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Learning from the games animals play: using behavior to assess spatial structure and stochasticity in natural populations

Douglas W. Morris

Department of Biology and Faculty of Forestry and the Forest Environment, Lakehead University, Thunder Bay, Ontario P7B 5E1, Canada

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Population densities are heterogeneous across a variety of spatial scales. The variation in density reflects a similar variety of processes ranging from density-dependent habitat selection at small scales to independently regulated populations at much larger ones. I measured each scale with experiments capitalizing on the behavior of individual deer mice foraging in badland habitats in Alberta, Canada. First, I used patterns in rodent density along transects crossing badland and prairie habitats to measure the scale of habitat selection. Consistent with theoretical predictions, differences in the intercepts of isodars (graphs of density in adjacent habitats assuming ideal habitat selection) comparing prairie and badland densities revealed a maximum scale of habitat selection on the order of only 140 m. Second, I used foraging experiments to estimate density-dependent declines in fitness measured by the surrogate of giving-up-density of mice foraging in artificial foraging patches. Habitat selection should tend to equalize giving-up-densities among replicated, but spatially segregated, grids containing different numbers of foragers. Contrary to predictions from habitat selection theory, giving-up-densities declined with increased forager density in the majority of grids. Giving-up densities in nine of 12 grids increased linearly as population density was reduced in 1997. Giving-up densities in eight of 10 grids increased linearly with resource supplements in 1998. The results of both experiments are consistent with independent resource harvest by varying numbers of foraging mice. The identity of "outlier" grids, that showed little response to either manipulation, varied between years. The combined results document spatially-structured populations and allow us to estimate the frequency of stochastic dynamics that may have a profound influence on evolution and conservation strategies in heterogeneous landscapes.

Introduction

One of the first observations made by any aspiring naturalist is that a species' population density varies from place to place. Ecological models point toward three dominant processes that can explain the variance.

1. The distribution and abundance of individuals reflect differences in population growth rates and fitness among habitats of variable quality.
2. Spatial variation in density is caused by density-dependent habitat selection (e.g., Fretwell & Lucas 1970).
3. Variation in density is caused by a variety of spatial processes where limits to dispersal produce aggregated populations (e.g., Tilman & Kareiva 1997).

Each process has dramatic effects on the dynamics of populations, on evolution, and on the way we should study ecology. If, for example, variation in density reflects simply different population growth rates and carrying capacities, then the mean performance by the population is a weighted average of the separate contributions made by each habitat. The population is the appropriate unit of evolution and of ecological study. If, on the other hand, density is modified by habitat selection, then relative densities in each habitat can be expected to vary with overall population size (Fretwell & Lucas 1970, Morris 1988). Population regulation is linked tightly to habitat selection, and evolution is both density and frequency dependent. Studies that ignore habitat do so with the risk of misinterpreting population dynamics and evolutionary processes. Finally, spatially-structured populations may each be regulated separately. Local variation in abundance may reflect the stochastic nature of "demographic accidents" as well as a host of environmentally variable processes. Such processes could include spatially variable abiotic events, as well as spatially-dependent dynamics of other trophic levels. Any understanding of the dynamics and evolution of the population must include an understanding of its spatial structure.

Our success at differentiating among these interdependent mechanisms hinges on our ability to estimate population growth or fitness in different habitats, to map spatial distribution, and to associate each with population density. I illustrate how we can streamline this complicated set of analyses by using the optimal behaviors of individuals. First, I review how one can use patterns of density to measure the effective scale of dispersal, then confirm the theory with deer mice. I illustrate how to determine whether spatially restricted dispersal also limits the spatial scale of habitat selection, especially its ability to homogenize spatial variance in fitness. I demonstrate how patterns of resource consumption can be used to estimate the spatial pattern in fitness. I then apply both approaches to assess the relative roles of habitat quality, habitat selection, and spatial structure on the population dynamics of deer mice living in prairie-badland mosaics. The results provide conclusive evidence for both habitat selection and spatially-structured populations. Habitat selection, at least for deer mice in southwestern Canada, operates over a small spatial scale beyond which populations respond independently to local quality and stochastic effects.

Using optimal behavior to test for spatially-structured populations

Measuring the scale of habitat selection

It might appear that one can test for spatially-structured populations in a straight-forward manner. Any spatial sampling regime, if conducted at a large-enough scale, should reveal either the presence or absence of persistent patterns in population density. But it is not just spatial pattern that is of interest. For theories of habitat selection, and their evolutionary consequences, we need to know how variation in spatial patterns of density reflect local variation in fitness. Moreover, we would also like to know the appropriate spatial scale of habitat selection so that we can look beyond it for patterns of spatially variable population densities.

Theories of habitat selection, independent of any problems associated with spatial scale, are notoriously difficult to test (e.g., Morris 1987b, 1989a, 1991). Ideal-free theory (Fretwell & Lucas 1970, Fretwell 1972) and its associated ideal-

free distribution (IFD), for example, predicts that the mean fitness of habitat selectors, regardless of density, should be equal among all occupied habitats. Even if we could measure simultaneously fitness and density in two or more habitats, how would we test the IFD prediction that mean fitness is identical? The problem can be solved, in many cases, by plotting the set of joint densities in a pair of habitats such that the expected fitness is the same in each (Morris 1988). The resulting regression, called a habitat isodar, is the solution, in density space, of ideal habitat selection. When organisms select habitat to maximize their individual fitness, the isodar represents the evolutionarily stable strategy of habitat selection. The isodar slope equals the relative density-dependent decline in fitness of the two habitats; its intercept is proportional to habitat differences in maximum fitness attained at low density (Morris 1988). Any process that influences maximum fitness in different habitats, or the density-dependence of fitness within them, will influence the isodar. The effects can often be measured by including appropriate variables in the isodar solution (Morris 1989b, 1999, Rodríguez 1995, Morris *et al*. 2000a, 2000b).

