing the margin of the river valley, Table 2). There was no difference in the sex ratio of adults ($G_4 = 1.29$, $0.5 < P < 0.9$) or in the age class of animals captured in prairie and badland habitats between areas with different sizes of prairie patches ($G_4 = 2.08$, $0.5 < P < 0.9$, Table 3).

Table 2. The number of different deer mice captured on 18 transects bisecting prairie and badland habitats in southern Alberta.

Transect	Landscape	Number of deer mice
1	Valley margin	5
2	Valley margin	9
3	Valley margin	3
4	Valley margin	14
5	Valley margin	8
6	Valley margin	7
7	Valley margin	8
8	Valley margin	8
9	Valley margin	8
10	Badland mosaic	5
11	Badland mosaic	7
12	Badland mosaic	10
13	Badland mosaic	13
14	Badland mosaic	7
15	Badland mosaic	8
16	Badland mosaic	9
17	Badland mosaic	10
18	Badland mosaic	12

Deer-mouse movements between habitats were similar to their movements within habitats

Most deer mice captured near habitat boundaries were captured at trap stations adjacent to a single foraging site (49 at one site vs 17 at two). There was no difference in capture ratio of the number of animals caught only in distant stations divided by animals caught in adjacent sets of stations in a single habitat and the capture ratio for both habitats in either the badland matrix (15/8 [single], 17/4 [both], likelihood ratio $\chi_1^2 = 1.39$, $P = 0.24$) or along the margin of the river valley (9/1 [single], 8/4 [both], Fisher's exact test, $P = 0.32$).

Giving-up densities declined as the density of foragers increased

When comparisons were made among transects, giving-up densities declined as the density of foragers increased (Fig. 2, Table 4). The data suggest an accelerating decline of GUD with density that could have major implications for population dynamics and our understanding of density-dependent foraging, but we need more field and experimental observations before rejecting the simpler linear model. Within transects, however, there was essentially no covariation
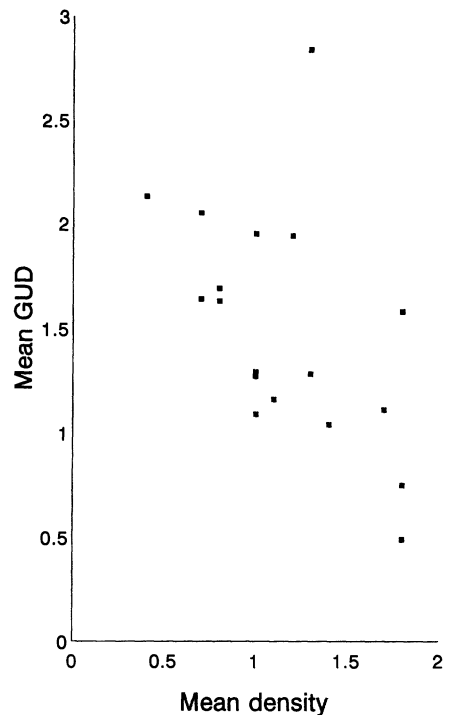

Fig. 2. The mean giving-up density of ten foraging sites on a transect declined significantly with the mean density of deer mice (mean number of mice captured in trap stations adjacent to foraging sites) on the same transect even though one transect in the badland matrix had a high giving-up density. Mean deer-mouse density as calculated here is highly correlated with the total number of different rodents captured on each transect ($r = 0.88$, $N = 18$, $P < 0.001$).

between giving-up density and forager density from one habitat to the other (the difference in mean giving-up density between habitats vs the difference in the mean density of foragers [$F_{1,15} = 0.02$, $P = 0.88$]). Increased numbers of conspecific competitors reduced quitting-harvest rates, but not at the scale where density-dependent habitat selection should act to equalize expected fitness.

Giving-up densities were higher in prairie than in badland habitat

Mean giving-up densities in the prairie habitat (1.8 g) were significantly higher than in badland (1.19 g, Table

Table 3. The proportions of male and of adult deer mice did not depend on either landscape or habitat ($G_4 = 1.29$ and 2.08 respectively [$0.5 < P < 0.9$ in each instance], analyses exclude animals captured in both habitats).

