# Tests of Density-Dependent Habitat Selection in a Patchy Environment

Douglas W. Morris

# TESTS OF DENSITY-DEPENDENT HABITAT SELECTION IN A PATCHY ENVIRONMENT[1]

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*Abstract.* A simple regression analysis can be used to assess the response of animal density to differences in habitat quality. The same test can evaluate general predictions of habitat selection theory as well as search for differences in the shapes of habitat suitability–density functions, something previous tests have been unable to do. Combined with demographic or other estimates of fitness, regression tests can provide new insights into the evolution of habitat selection.

Regression and fitness tests were used to explore the pattern of density-dependent habitat use in two temperate-zone rodents. The intensity of population regulation appeared to be inversely related to a habitat's carrying capacity. Variation in density-dependent habitat choice suggests new and unexpected dispersal strategies that vary with habitat heterogeneity. The predictions of the theory are complicated when habitat quality varies independently of population density. Sweepstake fitness rewards may be reaped by animals that would previously have been assumed to have made a suboptimal habitat choice. At the level of microhabitat, habitat selection models appeared to be much less capable of predicting variation in population density. Such a relation could be due to complex and inverse relationships between microhabitat quality and carrying capacity, or it could simply reflect scaling patterns in habitat selection.

*Key words: density dependence; dispersal; habitat selection;* Microtus; *patchiness;* Peromyscus; *population regulation; rodent; scale.*

## INTRODUCTION

Habitat determines the availability of resources, refugia, nest sites, and mates; the abundance of conspecific and interspecific competitors; the risks of predation, parasitism, and disease; and a host of other factors that influence reproductive success. An evolutionarily astute (ideal) individual will assess these interrelated costs and benefits and choose that habitat in which its reproductive success is maximized. The optimality decision will depend, in large part, on the basic quality or suitability of different habitats discounted by the density-dependent demands of the current population (Fretwell and Lucas 1970). Density-dependent interspecific interactions will further modify habitat choice (Rosenzweig 1974, 1979a, b, 1981, 1987, Grant 1975, Pimm and Rosenzweig 1981, Rosenzweig and Abramsky 1985, 1986).

According to the theory, habitat quality should generally decline with increasing population density (Svärdson 1949, Morisita 1950 [cited in Rosenzweig 1987], Fretwell and Lucas 1970, Fretwell 1972, MacArthur 1972, Partridge 1978, Whitham 1980, Pulliam and Caraco 1984, Emlen 1985, Krebs 1985). MacArthur (1972) suggested using the per capita rate of population increase ($[1/N_i][dN_i/dt]$ where $N_i$ is the density estimate in habitat $i$) as an appropriate estimate

of habitat quality. If habitat quality (suitability) is density dependent, then

$$(\delta/\delta N_i)([1/N_i][dN_i/dt]) = f_i N_i, \qquad (1)$$

where $f_i N_i$ (the so-called suitability–density function) specifies the form of population regulation. The intensity of regulation is given by the per capita feedback on population growth rate.