Thus, one way to measure the scale of habitat selection is to insert the cost of dispersal into the habitat isodar that one would measure at different distances from a common habitat boundary (Morris 1992). To construct an isodar, imagine that fitness declines linearly with density in each habitat such that

$$W_i = A_i - b_i N_i, \tag{1}$$

where W_i represents fitness in habitat i, A is maximum fitness at low density, and b is the decline in fitness with increasing density (N). Ideal habitat selectors should occupy habitats such that expected fitness is equal in each. For two habitats and ideal free habitat selection (Fretwell & Lucas 1970),

$$W_1 = W_2.$$

Solving the substituted values from equation (1) in terms of N_1 yields the linear isodar

$$N_1 = \frac{A_1 - A_2}{b_1} + \left(\frac{b_2}{b_1}\right) N_2. \tag{2}$$

But an individual habitat selector whose home range spans the habitat boundary must compensate for the cost of rejecting the poor habitat to exploit only the rich one (Rosenzweig 1974, 1981). The benefits of being able to forage in the rich habitat must pay for the costs of moving through the poor one. Thus, near the boundary where individuals subsidize their use of habitat j by exploiting habitat i, the isodar is given by

$$N_i = \frac{A_i - \left(A_j + c_i\right)}{b_i} + \left(\frac{b_j}{b_i}\right) N_j. \tag{3}$$

where c_i is the "loss" in fitness in habitat i caused by the individual's encounter with habitat j. Equation 3 represents the value of the isodar at the foraging scale (Morris 1987a, 1992). At the dispersal scale, the isodar becomes

$$N_i = \frac{A_i - \left(A_j - c_{i \to j}\right)}{b_i} + \left(\frac{b_j}{b_i}\right) N_j. \tag{4}$$

where $c_{i \to j}$ is the total cost of dispersal from i to j that devalues the quality of habitat j to any dispersing individual. Optimal individuals must pay off the costs of dispersal associated with time lost from reproduction, and other fitness-enhancing activities, as well as the risks associated with dispersal and establishment of a new home range (Morris 1987a, 1992). Thus, by building isodars at different distances from the shared habitat boundary, one can objectively measure the effective scales of habitat selection. The isodar intercept will be smaller at the foraging scale of habitat selection than it will be at the dispersal scale.

Deer mice confirm the theory

Morris (1992) tested the spatial predictions of isodar theory by contrasting the slopes and intercepts of isodars along 23 transects crossing sharp boundaries between prairie and badland habitats in southwestern Canada. A comparison of isodars constructed from data near the boundary with those constructed with data more distant from the border confirmed the theory. Isodars for stations within 30 m of the boundary (foraging scale) tended to have lower intercepts

than those calculated for isodars based on stations between 40 and 70 m (dispersal scale). Isodars calculated at greater distances were often non-significant confirming the expectation that, beyond the foraging scale, populations are not connected by habitat selection and tend to be self regulating (Fig. 1).

Despite these convincing data it is possible that the cumulative short-distance movements by deer mice (and other species) can, given enough time, tend to equalize fitness over rather large spatial scales. Definitive tests of the role of habitat selection, and its spatial extent, must include estimates of fitness tested against *a priori* predictions of its spatial relationship with population density.

Habitat selection or spatial structure?

Imagine that one has estimates of population density and fitness across a series of sites connected by ideal habitat selection. Expected fitness will be the same in each site, the relationship between fitness and density is flat, and any differences in density that do exist reflect local differences in habitat quality (Fig. 2A). Now imagine that the estimates are obtained at sites exceeding the scale of habitat selection (spatially-structured populations). Imagine, first, that all sites are of similar value, and that the density in each is regulated independently of all others. Local history and demography will interact to yield different population densities. Fitness, reflecting the difference between site quality and local density, will decline as density increases (Fig. 2B). The decline need not be linear, of course, but will likely be monotonic if the mechanisms of density dependence do not vary with population size. Finally, imagine spatially-structured populations where some sites are of lower or higher quality than are others. Poor sites will, for a given density, yield low fitness whereas rich sites will yield high fitness (Fig. 2C). If sites vary dramatically in quality, there may be no relationship whatsoever between fitness and density.

Figure 2 is intended only as a guide to general trends in fitness with density that may occur under the influence of habitat selection and spatial structure. Pitfalls await the unwary scientist. Population densities on different grids might simply reflect different carrying capacities. Near equilibrium, fitness would be the same in all sites (Fig. 2A). Away from equilibrium, population growth rates could be quite different in different sites. Both scenarios can be tested experimentally by manipulating density or resource abundance.

Even when the relationship between fitness and density is highly variable (e.g., Fig. 2C), sites of different density but similar fitness might correspond to neighboring locations connected by habitat selection (as in Fig. 2A). This possibility can be tested by examining the spatial array of sites in combination with experiments that modify density-dependence through a series of *per capita* adjustments to either population or resource density. Sites regulated by habitat selection should tend to occur at close distances to one another, and fitness within those sites should tend to be equalized regardless of the experimental treatment. At large scales, similar fitness will be maintained between spatially-structured populations only if the "degree of density dependence" (revealed by density and resource manipulations that are proportional to population density) is the same in a low-density and low-quality site as it is in a site of higher quality occupied by more individuals (Morris 1987b). Such a scenario is possible of course [for example, when an individual's fitness is proportional to the fraction of total resource consumed (Sutherland 1983, Fagen 1987)], but it is debatable whether such a process occurs at the landscape scales addressed here (Morris 1994). Regardless, the first and most crucial component of a successful test is to obtain a reliable estimate of fitness.

Estimating fitness of optimal foragers

Theories of optimal foraging, arguably the roots to theories of habitat selection (Rosenzweig 1974, 1981, Charnov 1976, Rosenzweig & Abramsky 1997), provide a wonderful method to measure a habitat's quality in terms of fitness. Optimally-foraging individuals should exploit resources in any patch as long as the benefits

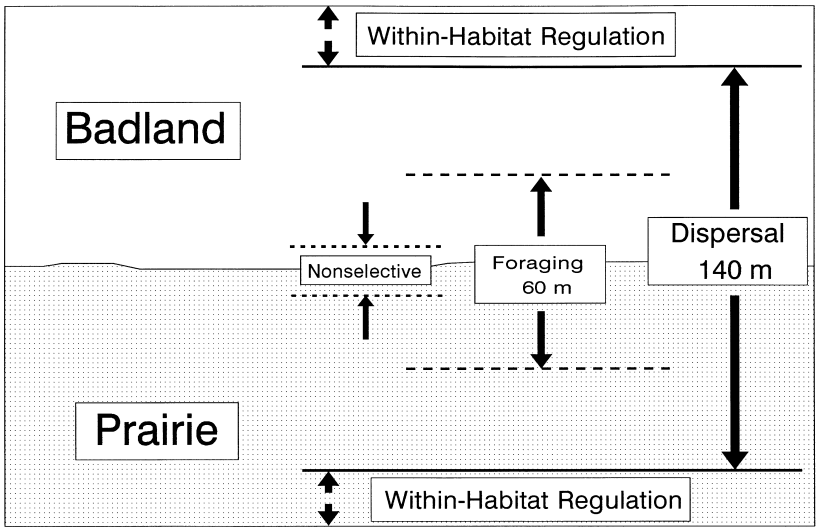

Fig. 1. An illustration of the spatial scales of habitat selection as demonstrated by deer mice occupying badland and prairie habitats in southwestern Canada. Isodars calculated for stations within 30 m of the boundary correspond to the foraging scale of habitat selection whereas isodars calculated for stations between 40 and 70 m correspond to dispersal. Non-significant isodars calculated at greater distances confirm that habitat selection is ineffective at regulating population densities beyond the dispersal scale. The nonselective scale where individuals cannot distinguish one habitat from the other has not been measured (modified after Morris 1992).