"Landscape"	Habitat	Adult males	Adult females	Juveniles
Badland mosaic	Badland	23	22	10
	Prairie	6	6	6
Valley margin	Badland	26	17	11
	Prairie	5	6	3

Table 4. Significant differences in mean giving-up density of deer mice foraging in artificial shrub-covered and unsheltered foraging stations along 18 transects crossing badland and prairie habitats in southern Alberta (repeated measures MANOVA with covariate [deer-mouse density]).

Comparison	Source	DF	F	P
Between transects	Regression	1,15	5.05	0.04
	Constant	1,15	38.26	<0.001
Within transects	Habitat	1,15	8.30	<0.01
	Shelter	1,16	20.65	<0.001

4). There was no difference in GUD between sets of transects found along the valley margin vs those in the badland mosaic (landscape effect, $F_{1,15} = 0.04$, $P = 0.85$), nor did differences between habitats depend on landscape (landscape × habitat interaction, $F_{1,15} = 1.05$, $P = 0.32$). Individuals extracted more value from foraging sites in the badland than prairie habitat regardless of whether large or small prairie patches were contrasted.

Giving-up densities were higher in unsheltered than in sheltered foraging sites

Mean GUDs were significantly higher in unsheltered bottles than in shrub-covered bottles in both habitats (unsheltered – 1.28 g in badland, 1.89 g in prairie; shrub-covered – 1.10 in badland, 1.72 in prairie, Table 4). There was no habitat (habitat × cover interaction, $F_{1,16} = 0.01$, $P = 0.93$) or landscape effect on these differences (landscape × cover interaction, $F_{1,16} = 0.22$, $P = 0.64$; landscape × habitat × cover interaction, $F_{1,16} = 2.15$, $P = 0.16$). The results suggest a difference in predatory risk between sheltered and unsheltered bottles. Relative differences in giving-up densities between sheltered and unsheltered bottles did not depend on landscape heterogeneity.

Giving-up densities within a habitat did not vary with distance

Mean GUDs did not vary with distance from the boundary (distance effect, Pillai's $V_{4,9} = 0.19$, $P = 0.71$, Fig. 3). None of the two-way interactions with distance, no three-way interaction, nor the four-way interaction (landscape × habitat × cover × distance) was significant (all $Ps > 0.2$). Again, there was no landscape effect.

Deer-mouse density in badland exceeded that in prairie and increased with distance from the habitat boundary

Deer-mouse density was higher in badland than in prairie habitat (Table 5). The difference increased linearly with distance from the habitat boundary (Fig. 4). As with GUDs, landscape had no influence on mean rodent density (landscape effect, $F_{1,16} = 0.61$, $P = 0.45$; no interaction terms involving landscape were significant, all $Ps > 0.16$).

The pattern of density change was asymmetrical in the two habitats. Density increased with increasing distance from the boundary in badland habitat (density = 1.34 + 0.018 distance in meters; $F_{1,88} = 4.75$, $P = 0.03$). There was no significant regression in the prairie ($F_{1,88} = 1.1$, $P = 0.3$).

Discussion

When foraging animals select habitats to maximize fitness, and have access to more than one habitat with
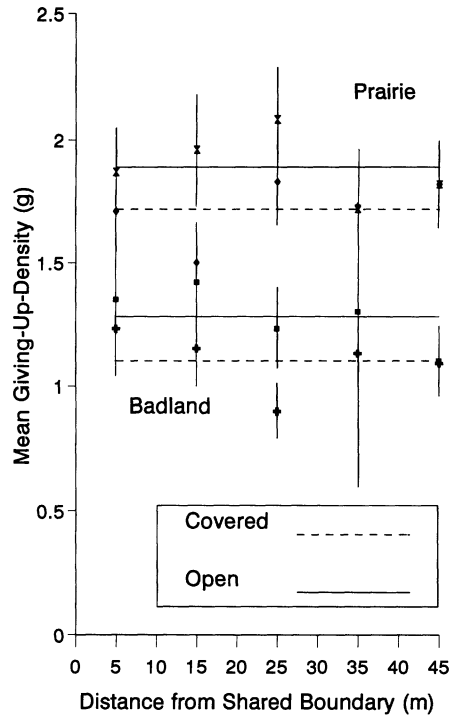