Most graphical representations of this remarkable model have depicted habitat selection among habitats as families of similar parallel (frequently linear) curves of declining habitat quality with increasing population density on an arithmetic scale. An ideal free distribution at any given population size is attained when the densities in different habitats are adjusted so that average fitness in each habitat is the same. For parallel curves this leads to an interesting paradox. For example, in a two-habitat system where A has a higher basic suitability than B, and both are currently occupied but not at equilibrium, each is expected to gain exactly the same number of individuals with any increase in population size. The result is that the subpopulation in habitat B, which had a lower initial density than that in A, has grown at a faster rate (Fig. 1 upper; see also Holt 1985). This appears to violate the model's assumption that average fitness in the two habitats is the same because the per capita rate of population increase in the habitats has been unequal. The degree of density-dependent feedback on reproductive
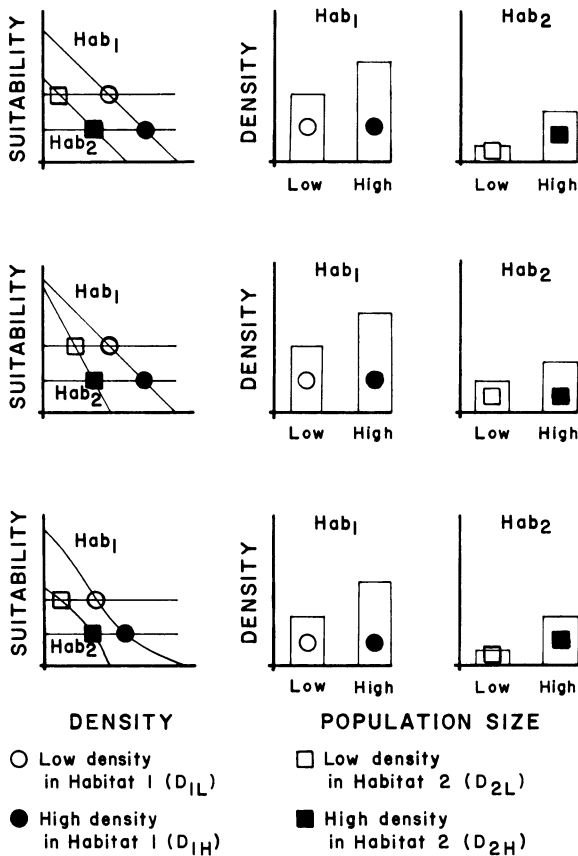
FIG. 1. Three alternative views of the relationship between population density and habitat quality (suitability) in a two-habitat system (Hab$_1$ and Hab$_2$). On the left side of the figure, habitat densities are inferred from the intersection of horizontal lines (upper = low $N$; lower = high $N$) representing habitat quality at two population sizes ($N$). The ideal free densities are plotted on the right side of the figure as bar charts. Upper: parallel suitability curves imply that population growth rates are unequal. Each has added the same number of individuals, but Hab$_2$ has a higher per capita growth rate than Hab$_1$; habitat densities become more equitably distributed with increased $N$ ($D_{1H} - D_{1L} = D_{2H} - D_{2L}$; $D_{1H}/D_{1L} < D_{2H}/D_{2L}$; $D_{1L}/D_{2L} > D_{1H}/D_{2H}$). Middle: if population growth rates are identical, suitability curves must diverge from one another, and relative habitat densities are unchanged ($D_{1H} - D_{1L} > D_{2H} - D_{2L}$; $D_{1H}/D_{1L} = D_{2H}/D_{2L}$; $D_{1L}/D_{2L} = D_{1H}/D_{2H}$). Lower: suitability curves may vary in shape as well as slope. Relative habitat densities may remain the same, become more similar (as here) ($D_{1H} - D_{1L} < D_{2H} - D_{2L}$; $D_{1H}/D_{1L} < D_{2H}/D_{2L}$; $D_{1L}/D_{2L} > D_{1H}/D_{2H}$), or less similar depending upon the relationship of habitat quality with density.

success is the same in each habitat, but the densities differ. As a consequence, habitats with lower densities must absorb migrating individuals from those habitats with higher densities if average fitness is to remain equal. Formally, according to Fretwell and Lucas,

$$dN_1/dt = dN_2/dt = W_1N_1 = W_1N_2 \qquad (2)$$

and average fitness ($W_1$) should be the same in the two habitats. But with parallel curves, $N_1 > N_2$, consequently

$$dN_1/dt = dN_2/dt = W_1N_1 = W_1N_2 + \epsilon N_1, \qquad (3)$$

where $\epsilon$ represents dispersal from habitat 1 to habitat 2.

Dispersal may also occur when there is a cost to habitat selection. With cost, individuals may begin to exploit poorer patches even though their fitness is greater elsewhere (Rosenzweig 1974, 1981). Consequently, per capita growth rates would remain higher in the better, high-density habitats, and result in directional dispersal to habitats of lower quality and density. Cost theories currently address individual foraging behavior (microhabitat) and dispersal predictions may have to be limited to that scale.

An alternative view is that different habitats should be identical in their rates of population growth (with no differential migration). Increased density in a particular habitat is then attained by reproduction and survival in that habitat and not by directional dispersal. This could easily be modeled by curves of diverging slopes (Fig. 1 middle), or by changing the density axis to a logarithmic scale. In this model, density-dependent effects on population growth rates, as well as reproductive success, are equal among habitats. Yet another alternative is that the slopes, shapes, and intercepts of the suitability–density curves differ (Fig. 1 lower). In this third view, the intensity and form of density-dependent feedback on reproductive success varies among habitats.