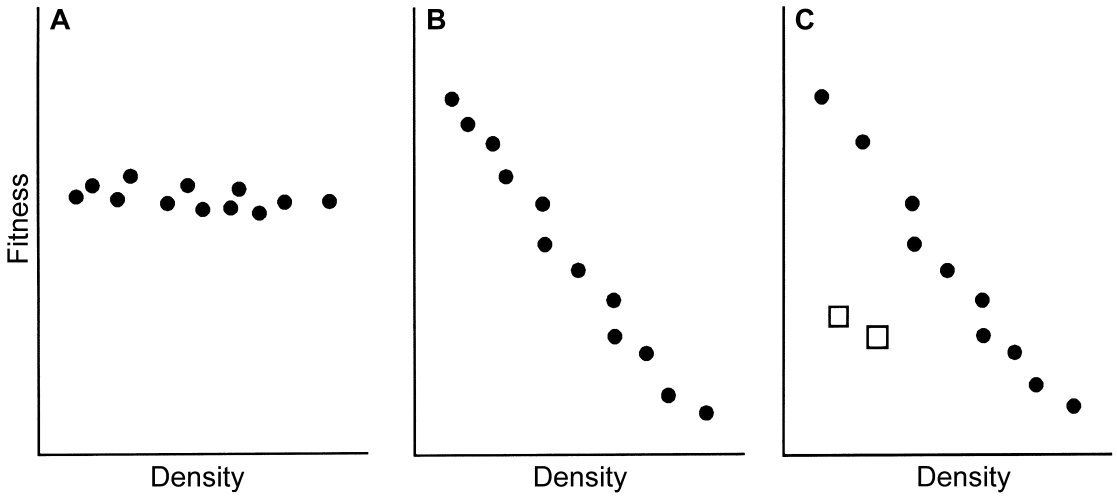

Fig. 2. An illustration of how different relationships between fitness and population density can be used to infer the relative importances of habitat selection, spatial structuring, and environmental variation on population regulation. The figure is intended only as a guide to the many possible patterns in fitness that can occur with population density. — **A**: Density-dependent habitat selection should equalize fitness at different sites that vary in quality. — **B**: Differences in population density without habitat selection (spatially-structured populations) should produce a tight, but not necessarily linear, negative relationship between fitness and population density across sites of similar quality. The pattern assumes that mechanisms of density dependence do not vary with population size. — **C**: One of many possibilities where variation in site quality can confound the relationship between fitness and population density. Here, sites of low quality (open squares) will tend, in spatially-structured populations, to produce lower than expected fitness. Sites of high quality could yield higher than expected fitness (not illustrated). Environmental stochasticity is inferred when the identity of such sites varies through time.

equal 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). The quitting-harvest rate when individuals abandon a depletable resource patch can be estimated by the giving-up density (GUD) of resources remaining in the patch. When an individual exploits 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).

Imagine animals feeding at a distance of slightly less than one foraging range on either side of the boundary. A given individual will exploit both habitats and harvest patches in each until the quitting-harvest rate (H) equals the combined costs of foraging,

$$H = E + P + \mathrm{MOC} \qquad (5)$$

where E represents the energetic costs of foraging, P equals predatory risks associated with foraging, and MOC corresponds to missed opportunities while foraging (Brown 1988, 1992). Each "cost" 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*. 1992a, Morris 1997)].

Within a single habitat, GUDs should also reflect local variation in habitat quality. A population of foragers occupying an area of reduced productivity will have lower *per capita* resource availability than will a population of the same density in an area of high productivity. Individuals in the low productivity site will place increased value on attaining energy for survival (increases the marginal value of energy). Foraging costs, as well as quitting-harvest rates and their associated GUDs, should decline. The same will occur when resource renewal is constant, but when population density varies.

GUDs may not reflect local resource availability when the cost of predation varies between sites, or when the state of the foragers changes in a way that is unrelated to the quality of the habitat. Predation effects can be controlled by comparing the GUDs of foragers in risky and safe foraging patches (Brown 1988, 1992, Brown *et al*. 1992b, 1994, Kotler *et al*. 1991, 1992, Morris 1997, Morris & Davidson 2000). Similar control on the state of foragers can be afforded by carefully assessing the relative densities of different age, sex, body size, and condition classes of individuals within each site. Thus, all things considered, one should be able to use spatial data on GUDs and density, and careful experiments that manipulate competition for resources, to assess for the existence of spatially-structured populations.

Spatial variation in density and fitness of deer mice

Field methods

I searched for spatial structure in a population of deer mice (*Peromyscus maniculatus*) occupying prairie and badland habitat in Dinosaur Provincial Park in southern Alberta, Canada. The deer mouse is the only common rodent in either habitat. Highly-eroded badlands created by sequences of post-glacial flooding are surrounded by residual short-grass prairie on the rim of the Red Deer River Valley. Smaller patches of prairie exist on small mesas within the badland complex. Deer mice are far more abundant in the low-productivity badlands than they are in the upland prairie. Predatory risk, measured by higher GUDs from mice foraging in resource trays in the open versus those protected by artificial shrubs, is greater in the low-density prairie habitat (Morris 1997).

Using isodars, I measured the dispersal scale to be approximately 70 m either side of the habitat boundary (approximately 140 m total distance, Morris 1992). Accordingly, in August 1997 my assistants and I established 12 permanent 30 m × 30 m trapping grids (16 trap stations spaced at 10 m intervals) spaced between 200–400 m apart from one another in badland habi-

tat. We located each grid on similar slopes and substrates (bentonite clay and sandstone with a scattering of surface rocks).