Fig. 3. Mean giving-up densities of foraging deer mice were higher in prairie than in badland, were lower in artificial shrub-covered foraging stations than in unsheltered (open) ones and did not vary with distance from the habitat boundary. Vertical lines represent one standard error about the mean. Note that the standard errors inflate estimates of variance because all analyses were based on paired comparisons, not on the pooled data used to calculate the standard errors. Symbols as follows: hourglasses – unsheltered bottles in prairie, diamonds – covered bottles in prairie, squares – unsheltered bottles in badland, crosses – covered bottles in badland.

limiting resources, giving-up density in identical foraging patches can be used as an inverse measure of habitat quality (Ziv et al. 1995). The lower the GUD, the more value individual foragers attain from the habitat. If relative population density between habitats is determined by differences in habitat quality (e.g., Fretwell and Lucas 1970, Rosenzweig 1974, 1981, Pulliam and Caraco 1984, Fagen 1987, 1988, Morris 1994), high-quality habitats should have higher density and lower GUDs than low-quality habitats. Deer-mice for-

Table 5. Significant differences in mean deer-mouse density along 18 transects crossing badland and prairie habitats in southern Alberta (repeated measures MANOVA).

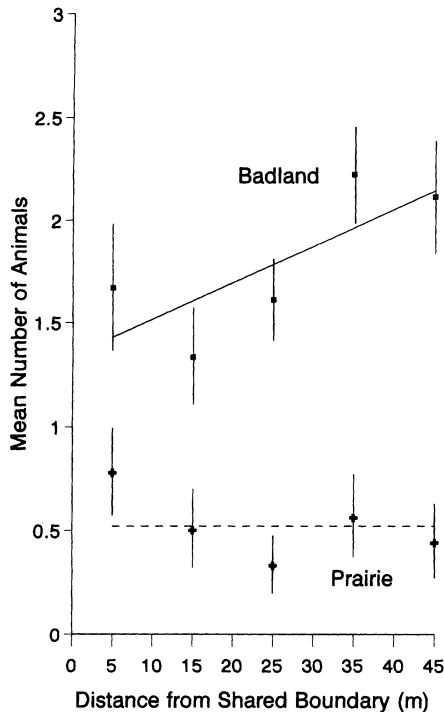| Comparison	Source	DF	F or V*	P
Between transects	Constant	1,16	133.74	<0.001
Within transects	Habitat	1,16	58.81	<0.001
	Habitat × Distance	4,13	0.52*	0.04
Polynomial contrast	Linear component	1,16	9.81	0.006

* Pillai's trace.

Fig. 4. Mean rodent density was higher in badland than in prairie habitat. The difference in density depended on how far the estimate was taken from the shared habitat boundary. The solid and dashed lines correspond to the solutions of within-habitat regressions. Vertical lines represent one standard error about the mean. The standard errors inflate estimates of variance because all analyses were based on paired comparisons, not on the pooled data used to calculate the standard errors.

aging across boundaries between badland and prairie habitats agreed with these predictions. Deer mice had lower GUDs and higher densities in the badland habitat.

The patterns of deer-mouse GUDs and density also support predictions of habitat selection theory. There was a strong negative relationship between mean GUD and mean deer-mouse density on different transects. Within transects, however, giving-up density did not vary with increasing distance from the habitat boundary whereas density increased with increasing distance into the better (badland) habitat. There was no relationship between GUD and density at the foraging scale. Animals moved between adjacent foraging sites on opposite sides of the badland/prairie boundary with the same frequency that they moved among adjacent foraging sites within a single habitat. Thus, the general patterns of resource harvest, density and movement by deer mice suggest that they are both optimal foragers and ideal density-dependent habitat selectors.