In principle, tests of the theory should be simple. We need only to estimate reproductive fitness with changing population density across a spectrum of habitats and plot the resulting suitability–density functions. But in practice, measuring reproductive success has eluded generations of field biologists. How else can we proceed to test the model?

Fraser and Sise (1980) and Rosenzweig and Abramsky (1985) have suggested the following: Monitor populations through time or space and evaluate the distribution of individuals across habitats with changes in population size. If individuals become less selective in their choice of habitat as the population increases, there should be an increase in the equitability of dispersion of individuals among habitats. Equitability predictions depend critically on the form and steepness of the suitability–density functions (Fig. 1), and no change, or even a decline in equitability of dispersion,

TABLE 1. Hypothetical population density data for two macrohabitats at low and high population sizes.

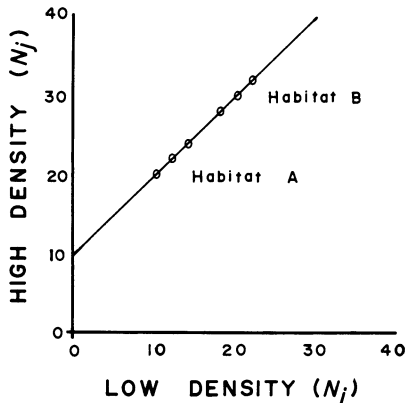| Habitat | Low $N$ ($N_i$) | High $N$ ($N_j$) |
| --- | --- | --- |
| A | 10 | 20 |
|   | 14 | 24 |
|   | 12 | 22 |
| B | 18 | 28 |
|   | 20 | 30 |
|   | 22 | 32 |

FIG. 2. Density regression of the data in Table 1. Equal numbers of individuals (10) were added to each replicate of the two habitats. The density regression specifies a perfect linear relationship with slope = 1.0.

does not necessarily imply continued habitat selection. How can we reveal the underlying shapes and slopes of these curves?

## A TEST FOR DENSITY-DEPENDENT
## HABITAT SELECTION

Consider a field protocol in which two occupied habitats are censused with replicated plots. Further, let population size vary between population estimates. This could be accomplished by density manipulation experiments or by temporal sampling during periods of population change (e.g., Fraser and Sise 1980). Each habitat will now have replicated estimates of population density at low and high population sizes. If we

plot these paired estimates one against the other for both habitats on a single graph, we can specify the relative slopes of their respective suitability–density functions. Thus, for parallel linear functions the relation between $N_j$ and $N_i$ (density estimate at high and low population sizes respectively) in habitat A is identical to that in habitat B, and a single linear regression of $N_j$ against $N_i$ for both habitats specifies a straight-line relation of slope 1.0. I provide a proof of this later (Eq. 8), but for now, a simple example will make it clear.

Assume we have replicated estimates of population density for each of the two habitats (Table 1). Note that each has a constant arithmetic increase in density that reflects parallel suitability–density curves (the number of additional individuals is the same for both habitats). When the paired densities are plotted one against the other, they give a perfect linear relationship with slope 1.0 (Fig. 2, Fig. 3A). This example also demonstrates the paradox of parallel suitability–density functions. Mean population density in the better habitat (B) has increased by 50%, that in the poorer habitat (A) has increased by 83%. The per capita population growth rates in the two habitats are unequal.