We conducted two different foraging experiments on the grids in 1997 and approximately 12 months later in 1998. In 1997, we placed three pairs of opaque 2.5 US gallon (9.463 litres) plastic bottles with a single 3.4-cm opening at the vertices of a 2 m × 2 m × 2 m equilateral triangle in the center of each grid. Each bottle contained millet mixed in 1.5 litres of screened (70 grain) silica sand. The millet-in-sand mixture has been used extensively to assess GUDs of seed-eating rodents in the 15–100 g body-mass range (e.g., Brown 1988, 1989, Kotler & Brown 1990, Kotler *et al*. 1993, Ziv *et al*. 1995, Morris 1997, Morris & Davidson 2000). The bottles eliminated complications associated with rain, wind, and diurnally foraging birds. One bottle of each pair (1-m spacing) was covered with an artificial shrub made from an expanded-aluminum frame (82 cm × 40 cm) overlain by camouflage netting (Morris 1997). Quonset-shaped (inverted U) "shrubs" extended approximately 10 cm on all sides of the foraging bottles. We thoroughly mixed 4 g of unhusked and pre-screened (> 2-mm diameter) millet seeds into one pair of bottles, and 2 g into another pair. We grouped the grids randomly into two sets for the third pair of bottles; each group received either 6 g of millet in those bottles, or none, on alternate days.

Animals were trained to forage in the bottles for 5 consecutive nights before we collected experimental data. Following each night of foraging, we sieved the remaining millet, cleaned it of dirt and faeces, and recharged each bottle. My purpose was to use comparisons between covered and open bottles to control for potential grid differences in predatory risk, (e.g., Brown 1989, Brown *et al*. 1988, Brown *et al*. 1992b, Kotler *et al*. 1991, Kotler & Blaustein 1995, Ziv *et al*. 1995) and to use contrasts between 2-g and 4-g bottles to assess patch leaving rules (Brown 1989, Brown & Mitchell 1989, Valone & Brown 1989, Morris 1997). If animals leave patches at similar harvest rates, for example, proportionately more resources would be harvested from 4-g than from 2-g bottles (Valone & Brown 1989). Animals using a fixed search-time would consume a higher proportion of resources from poor, relative to rich, patches (Valone & Brown 1989). Comparisons between 6 g versus zero millet in the third pair of bottles was designed to gain insights into missed opportunity costs of foraging mice. The value of grids with 6 g of additional millet should exceed the quality of grids with none. If foragers recognize these differences, GUDs should be higher when extra millet is present because rodents would forage profitably outside of the 4-g bottles. Here, my emphasis is on spatial structure and stochasticity, so I concentrate on the results from 4-g bottles.

We live-trapped nocturnal deer mice for three consecutive nights during the training period to estimate the number of different animals exploiting each grid. All rodents were marked with individual metal ear tags, weighed to the nearest g, measured (body length, tail length), sexed and released at the point of capture. Soiled or dirty traps were thoroughly washed with detergent, soaked in a bleach-water solution, rinsed in clean water, dried, and baited with a peanut-butter and flour mixture, rolled oats, and potato before being reset. Once the experiment began, we set just enough live traps to capture either one quarter, one half, or none of the rodents known to occupy each grid. Rodent "removals" were designed to evaluate short-term density-dependent differences in GUDs that I could use to verify presumed density-dependent differences in GUD among grids. Thus, the overall design included four factors consisting of cover (two levels; artificial shrub or not), resource density (two levels; 2 g vs 4 g), missed opportunities (two levels; 6 g or none), and rodent density (three levels; control, $^1/_2$, and $^1/_4$ "removal"). We arranged the 24 cells ($2 \times 2 \times 2 \times 3$) in a double Latin-square design spanning six consecutive days of foraging (144 observations in each of 2-g and 4-g bottles). We also collected control data (no trapping) one day previous to, and one day following, the Latin-square experiment.

Intense thunderstorms on the fifth day forced us to seal the bottles overnight, and to postpone trapping. On day six, we repeated the previous day's treatment to standardize any carryover effects, discarded those data, then resumed data collection within the Latin-square design.

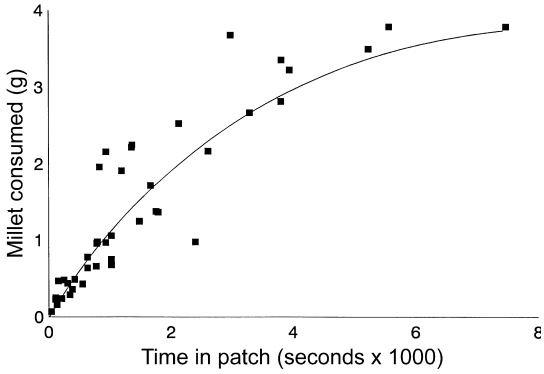

Fig. 3. The rate of millet consumption by deer mice declines with the length of time that the rodents spend foraging in artificial resource patches (curve for illustration only).

We conducted a second experiment on the same grids in 1998. We again superimposed an equilateral triangle (2 m × 2 m × 2 m) at the center of each grid. We placed either an "open" or "shrub"-covered foraging bottle with 1.5 l of sand and 4 g of millet at two randomly selected vertices. We placed a large plastic foraging tray ("Rubbermade 2221", approximately 40 cm × 55 cm × 15 cm deep with 3 entrance holes) containing 3 l of 70 grain silica sand, protected from wind, rain, and birds by a green lid, at the third vertex. Our intent was to manipulate resource density in an experiment parallel to our 1997 manipulation of the number of foraging rodents. Results similar to those of the rodent removals would suggest that any density-dependent result in 1997 was related to resource competition. Divergent results would suggest that the density-dependent response of 1997 included interference among individuals. We placed 30 cm long PVC tubes (4 cm diameter) containing ink and tracking paper (van Apeldoorn *et al*. 1993) in line with the holes of each bottle. We collected the tracked paper every day, and recorded the presence/absence of tracks in a symmetrical matrix superimposed onto the paper (56 cells) as a covariate to control for possible differences in rodent activity among foraging grids.

We live-trapped deer mice, as in 1997, for three consecutive days to estimate the number of different animals using each grid. We allowed rodents to forage in bottles (4 g) and trays (8 g) for nine nights while we attempted to obtain consistent foraging in another set of 12 grids located in prairie habitat near the badlands. On the 10th day we randomly assigned two grids to controls (8 g millet in their respective trays), then initiated a 5-day balanced double Latin-square design with the remaining 10 grids (two factors, cover with two levels, open versus shrub-covered, and resource density in the trays with five levels, 1, 2, 3, 4 or 5 g of millet for every rodent using the grid; 10 cells, 100 observations). We added an extra day during which all 10 trays were allocated 8 g of millet for each known forager, then concluded the experiment with a final night of live-trapping to estimate deer-mouse population change from the beginning to end of the experiment.