The pattern of declining density from badland toward prairie is consistent with an alternative explanation that the quality of the badland habitat declines toward its boundary with prairie habitat. But this is,

after all, the point made by theory. Average habitat quality declines as individuals allocate more of their foraging range and time to the poorer habitat.

Contrary to theory, there was no decline in density away from the boundary in the poor (prairie) habitat. This may have been an artefact caused by extremely low rodent density in the prairie. Traps at many stations failed to capture any mice at all. The result was a high variance in density at all distances from the boundary (many stations with zero density and a few recording more than a single individual). Even with low densities, however, all bottles were actively foraged in by the end of the experiment.

The tests for a landscape effect were even clearer. The patterns of GUDs and deer-mouse density were not different between the scale of the badland river valley with adjacent upland prairie and that of small prairie isolates within the badland mosaic. From the perspective of foraging deer mice encountering prairie/ badland borders, all patches of prairie appeared similar regardless of size.

Habitat fragmentation, at least below critical thresholds, is generally assumed to have far-reaching and often catastrophic consequences to biodiversity (e.g., Andrén 1994, With and Crist 1995). It is obvious that the dynamics of colonization and extinction, as well as the associated distribution and persistence of metapopulations (e.g., Hanski 1996), will often change as populations become ever more isolated in shrinking areas of habitat. But there is a dearth of data on how other crucial ecological and evolutionary processes may vary with fragmentation. For deer mice occupying prairie-badland landscapes in southern Alberta, landscape configuration and composition appear to have no effect on the nature of density-dependent habitat selection or the costs and benefits of foraging within and between landscape elements.

Average population density will, nevertheless, vary with the ratio of badland to prairie patches and influence local extinction and colonization. There appear to be no other effects of landscape on the distribution and abundance of deer mice in this ecosystem, presumably because the residual landscapes, for the moment at least, represent a viable interconnected network of habitats, and maintain a suite of predators and other species that continue to occupy the prairie/badland landscape as a whole. As patches of the landscape themselves shrink and become fragmented with a smaller complement of species we can expect that the nature of the habitats, including foraging costs, will change as will the pattern of density-dependent habitat selection. Comparative studies on carefully selected common species, similar to the one I report here, could thus serve as useful indicators of changes in the ecological function of reserves and other fragmented landscapes.

It is also noteworthy that the pattern of density variation between habitats was invariant between the two landscape extremes (there was a nonsignificant trend toward higher density in the badland mosaic). This result suggests that spillover of deer mice from badland to prairie habitat is negligible at the scales addressed here. Spillover should be most pronounced when individuals interfere with the habitat occupation of others (e.g., Pulliam 1988, 1996). Interference will often produce curvilinear or nonlinear isodars (Morris 1994) and differences in spillover into poor patches in different landscapes, or within landscapes varying in heterogeneity, should magnify differences in habitat quality detectable by GUDs. The deer-mouse isodars in these prairie/badland landscapes appear linear (Morris 1992) and the pattern of GUDs does not vary between very large and small patches. Furthermore, there was no detectable difference in the sex and age composition of deer mice occupying areas with small vs large prairie patches or living in different habitats. The absence of a landscape effect may be at least partly associated with a relatively small role for interference in habitat selection by these deer mice.

Why were giving-up densities lower in badland? Badlands contain numerous rocks and crevices under and within which deer mice can seek shelter from predators. Prairie, on the other hand, has few obvious shelters, even for small rodents. Thus, even if the incidence of predators is similar in the two habitats, differences in shelter and "escape substrate" (e.g., Ziv et al 1995) may act to create a higher risk of predation in prairie that would be reflected in its higher giving-up density by foraging deer mice.

The differences in giving-up densities between sheltered and unsheltered bottles are consistent with differences in predatory risk provided that deer mice exploit bottles with diminishing returns (Fig. 5). The figure compares the quitting-harvest rates of three animals that consume different numbers of prey (seeds) in foraging trays with identical initial resource densities (the number of prey eaten is inversely proportional to giving-up density). The difference in number of prey consumed, and the difference in giving-up density, is the same for the three animals, but the difference in quitting-harvest rates between A and B is twice that of B vs C. Thus, the difference in quitting-harvest rates between shrub-covered and unsheltered bottles in the prairie (high giving-up density) would be greater than the difference in badland (low giving-up density). Predatory risk is greater in the prairie than it is in the badland.