The examples of predicted density curves in Fig. 3 were generated by plotting the paired densities of each habitat from parallel, divergent, convergent, and cross-over suitability–density curves. Parallel functions, for example, give density regression slopes of one (Fig. 3A). When the regression slopes are significantly different from one, density-dependent feedback on habitat suitability is unequal in the two habitats. Signifi-
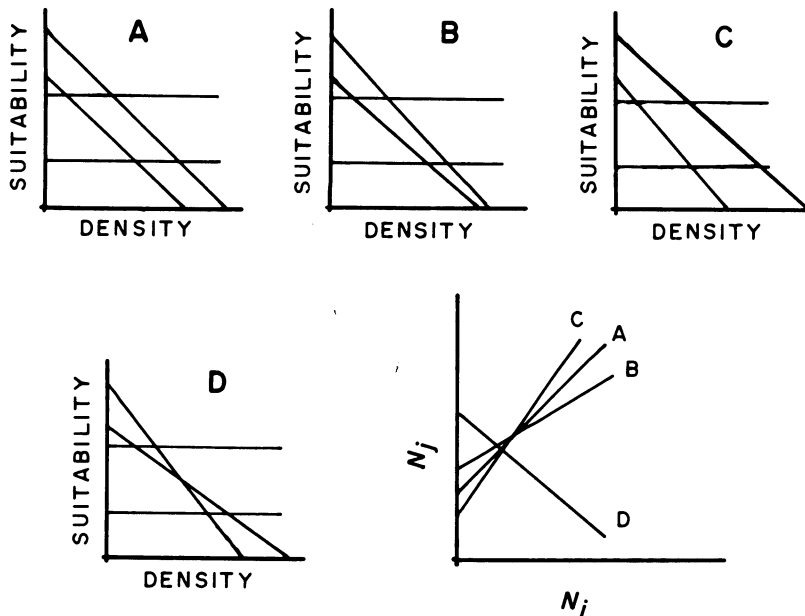


FIG. 3. The effect of different relative shapes of habitat suitability functions on the slopes of the density regressions (lower right graph). Parallel functions (A) give density regression slopes of one, converging functions (B) less than one, diverging functions (C) greater than one, and cross-overs (D) produce negative slopes.
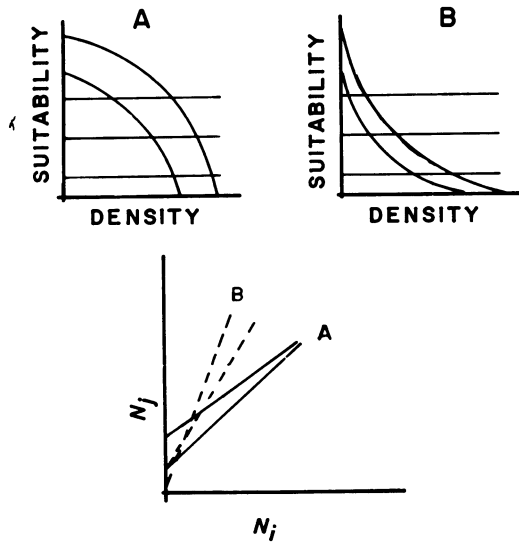
FIG. 4. Curvilinear responses can be assessed by comparison of paired regressions over three or more density treatments. For concave-downward functions, the slopes of the linear regressions will be significantly different from one another, and both will be less than unity (A); convex functions will generate significantly different linear regressions with slopes greater than one (B). Whether the regressions themselves converge or diverge will depend upon the relative degree of density dependence at high, compared with low, density. Similar tests could be used to describe the suitability–density function across any density range.

cant slopes less than unity (converging curves) imply that the per capita density-dependent feedback mechanisms on reproductive success are more severe in the "better" habitat (Fig. 3B). A smaller number of individuals in the high-density habitat cause an equal reduction in fitness as do a larger number in the low-density habitat. Significant slopes greater than one (diverging curves) imply that those mechanisms are less severe (Fig. 3C). We can assess the fit of the empirical curve to the predicted one by linear regression. A significant regression verifies the overall prediction of consistent density dependence. The relative shape of suitability functions will be revealed by the slopes of the significant regressions.

What if the curves cross over, as they would if the habitat with the highest per capita growth rate also had the most intense density dependence but a lower carrying capacity? If both densities being compared occurred above the cross-over point, linear regression would produce a slope less than unity (curves converging); if both were below, the regression slope would be greater than one (curves diverging). If we were lucky enough to compare densities above and below the junction of the suitability curves, the linear regression would be negative (Fig. 3D). This relation is easy to show for two habitats. If several habitats are compared, we may be unable to distinguish between a null hypothesis of no density dependence, and cross-overs among habitats (both could give nonsignificant linear regressions).