We tested the GUD assumption of diminished foraging returns through time by allowing six different deer mice to forage in bottles in experimental 60 cm × 60 cm × 30 cm high chambers under red light. We cut the bottles in half so that we could observe foraging rodents and, with a separate stop watch, recorded the amount of time each foraged. I used the resulting curve of diminishing returns (Fig. 3) to convert our 1998 field data, when we used 4-g bottles only, on GUD to quitting-harvest rate by solving the integral of Holling's disk equation.

Following Kotler and Brown (1990), the rate of millet harvest in our resource patches given by Holling's disc equation is

$$\frac{dM}{dt} = \frac{-aM}{(1+ahM)} \qquad (6)$$

where M is the final mass of millet (GUD), a is a deer mouse's attack rate, and h is a mouse's handling time for millet. Inverting the disc equation and subsequent integration yields an equation for time foraging in the patch, t, by which one can use regression to calculate a. Specifically,

$$t = \left(\frac{1}{a}\right)\ln\left(\frac{M_o}{M_f}\right) + h\left(M_o - M_f\right), \qquad (7)$$

where subscripts denote initial and final amounts of millet in the patch (Kotler & Brown

1992). For deer mice the regression was highly significant ($F_{2,39} = 228.03$, $P < 0.0001$), with $a = 6.95 \times 10^{-4}$ s^{-1} ($t_{39} = 4.40$, $P < 0.0001$) and $h = 422.8$ s g^{-1} ($t_{39} = 2.35$, $P = 0.024$). The quitting-harvest rate (g millet hr^{-1}) for any GUD is found by converting seconds to hours, then substituting a and h into the disc equation (Kotler & Brown 1990). Estimates of quitting-harvest rates obtained by this procedure are virtually redundant with those based on other curve-fitting methods (Morris & Davidson 2000). The deer-mouse results, using quitting-harvest rates in place of GUDs, were qualitatively identical to those I report below.

Our estimates of quitting-harvest rates assume that the foraging behavior of captive and wild rodents is similar. We attempted to minimize any differences by careful observations that recorded only the time of active foraging by captive rodents. Even so, we cannot exclude the possibility that wild rodents forage more or less efficiently. Regardless of this potential effect, GUD will be correlated closely with quitting-harvest rate across a wide range of foraging times, and analyses based on GUD can be assumed to reflect quitting-harvest rates (Morris & Davidson 2000).

Analysis

I analyzed each experiment with a repeated-measures mixed model ANOVA (Norušis 1992), including deer-mouse density as a covariate (Table 1). The covariate of population density should be significant only if density is strongly related to GUD (using GUD as an estimate of fitness, Fig. 2B). As noted above, two factors might destroy the relationship. (1) Density-dependent habitat selection should tend to equalize GUDs across grids within a single habitat (Fig. 2A). Even in the presence of habitat selection, grid differences in predation risk, or in the state of foragers, including vigilance (Brown *et al*. 1999), could cause GUDs and population densities to differ among grids (Fig. 2B). (2) Environmental varia-

Table 1. A summary of tests for habitat selection, spatial structure, environmental stochasticity and the form of density-dependent resource harvest in 12 sub-populations of deer mice occupying badland habitat at Dinosaur Provincial Park in Alberta, Canada.

Hypothesis	Prediction	Test
Habitat selection	Constant GUD with density	A graph of GUD versus population density should yield constant GUDs even though density varies.
Spatially-structured populations	Monotonic decline in GUD with increased density	GUDs on all grids should respond equally to experimental treatments.
Environmental stochasticity	Heterogeneous GUDs	Despite a general trend in GUD with density, some grids should possess "unusual" GUDs. GUDs in these "outlier" grids should respond differently to treatments, and the identity of unusual grids should vary among years.
Independent resource harvest	Linear increase in GUD with proportional reductions in density and increased resource supply	Polynomial contrasts in a repeated measures ANOVA reveal only a linear response.
Non-independent resource harvest	Curvilinear or nonlinear increase in GUD with proportional reductions in density and increased resource supply	Polynomial contrasts in a repeated measures ANOVA reveal higher-order responses.

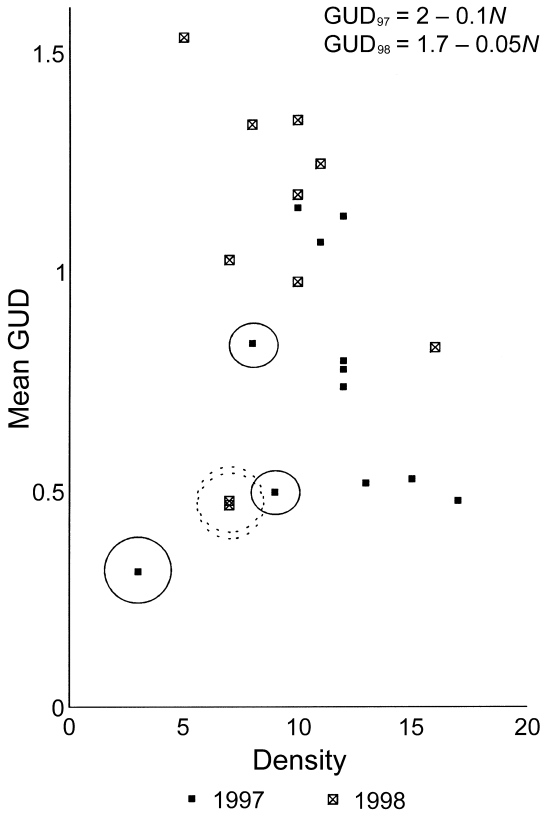

Fig. 4. Mean giving-up-densities (GUD) in bottles with 4 g millet varied with the population density of deer mice in both 1997 (solid symbols) and in 1998 (open symbols). In 1997, three plots with low density had lower-than-expected GUDs (solid circles). In 1998, two different plots with low density had lower-than-expected GUDs (dotted circles).

tion in resource supply might also affect population densities. At one extreme, all "populations" might grow according to their respective resource supplies. Such a process could appear similar to that for density-dependent habitat selection (e.g., each density corresponds to local carrying capacity, and at any point in time, population growth rates are similar among grids). Alternatively, environmental stochasticity could produce some grids with very low resource levels that should possess lower GUDs than expected on the basis of their population density (Fig. 2C). Grids with extremely high resources could produce GUDs higher than expected on the basis of deer-mouse density. Only scenario (1) is inconsistent with spatially-structured populations. Thus, I began the analysis by contrasting the rank order of population densities in the grids between the two years. I reasoned that stochastic effects should destroy any inter-annual correlation in population density.