Are there other reasons why the habitats yield different GUDs? One possibility is that, contrary to the circumstantial evidence against interference, deer mice actively interfere with one another's habitat selection. Optimal habitat selection will not equalize GUDs if they reflect dominance by individuals occupying the

superior badland habitat. Differences in giving-up density could be caused by the exclusion of subordinate individuals from the preferred badland habitat (e.g., ideal despotic [Fretwell and Lucas 1970] or ideal preemptive distributions [Pulliam 1988]). Subordinates may be in a different state than dominant individuals and possess higher state-dependent foraging costs (e.g., Brown 1988). The hypothesis awaits experimental testing.

Habitat differences in the energetic costs of foraging and missed opportunities could also generate habitat differences in giving-up densities. Missed opportunities in the prairie may increase with increasing distance from the habitat border (e.g., associated with the time or costs required to travel to the more rewarding badland habitat). Differences in missed opportunities between habitats should be minimal when stations are located in close proximity to the habitat boundary (a common suite of foragers exploit both habitats, e.g., Brown and Alkon 1990). Stations located 5 m either side of the boundary yielded similar differences in giving-up density as did stations located at a 45-m distance. It thus appears that missed opportunity costs have little or no influence on the observed differences in giving-up density between habitats that, at present, are best explained by higher predatory risk in prairie than in badland habitat.

By way of contrast, Brown et al. (1992b) documented increased giving-up densities for Allenby's gerbil (*Gerbillus allenbyi*) in rock habitat as distance increased
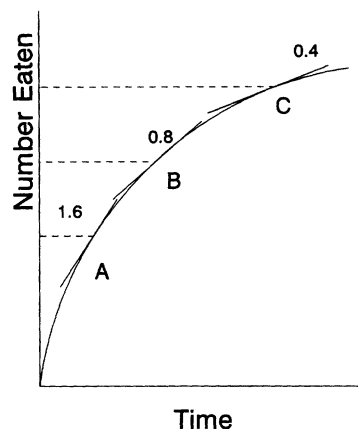

Fig. 5. An example of the bias in differences between quitting-harvest rates relative to the number of prey (seeds) consumed by animals foraging in a patch with diminishing returns (when different patches contain the same initial resource density, the amount of resource consumed is inversely proportional to the giving-up density). Upper-case letters correspond to three levels of consumption (different giving-up densities A > B > C). Tangents correspond to the instantaneous harvest-rates, numbers represent their slopes (again, A > B > C). Note that the difference in slope of the tangents between A and B is much greater (twice as great in this example) than the difference in slopes between those of B and C even though the difference in amount of resource consumed is equal.

from the preferred sand habitat. The increase in GUDs was attributed to increased predatory risk. Why the difference for deer mice? Gerbils exploit the rock habitat along the sand border, but do not maintain populations located only in rock habitat (Brown et al. 1992b). Density-dependent habitat selection cannot equalize fitness between the habitats and gerbils subsidize their use of the rock border by preferentially exploiting the sand habitat. Use of the sand allows individual gerbils to exploit the rock border up to a distance where predatory risks become unacceptably high for continued foraging. Within rock habitat alone, predatory risks appear so high that the habitat cannot sustain populations of Allenby's gerbil.

Ziv et al. (1995) documented a similar pattern of declining giving-up densities for Allenby's gerbil from loess plateau to adjacent semistabilized dune habitat. Semistabilized dunes are the preferred habitat for the dominant *Gerbillus pyramidum* that displace Allenby's gerbil in both time (Kotler et al. 1993) and habitat (Abramsky et al. 1990, 1991, 1992). Allenby's gerbil could encounter increasing predation risks with increased distance into the loess habitat as it does in rock habitat elsewhere in the Negev (Brown et al. 1992b). Giving-up densities would decline with increased distance in the semistabilized dune habitat if loess, like rock, is not occupied by Allenby's gerbil. In this regard, it is important to note that the sand pattern emerged only at 25 m from the habitat border (Ziv et al. 1995: Fig. 3). GUDs were similar at 5 and 15 m, as they were at 2.5 and 7.5 m in the Brown et al. (1992b) study.