Such an artifact would be quite common unless all of the curves had the same junction point. Similar constraints would apply in the absence of cross-overs if some curves were converging while others diverged. When data are available for several habitats, they should probably be compared two at a time.

The linear approximation technique for only two density comparisons will be unable to differentiate between linear and curvilinear functions. A simple test for curvilinearity can be accomplished with comparisons among three or more densities (Fig. 4). In a linear function, sequential paired regressions should produce equal slopes, whereas in a concave-downward function, increased overall population density will result in density regressions of significantly lower slope. The opposite will be true of convex functions. In this way, the shape of the suitability curves can be determined across any range of densities.

It may even be possible to use a similar approach to evaluate density dependence within homogeneous patches enclosing one or more home ranges (macrohabitat). If the variation in microhabitat quality within macrohabitats is significantly less than that among macrohabitats (Fig. 5), the suitability–density functions among macrohabitats can be modeled as narrow bands in the suitability–density regressions (Fig. 6 upper). Each band is composed of a series of similar functions representing microhabitat variation in suitability–density curves in that habitat (Fig. 6 lower). It follows that for microhabitats, suitability–density functions can be assessed by paired linear regressions in the same way as macrohabitats.

If total population density within a macrohabitat changes (or is manipulated) during the period of study $(N_i < N_j)$, then the densities at replicated subplots
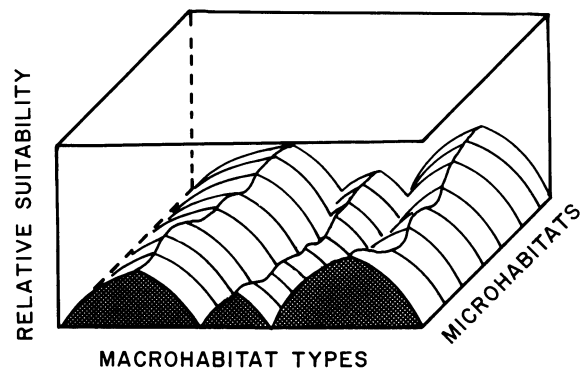


FIG. 5. The scaling of habitat quality into macrohabitat and microhabitat effects. If one were to measure habitat quality at several points in different macrohabitats, distributions of macrohabitat quality could be generated as on the face of this figure. If different sets of points (microhabitats) are sampled, or the same points sampled at different times, slightly different distributions would be generated. When these are "stacked" in rows, they create macrohabitat density ridges whose undulations reflect spatial and temporal variation in microhabitat (from Morris 1985).

$(n_i < n_j)$ should change similarly. If we assume that the suitability–density function defined by the two densities is linear, then

$$S_i = S_1 - bN_i \qquad (4)$$

and

$$S_j = S_1 - bN_j, \qquad (5)$$

where $S_i$ and $S_j$ are the habitat suitabilities in habitat 1 at densities $N_i$ and $N_j$, $S_1$ is a constant and is an appropriate linear estimate of the basic suitability of habitat 1, and $b$ is the slope of the habitat-suitability function with density. Assuming a constant difference between $N_j$ and $N_i$ and rearranging,

$$N_j = S_1/b - S_j/b, \qquad (6)$$

and

$$N_j - N_i = (S_1/b - S_j/b) - (S_1/b - S_i/b)$$
$$N_j - N_i = (S_i - S_j)/b, \qquad (7)$$

and the density response for habitat 1 is given by

$$N_j = (S_i - S_j)/b + N_i, \qquad (8)$$

where $(S_i - S_j)/b$ is the intercept on $N_j$, and the slope of $N_j$ vs. $N_i$ equals one. Since $N_i = \sum n_i$ and $N_j = \sum n_j$, the regression in habitat 1 can be estimated by

$$n_j = a + bn_i + e, \qquad (9)$$

where $a$ is the constant corrected difference in suitability for the given density treatment, $b$ is the slope estimate that should equal one, and $e$ is a normally distributed error term with a mean of zero and standard deviation equal to the standard deviation in animal abundance.