I evaluated the shape of the empirical relationship between GUD and population density by analyzing the 1997 density-reduction experiment, and the 1998 resource-supplementation experiment, with polynomial contrasts. Significant first terms in the polynomials would demonstrate linear density-dependence (1997 experiment), and linear consumption in relation to resource renewal (1998 experiment). If both analyses yield linear effects only, the results would support the hypothesis that density-dependent foraging represents the summed effects of independent foragers (Table 1). Significant higher-order terms would document curvilinear relationships between GUD, population density, and resource renewal that would suggest non-independent foraging (Table 1).

Results

Density and density manipulations

The number of different deer mice captured on each grid varied between 3 and 17 in 1997, and between 5 and 16 in 1998. There was no correlation between the densities in the two years (Kendall's $\tau = 0.03$, $P = 0.89$). Grids with high densities in 1997 were not the same as those with high densities in 1998. Despite the substantial differences in density among grids, densities appeared to vary little during the course of the experiments. Sixty-one of the 70 deer mice captured on the final night of the 1998 experiment had been captured during the three-day census two weeks earlier.

The 1997 removal experiments were an unqualified success. We captured 208 mice of those targeted by 222 traps set during the density reduction phase of the experiment (93.7% success). Faeces in another 12 empty traps demonstrated that deer mice had been captured, but escaped from traps before dawn. Only two traps failed to capture rodents.

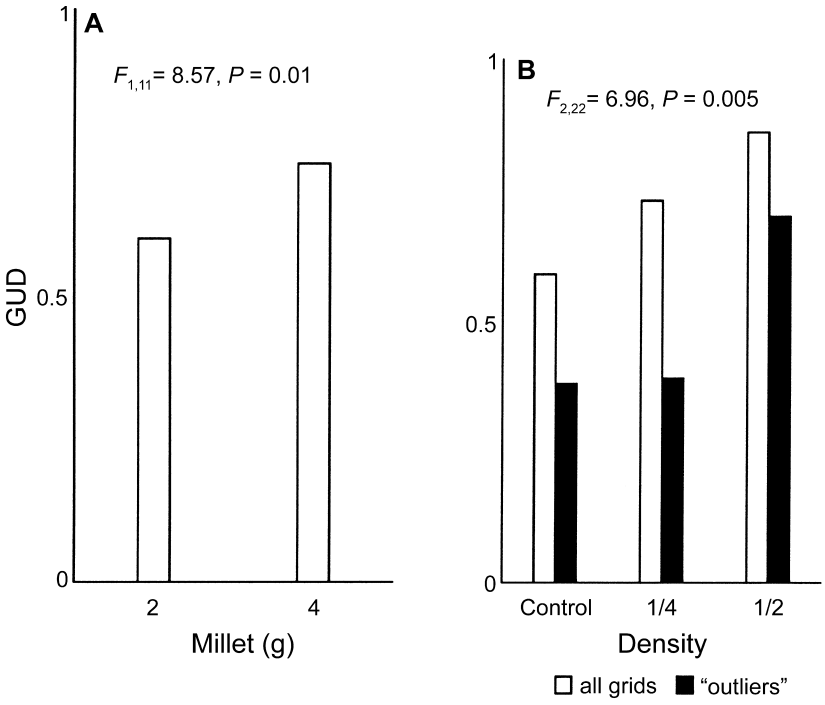

Fig. 5. Giving-up-densities (GUD) of deer mice in 1997. — **A**: GUDs were lower in bottles with 2 g of millet than in bottles with 4 g. — **B**: When all grids were included (open bars), GUD increased linearly when either one quarter or one half of the known population of deer mice on a grid was restrained from foraging. When grids with low GUDs and densities were contrasted separately, GUD increased only when one half of the rodents were restrained.

Giving-up densities

Giving-up densities were unequal across grids even though population densities varied (Fig. 4). Three patterns were readily apparent. (1) In the majority of grids, GUD appeared to decline more-or-less linearly with increasing population density. (2) Some grids with low density also had low GUDs, but grids that had abnormally low GUDs in 1997 were not those with low GUDs in 1998. (3) There were no grids with high density that also had high GUDs. The three patterns are consistent with spatially-structured populations and with environmental variation (Fig. 2C, Table 1).

The covariate of density was not related significantly to GUD in either year (1997: $F_{1,10}$ = 0.14, P = 0.72; 1998: $F_{1,8}$ = 0.04, P = 0.85), nor, in 1998, was the number of tracks ($F_{1,8}$ = 0.31, P = 0.6). The 1998 results for quitting-harvest rates were similar (density: $F_{1,8}$ = 0.02, P = 0.90; tracks: $F_{1,8}$ = 0.08, P = 0.78). I repeated each analysis in the absence of the covariate (Tables 2 and 3). In 1997, GUDs were lower in bottles

Table 2. The influence of cover, initial resource density, supplemental resource, and population reduction on the giving-up-density of millet left behind by deer mice foraging on 12 sample grids in badland habitat during 1997. Analysis by mixed model repeated measures ANOVA. No interaction was statistically significant.

Source	df	*F*	*P*
Constant	1,11	110.16	< 0.001
Cover	1,11	0.83	0.4
Initial Resource Density	1,11	8.57	0.014
Resource Supplement	1,11	1.03	0.33
Population Reduction	2,22	6.96	0.005

Table 3. The influence of cover and resource supplements on the giving-up-density of millet left behind by deer mice foraging on 10 sample grids in badland habitat during 1998. Analysis by mixed model repeated measures ANOVA

Source	df	*F*	*P*
Constant	1,9	81.50	< 0.001
Cover	1,9	5.65	0.04
Resource Supplements	4,36	3.24	0.02
Cover × Resource	4,36	0.74	0.6

with 2 g millet than in those with 4 g millet ($F_{1,11}$ = 8.57, P = 0.014; Fig. 5), and GUDs increased linearly with density reduction ($F_{2,22}$ = 6.96, P = 0.005, linear contrast t = 4.04, P = 0.002, quadratic term NS; Fig. 5). No other main effect, or interaction of effects, was statistically significant.

Figure 2C illustrates how difficult it might be to understand density-dependent foraging in natural systems. Environmental stochasticity could produce enough variation in the relationship between GUD and density to destroy any consistent pattern (e.g., Fig. 4). One can predict, *a priori*, that "stochastic" grids should respond differently to density reduction and resource addition experiments than do the remaining grids. I searched for these potentially "biassed" grids in each of 1997 and 1998 by sequential repeated-measures ANOVAs. I eliminated, in order, the most extreme residuals until the covariate of density was statistically significant (P = 0.05), then calculated the regression of mean GUDs in 4-g bottles versus the number of mice on a grid. I used only the data from 4-g bottles so that the results would be comparable between years.