One dominant and persistent interpretation emerges from all studies contrasting GUDs along transects that cross habitat boundaries. Differences in giving-up densities between habitats reflect, primarily, differences in predatory risk. It seems likely that the differences in risk will also be mediated by density-dependent habitat selection (by the predators).

Deer-mice occupying prairie/badland habitats provide several insights into the relative importance of habitat selection and landscape to patterns of animal abundance. The results strongly suggest that population density is adjusted by optimally foraging deer-mice attempting to maximize the rate of energy gain obtained from prairie and badland habitats. At the foraging scale analyzed here, deer mice appeared not to discriminate between large continuous patches of prairie versus small ones embedded in the badland mosaic. But they did discriminate between prairie and badland habitat. They clearly recognized, and responded, to the boundary between the two habitats, but not to the landscape context in which it occurred.

References

Abramsky, Z., Rosenzweig, M. L., Pinshow, B., Brown, J. S., Kotler, B. P. and Mitchell, W. A. 1990. Habitat selection: an experimental field test with two gerbil species. – Ecology 71: 2358–2379.

–, Rosenzweig, M. L. and Pinshow, B. 1991. The shape of a gerbil isocline measured using principles of optimal habitat selection. – Ecology 72: 329–340.

–, Rosenzweig, M. L. and Subach, A. 1992. The shape of a gerbil isocline: an experimental field study. – Oikos 63: 193–199.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – Oikos 71: 355–366.

– 1996. Population responses to habitat fragmentation: statistical power and the random sample hypothesis. – Oikos 76: 235–242.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. – Behav. Ecol. Sociobiol. 22: 37–47.

– 1989. Desert rodent community structure: a test of four mechanisms of coexistence. – Ecol. Monogr. 59: 1–20.

– 1992. Patch use under predation risk: I. Models and predictions. – Ann. Zool. Fenn. 29: 301–309.

– and Mitchell, W. A. 1989. Diet selection on depletable resources. – Oikos 54: 33–43.

– and Alkon, P. U. 1990. Testing values of crested porcupine habitats by experimental food patches. – Oecologia 83: 512–518.

–, Kotler, B. P., Smith, R. J. and Wirtz, W. O. II. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. – Oecologia 76: 408–415.

–, Morgan, R. A. and Dow, B. D. 1992a. Patch use under predation risk. II. A test with fox squirrels, *Sciurus niger*. – Ann. Zool. Fenn. 29: 311–318.

–, Arel, Y., Abramsky, Z. and Kotler, B. P. 1992b. Patch use by gerbils (*Gerbillus allenbyi*) in sandy and rocky habitats. – J. Mammal. 73: 821–829.

Connor, E. F. and McCoy, E. D. 1979. The statistics and biology of the species-area relationship. – Am. Nat. 113: 791–833.

Fagen, R. 1987. A generalized habitat matching rule. – Evol. Ecol. 1: 5–10.

– 1988. Population effects of habitat change: a quantitative assessment. – J. Wildl. Manage. 52: 41–46.

Fretwell, S. D. and Lucas, H. L., Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. – Acta Biotheor. 19: 16–36.

Hanski, I. 1996. Metapopulation ecology. – In: Rhodes, O. E., Chesser, R. K. and Smith, M. H. (eds), Population dynamics in ecological space and time. Univ. of Chicago Press, Chicago, pp. 13–43.

Kotler, B. P. and Brown, J. S. 1990. Rates of seed harvest by two species of gerbilline rodents. – J. Mammal. 71: 591–596.

– and Blaustein, L. 1995. Titrating food and safety in a heterogeneous environment: when are the risky and safe patches of equal value? – Oikos 74: 251–258.

– , Brown, J. S. and Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. – Ecology 72: 2249–2260.