## How to Apply the Test

The density-regression method can be applied to any set of field data where replicated and independent estimates of population density vary through time. The test is easiest to perform when only two treatments corresponding to low and high population density are compared. The density estimates for each replicate of the high population density treatment are plotted against their corresponding estimate for the low population density treatment and the data analyzed by model II regression. Confidence intervals about the regression coefficients enable tests for parallel, convergent, and divergent regulation. In this way, any pair of habitats can be contrasted in terms of their relative degrees of density-dependent feedback on population growth rates.

Comparisons between only two density treatments assume that density-dependent feedback on population growth rate is linear with increasing density. The linearity assumption is not crucial when the objective of the study is to evaluate the relative degrees of density dependence between pairs of habitats. As long as the general shapes of the curves are similar, a linear approximation is capable of specifying whether the in-
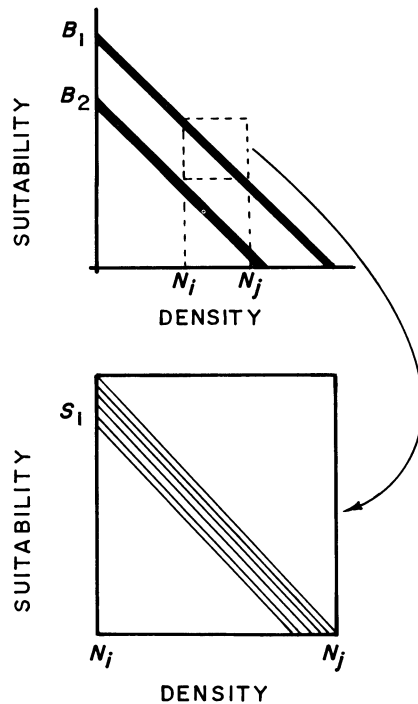


FIG. 6. The Fretwell-Lucas-Rosenzweig theory expanded to include microhabitat. $B_1$ and $B_2$ are the basic suitabilities of habitats one and two respectively, $S_1$ is the estimate of $B_1$ at density $N_i$. With consistent variation in microhabitat quality, the shapes of the individual microhabitat suitability–density functions mirror that of the overall habitat, and a regression demonstrating their slope can be used to estimate that of the macrohabitat. The relative quality of different macrohabitats corresponds with the intercepts of the microhabitat density regressions. Higher quality macrohabitats will have higher intercepts.

tensity of density dependence is similar between the two habitats. In Fig. 4A, for example, the per capita growth rate in the low-density habitat exceeds that of the high-density habitat. The curves are parallel, and so too are linear projections of those curves between any pair of densities (draw a straight line joining any pair of densities for the upper curve and contrast it with a similar line on the lower curve). A linear regression captures the essence of parallel regulation between the habitats.

Replicated density estimates for more than two density treatments provide a greater scatter of data and the ability to assess for shape differences in suitability–density functions. This design enables regression tests for curvilinear density dependence in addition to contrasts between pairs of habitats. An appropriate protocol with more than two density estimates would first contrast sequential paired regressions within habitats to test for curvilinearities before making comparisons between habitats. Similarly, when data exist for several different habitats, the relative shapes of suitability–density curves among them can be deduced by the regression analyses of habitats taken two at a time.

While I have developed paired density regressions as a test of density-dependent habitat selection, in practice, it may be difficult to differentiate from a null hypothesis of density-independent selection. Density-dependent habitat selection assumes that individuals assess the density-dependent habitat rewards of alternative habitats and use those habitats in a way that maximizes fitness. This leads to consistent relationships of density with habitat quality.

In contrast, density independence can lead to no relationship between density and habitat quality. Unfortunately, it can also lead to abundance patterns similar to those of density-dependent habitat selection. This occurs when populations in different habitats possess different per capita growth rates. The abundance of individuals across habitats reflects the different growth rates, even if individuals move among habitats independent of density and independent of expected fitness rewards. This is not a problem if our interest is focused on the actual patterns of abundance. It can be a serious problem if we wish to understand the processes leading to those patterns. When habitat selection is the prime focus of research, additional tests for actual selectivity and fitness rewards should be incorporated into the design. As I show in the accompanying example, fitness correlates can often be obtained as by-products of the replicated estimates of population density.