The analysis created two groups of grids, those with "biassed" residuals, and those with a monotonic decline of GUD with density. I analyzed each group separately for each experiment (density reduction and resource addition) to confirm:

1. That the expected pattern of GUD with density and resources corresponded with that revealed by the grids retained in the ANOVA.
2. That the residual grids responded differently to the experimental treatments than did the others. Thus, the deletion of residuals was used to identify groups for subsequent analysis, and to predict what each experiment should reveal. There was no attempt to use this statistical sleight of hand to assess, without subsequent tests, the relationship between GUD and density.

The significant regressions from the two years were similar (Fig. 4; $GUD_{97} = 2.01 - 0.1N$, P = 0.008; $GUD_{98} = 1.66 - 0.05N$, P = 0.05). The results suggest, despite the lower densities in 1998, and despite different identities for the plots with low density in the two years, that GUD had a characteristic linear relationship with density in the badland habitat. Each individual forager appeared to have an additive effect on resource consumption. More importantly, the regressions identify the three plots with unusually low GUDs for their density in 1997, and the two in 1998 (Fig. 4) as likely candidates where environmental stochasticity influenced both GUD and population density.

Environmental stochasticity

I attempted to gain insight into the relative importance of stochastic effects by separately comparing the response to density reduction in the three grids with unusually low GUDs during 1997. Contrary to the overall pattern, there was no increase in mean GUD with the one-quarter reduction. Mean GUD increased substantially when density was reduced by one half (Fig. 5). Not only did the three plots have low initial GUDs for their density, but they yielded a different response to the density treatments than did the other grids. When density was reduced by 25% on these grids, mice continued to forage in the bottles to the same low harvest rate. Mice in the remaining grids, including those of similar density, foraged less in the bottles when densities were reduced. Thus, the manipulations had different effects on foraging costs between the two sets of grids. Missed opportunities were less in the three unusual grids than in the others. The patterns suggest that background resource levels, on these three grids, were less than those on the remaining grids (environmental stochasticity).

The 1998 analysis yielded similar results. GUDs and quitting-harvest-rates were lower under cover than in the open ($F_{GUD\ 1,9}$ = 5.65, P = 0.041; $F_{QHR\ 1,9}$ = 7.00, P = 0.027) and both increased linearly across resource-supplement treatments ($F_{GUD\ 4,36}$ = 3.24, P = 0.023; $F_{QHR\ 4,36}$ = 3.38, P = 0.019, linear contrast t_{GUD} = 2.64, P = 0.027; t_{QHR} = 2.71, P = 0.024, no higher term significant; Fig. 6). There was no influence of cover on the density-dependent pattern in GUD. The two-way interaction between cover and resource supplementation was nonsignificant

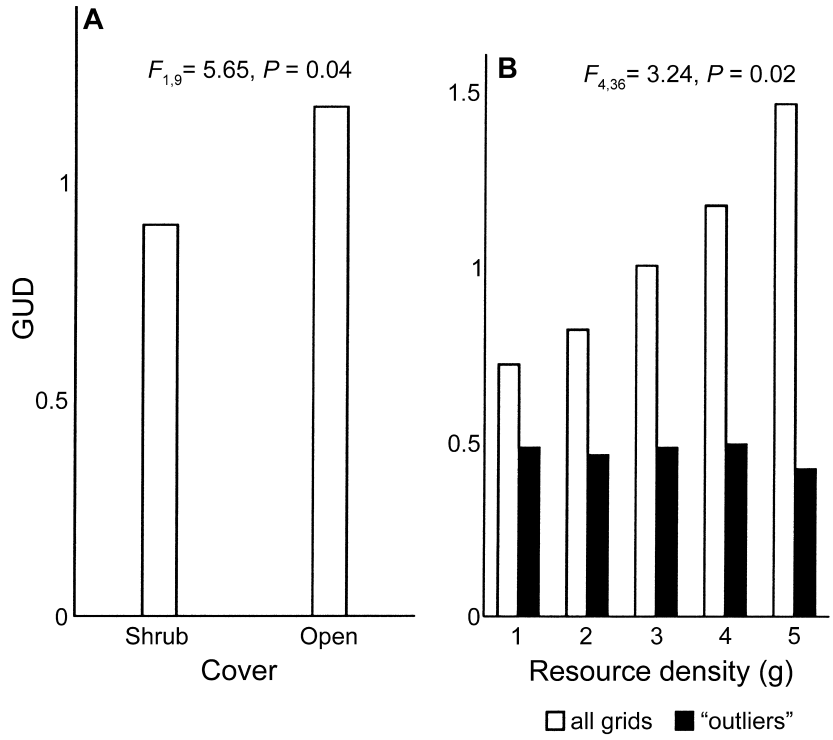

Fig. 6. Giving-up-densities (GUD) of deer mice in 1998. — **A**: GUD was higher at open bottles than at those protected by artificial shrubs. — **B**: When all grids were included (open bars), GUD increased linearly with increasing resource supply. When grids with low GUDs and densities were contrasted separately, GUD did not vary with resource supply.

($F_{\text{GUD } 4,36} = 0.74$, $P = 0.57$; $F_{\text{QHR } 4,36} = 0.58$, $P = 0.68$).

As in 1997, I evaluated the treatment response of the two unusual grids separately. Mean GUD in these grids did not respond to increased resource availability (Fig. 6). Again, the result is consistent with differences in missed opportunities associated with low initial resource levels on the two unusual grids (environmental variation).

Discussion

Deer-mouse populations in badland habitat illustrate a clear and dramatic spatial structure where the ability of density-dependent habitat selection to equalize fitness is quickly attenuated by spatially-limited dispersal (Morris 1992, 1997). The insight is possible because we can indeed use the adaptive behaviors of individuals to understand issues of spatial scale and to explore, experimentally, questions of broad extent and significance to ecology. The implications are profound. Spatially-structured populations are the fodder of metapopulation dynamics (Levins 1969, Hanski 1991, 1994, 1999, Hanski & Gilpin 1997, and many others) that provide numerous "natural experiments" for adaptive evolution (Wade & Goodnight 1998). Similarly, the success of the experiments demonstrates an improved ability to map processes at small scales with larger-scale events.