– , Brown, J. S. and Subach, A. 1993. Mechanisms of species coexistence of optimal foragers: temporal partitioning by two species of sand dune gerbils. – Oikos 67: 548–556.

MacArthur, R. H. and Levins, R. 1964. Competition, habitat selection and character displacement in a patchy environment. – Proc. Natl. Acad. Sci. USA 51: 1207–1210.

Morris, D. W. 1987. Spatial scale and the cost of density-dependent habitat selection. – Evol. Ecol. 1: 379–388.

– 1988. Habitat-dependent population regulation and community structure. – Evol. Ecol. 2: 253–269.

– 1992. Scales and costs of habitat selection in heterogeneous landscapes. – Evol. Ecol. 6: 412–432.

– 1994. Habitat matching: alternatives and implications to populations and communities. – Evol. Ecol. 8: 387–406.

– 1995. Habitat selection in mosaic landscapes. – In: Hansson, L., Fahrig, L. and Merriam, G. (eds), Mosaic landscapes and ecological processes. Chapman and Hall, New York, pp. 111–135.

– 1996. Coexistence of specialist and generalist rodents via habitat selection. – Ecology 77: 2352–2364.

Norušis, M. J. 1992. SPSS SPSS/PC+ advanced statistics version 5.0. – SPSS Inc., Chicago.

Oksanen, T. 1990. Exploitation ecosystems in heterogeneous habitat complexes. – Evol. Ecol. 4: 220–234.

– , Oksanen, L. and Gyllenberg, M. 1992. Exploitation ecosystems in heterogeneous habitat complexes II: impact of small-scale heterogeneity on predator-prey dynamics. – Evol. Ecol. 6: 383–398.

Pulliam, H. R. 1988. Sources, sinks and population regulation. – Am. Nat. 132: 652–661.

– 1996. Sources and sinks: empirical evidence and population consequences. – In: Rhodes, O. E., Chesser, R. K. and Smith, M. H. (eds), Population dynamics in ecological space and time. Univ. of Chicago Press, Chicago, pp. 45–69.

– and Caraco, T. 1984. Living in groups: is there an optimal group size? – In: Krebs, J. R. and Davies, N. B. (eds), Behavioural ecology, 2nd ed. Blackwell, Oxford, pp. 122–147.

– and Danielson, B. J. 1991. Sources, sinks and habitat selection: a landscape perspective on population dynamics. – Am. Nat. 137: S50–S60.

Recer, G. M., Blanckenhorn, W. U., Newman, J. A., Tuttle, E. M., Witham, M. W. and Caraco, T. 1987. Temporal resource variability and the habitat-matching rule. – Evol. Ecol. 1: 363–378.

Rosenzweig, M. L. 1974. On the evolution of habitat selection. – In: Proc. first international congress of ecology. Centre for Agricultural Publishing and Documentation, The Hague, pp. 401–404.

– 1981. A theory of habitat selection. – Ecology 62: 327–335.

Sokal, R. R. and Rohlf, F. J. 1981. Biometry, 2nd ed. – Freeman, San Francisco.

Stickel, L. F. 1968. Home range and travels. – In: King, J. A. (ed.), Biology of *Peromyscus* (rodentia). Am. Soc. Mammal., Stillwater, OK, pp. 373–411.

Valone, T. J. and Brown, J. S. 1989. Measuring patch assessment abilities of desert granivores. – Ecology 70: 1800–1810.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures. – In: Scheiner, S. M. and J. Gurevitch, J. (eds), Design and analysis of ecological experiments. Chapman and Hall, New York, pp. 113–137.

Wiens, J. A., Stenseth, N. C., Van Horne, B. and Ims, R. A. 1993. Ecological mechanisms and landscape ecology. – Oikos 66: 369–380.

With, K. A. and Crist, T. O. 1995. Critical thresholds in species' responses to landscape structure. – Ecology 76: 2446–2459.

Ziv, Y., Kotler, B. P., Abramsky, Z. and Rosenzweig, M. L. 1995. Foraging efficiencies of competing rodents: why do gerbils exhibit shared-preference habitat selection? – Oikos 73: 260–268.