## AN EXAMPLE: HABITAT SELECTION OF SMALL MAMMALS

I applied the regression test to data on the abundance of two species of small mammals in Point Pelee National Park, southern Ontario (42°00' N, 82°31' W; Morris 1983, 1984a). Small mammals were censused by live-traps in two wooded (forest and sumac) and two open (grassland and old-field) habitats. The habitats were adjacent to one another along a north–south gradient, and were ordered linearly as grassland-sumac-old field-forest. Complete descriptions of the habitats can be found in Morris (1984b). I established a live-trap grid with 15-m spacing between trap stations in each habitat. The smallest grid (9 × 15 traps) was in the sumac; that in the old field was slightly larger (9 × 16 traps). Grassland and forest grids were of equal size (9 × 17 traps). Ecotones between plots were distinct and reflected differential successional histories of each habitat since agricultural abandonment. To protect against ecotone effects and to achieve equal-sized plots for comparisons among habitats, the analyses presented here eliminate the peripheral lines in the forest and grassland, and the fencerow ecotone between the sumac and old field. All plots were effectively 9 × 15 trap grids (135 stations each).

From 3 May to 10 November 1978, and again from 16 May to 29 October 1979, each station was live-trapped at monthly intervals. In order to sample the entire area, each interval consisted of three trap rotations where traps were set out at dusk on every third line and collected at first light the next morning. The subsequent rotation trapped the adjacent line, so that each station was censused once each interval. Except for a few stations in the forest that were submerged by spring floodwaters, all stations were trapped six times during each of 1978 and 1979 (6402 total trap nights). Longworth traps containing mattress stuffing as bedding, and baited with a peanut butter–flour mixture, oatmeal, and a slice of potato, were placed within 1 m of each station. Soiled traps were washed with detergent, rinsed in clean water, and dried before being reset. All captured rodents were individually marked with metal ear tags. Age, sex, reproductive status, and body measurements were recorded, and the animals were released.

I performed three analyses. First, I tested for interdependence in numbers of individuals among habitats and years by contingency analysis. A significant result implies a shift in habitat use that may or may not be related to overall density. A nonsignificant outcome implies that, for the entire population, the relative abundance of individuals among habitats has not changed between years. It is still possible, however, that pairs of habitats show different degrees of density dependence, which is masked by the lack of replicated estimates of density at the macrohabitat scale. To obtain this replication, I created five adjacent belt transects of 3 × 9 "grids." The number of different individuals captured in each of these transects represented my replicated estimates of population density within habitats. The second analysis was a density regression of these estimates between pairs of habitats. Third, to create subplots for the microhabitat regressions, I grouped sampling stations into square 3 × 3 grids and estimated rodent density similarly. I evaluated the significance of the relation between $N_j$ and $N_i$ by Pearson product-moment correlation. Linear regressions were generated for each of the significant correlations, and the slope of the reduced major axis (Sokal and Rohlf 1981:547–555) and its confidence interval were calculated to allow comparison with the predicted slope of 1.0.

Two caveats are in order regarding the density estimates. Simple enumeration of the number of different animals captured may give a biased estimate of population density (Burnham and Overton 1979), and when possible, should be replaced with an appropriate capture-recapture technique. These techniques are most suitable when intensive and replicated sampling occurs over a short time interval. Such a sampling regime was logistically impossible in my study. In any case, more sophisticated estimates of population density appear unnecessary for two reasons. First, my density values correspond to the minimum number of different rodents known alive over the sampling period, an estimate that accurately reflects changes in rodent population sizes (Hilborn et al. 1976). Second, I am

concerned more about changes in relative density among habitats than I am in an unbiased estimate of overall population size. My census data would be inappropriate for these analyses only if the degree of bias itself varied substantially between habitats or with population density.

The second caveat concerns my practice of subdividing large plots into smaller ones. Some animals were captured in more than one plot and critics have suggested that these individuals inflate the plotwise density estimates, as well as make those estimates interdependent. I accept this criticism, but suggest that it is not crucial to my analysis of habitat selection, the primary purpose of which is to serve as an empirical example of the regression technique. Future studies should pay close attention to adequate replication at all scales of analysis. Nevertheless, the number of individuals using a plot should be well represented by the number of animals captured there. The number of individuals using that plot and other nearby areas will be the same regardless of whether an adjacent area is sampled or not. The only way the density estimates become strictly interdependent is if the sampling regime precludes individuals from being captured at least once in the different plots they exploit because they are consistently captured elsewhere. This is unlikely in any long-term sampling, and is much more unlikely under my protocol of rotated simultaneous trapping of every third trap-line.