The experiments also demonstrate, for deer mice in badland habitats, that mean resource consumption varies linearly with changes in density and with changes in resource renewal. Above some lower threshold of habitat quality, each deer mouse appears to have an equal and additive effect on resource consumption. Moreover, when we substituted quitting-harvest rate for GUD as a better estimate of fitness, the linear response remained. Even though deer mice foraged in our patches with diminishing returns, the range of GUDs observed in the field occurred in the region where there was more-or-less a linear correspondence between GUD and quitting-harvest rate. Each deer mouse had an additive negative effect on fitness. The result is inconsistent with classical theories of habitat matching (e.g., Sutherland 1983, Pulliam & Caraco 1984, Fagen 1987, Morris 1994, 1995)

where individuals are assumed to consume equal proportions of the renewing resource. A linear decline is, however, consistent with the expectations of foragers in real-life mosaics (Morris 1995). Regardless as to cause, linear relations between fitness and density suggest that many or our concepts about density-dependence and habitat use may be encapsulated in relatively simple models.

Environmental, demographic or historical stochasticity?

In each of the two years of this study approximately 20% of the grids had unusually low GUDs for their population density. The identity of similar and dissimilar grids varied between years. It is too early to speculate whether or not this degree of stochasticity characterizes either badland habitat, or habitat use by deer mice. The implication is that the remaining 80% of grids possessed similar carrying capacities. The more important point is that we now have the demonstrated potential to measure variation in density and fitness with relatively simple experiments that can reveal underlying patterns and stochasticity in spatial distribution. The experiments open a wealth of opportunities that will allow us to explore the patterns, causes, and consequences of variation in habitat quality and population density.

If 20% of the sites are influenced by environmentally stochastic effects, what process accounts for the variation in abundance among the remaining sites? It would be unrealistic to ascribe all of the 'residual' variance in density in the otherwise similar grids to the usual alternative of demographic effects (e.g., Gotelli 1998). A variety of historical influences representing past environmental and demographic events, as well as their associated time lags, are the more likely explanation for the variable densities. Temporal variation in the activity of predators among sites, for example, could leave long-term signatures on the future pattern of population dynamics. At the time when predators were active, reduction in prey density would be caused by environmental variation (e.g., reduced carrying capacity), and possibly to changes in demography linked to predator selectivity. Similarly, the future dynamics of the sub-populations occupying the 20% of the grids whose quality is reduced during the reproductive season will include a variety of time-lagged influences when their sites 'recover'. The future consequences of these sorts of effects are more properly subsumed under the collective term of historical stochasticity/contingency rather than to their root causes, that may, in any case, be impossible to uncover. Regardless, it is clear that one can use current densities, in concert with the behavior of individuals, to infer stochastic dynamics, and to help guide management and conservation efforts.

The ability to measure stochastic influences is particularly satisfying. We now have the potential to gain new insights into the role of stochasticity in population dynamics. We should be able to improve our forecasts, both in terms of density, and in terms of the persistence of threatened populations.

Do we anticipate that other stochastically dynamic populations should mimic those measured here? The answer will depend, in addition to local conditions, on the temporal scales of heterogeneity in the environment, on life history and on habitat selection. It is intriguing that long-term studies of white-footed mice (*Peromyscus leucopus*) occupying forest habitat also reveal spatial structure that mimics our observations on *P. maniculatus* (Krohne & Burgin 1990). Demographic patterns of white-footed mice varied among sample grids in each year, and grids with high density in one year often had low density in others (Krohne & Burgin 1990).

Habitat selection, a rapid process because it is intimately linked to behavior, may be far more effective at equalizing expected fitness and regulating populations of species with prolonged life histories and small population growth rates than it is in the highly dynamic populations of small rodents. One might also anticipate that the role for habitat selection would increase with a species' vagility. It would be interesting to know, for species sharing similar body plans, how similar the allometric relations are for dispersal, migration and the characteristics of life history that determine population growth.

Caveats

Despite their potential, foraging experiments often reveal unexpected quirks of behavior that beg explanation. Why, for example, did deer mice harvest millet to lower densities under artificial shrubs than in the open in 1998 (and in the previous studies, Morris 1997), but not in 1997? The answer is probably related to differences in shrub placement. In 1997, we placed shrub-covered bottles 1 m distant from open ones, instead of at our usual 2-m distance. From the perspective of deer mice, a shrub-covered foraging bottle apparently affords no more protection than one located in the open 1-m away. The result is consistent with the behavior of fox squirrels where GUD increases with distance from trees that they use to escape predators (Brown & Morgan 1995). The more important result is that there was no interaction between cover and density or cover and experimental treatments in either year. The decline in GUD with density was not caused by grid differences in predatory risk.

The 1997 results associated with supplemental millet are also at odds with the data from 1998. In 1997, there was no noticeable increase in GUD when we added 6 g of millet in two bottles at each foraging station (12 g total). There may be, again, a simple explanation. The 1997 6-g treatment was, on a *per capita* basis, similar to our initial millet densities (1-g supplement) in the 1998 experiment. The results of the two experiments are not comparable and suggest that, in 1997, our supplements were too low to detect a response in the giving-up-density of deer mice.

Evolutionary implications

Though I have couched this contribution primarily in terms of detecting spatial structure and environmental stochasticity, the approach speaks to a much larger issue of evolution in heterogeneous landscapes. Two long-standing perspectives dominate the field. One, the so-called large population size theory of R. A. Fisher (Fisher 1930, Wade & Goodnight 1998) argues that evolution occurs by a gradual process of mass selection where the slow accumulation of beneficial mutations increases mean fitness. The resulting adaptive landscape has a single peak. The alternative shifting-balance hypothesis of Sewall Wright (Wright 1931, 1988) argues that epistatic rearrangements driven by drift in small populations improve local fitness of spatially segregated demes. Successful demes lie on a higher adaptive peak than do others with lower mean fitness. The combination of drift and inter-demic selection allows adaptive genotypes to migrate throughout the population, and across its heterogeneous adaptive landscape (Coyne *et al*. 1997, Wade & Goodnight 1998). Wright's more complicated and contentious view of evolution (Coyne *et al*. 2000, Goodnight & Wade 2000, Peck *et al*. 2000) has enjoyed a resurgence of sorts with increased evidence that many species are composed of metapopulations with the requisite extinction and recolonization rates that allow successful migration and inter-demic selection (Wade & Goodnight 1998). Spatially-structured populations, particularly at the small scales observed here, enhance Wright's interpretation of evolution, but via an ecological route that also incorporates density-dependent habitat selection. Whether Wright's model applies or not, it is clear that ecologists must incorporate an evolutionary perspective into studies of spatial structure, and that evolutionary biologists must pay closer attention to the role that adaptive behaviors can play in the patterns and processes of evolution.

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