Arbitrary assignment of microhabitat to nested subplots inevitably obscures patterns of microhabitat use that might be more closely associated with microhabitat structure than with uniform partitions of spatial variation. These problems are likely not as severe as the logistical and statistical difficulties encountered in other methods of discriminating microhabitats for density comparisons (Morris 1987a).

My data are inappropriate for general comparisons of *Peromyscus* and *Microtus* densities among open and wooded habitats because the subplots are pseudoreplicates at that scale (e.g., Hurlbert 1984). Pseudoreplication is itself a problem of scale, and pseudoreplicates at one scale may themselves have adequate replication within that scale. This restricts my analysis to comparison of *P. leucopus* and *M. pennsylvanicus* abundances between macrohabitats at Point Pelee, but it does not affect the statistical analysis of abundance data replicated at that scale (e.g., Stewart-Oaten et al. 1986). Moreover, density-dependent habitat selection occurs by individual decisions on habitat quality, and any density patterns I observed can be taken to represent the nature of habitat selection of these small mammals at Point Pelee.

I augmented the regression test by searching for fitness differences among habitats with contrasts of time-specific demographic estimates of disappearance, recruitment, and reproduction. Disappearance and recruitment data were standardized as percentages per

TABLE 2. The number of different individuals of *Microtus* and *Peromyscus* captured in four adjacent macrohabitats (9 × 15 trap grids with 15-m spacing) in Point Pelee National Park during 1978 and 1979 (from Morris 1984c).

| Species | Year | Habitat | | | |
|---|---|---|---|---|---|
| | | Grass-land | Old field | Sumac | Forest |
| *Peromyscus* | 1978 | 10 | 11* | 31 | 59 |
| | 1979 | 11 | 39 | 84 | 121 |
| *Microtus* | 1978 | 97 | 26 | 0 | 5 |
| | 1979 | 147 | 30 | 0 | 2 |

\* In 1978, most *Peromyscus* in the old field were captured only during the autumn trap interval.

trap interval and matched estimates were analyzed among habitats by nonparametric analysis of variance (Friedman's two-way ANOVA, SPSSx: SPSS 1983). A posteriori contrasts of significant results and two-habitat comparisons were analyzed using Wilcoxon's matched-pairs signed-ranks test (SPSSx). Adult animals were classified as reproductive (females: pregnant or lactating; males: testes descended) or not, and total captures in each category contrasted among habitats and between years by contingency analysis. Unless otherwise indicated, tests were considered statistically significant with a type I error rate of 0.05 or less.

It is possible that comparisons of percentages inflate the apparent demographic differences among habitats. Rates of change for relatively small populations may be unreliable or inaccurate indicators of demography. This could be a problem if my intent was to contrast mean differences in rates between habitats. In contrast, a significant nonparametric ANOVA indicates statistically consistent trends in the rank of the percentage differences among habitats. If my demographic estimates are imprecise, it would be unlikely that I could generate any statistically significant differences.

## RESULTS

White-footed mice (*Peromyscus leucopus*) were abundant in the sumac and forest habitats and common in the old field, whereas the meadow vole (*Microtus pennsylvanicus*) was prevalent in the old field and grassland. Between the 2 yr of the study *Peromyscus* increased by ≈130%; *Microtus* increased by ,40% (Table 2). The overall abundances of *Peromyscus* among forest, sumac, and old field, and of *Microtus* between grassland and old field, were independent of yearly comparisons ($G = 2.68$, NS, and $G = 1.26$, NS, respectively). Variances of rodent density estimates were homogeneous among habitats and years ($F_{max} = 10.86$, df = 4, NS; Sokal and Rohlf 1981:405) and had no significant covariation with mean density ($r = 0.46$, df = 8, NS).

All four of the regressions comparing annual rodent density estimates between habitats were highly statistically significant and consistently accounted for a sub-
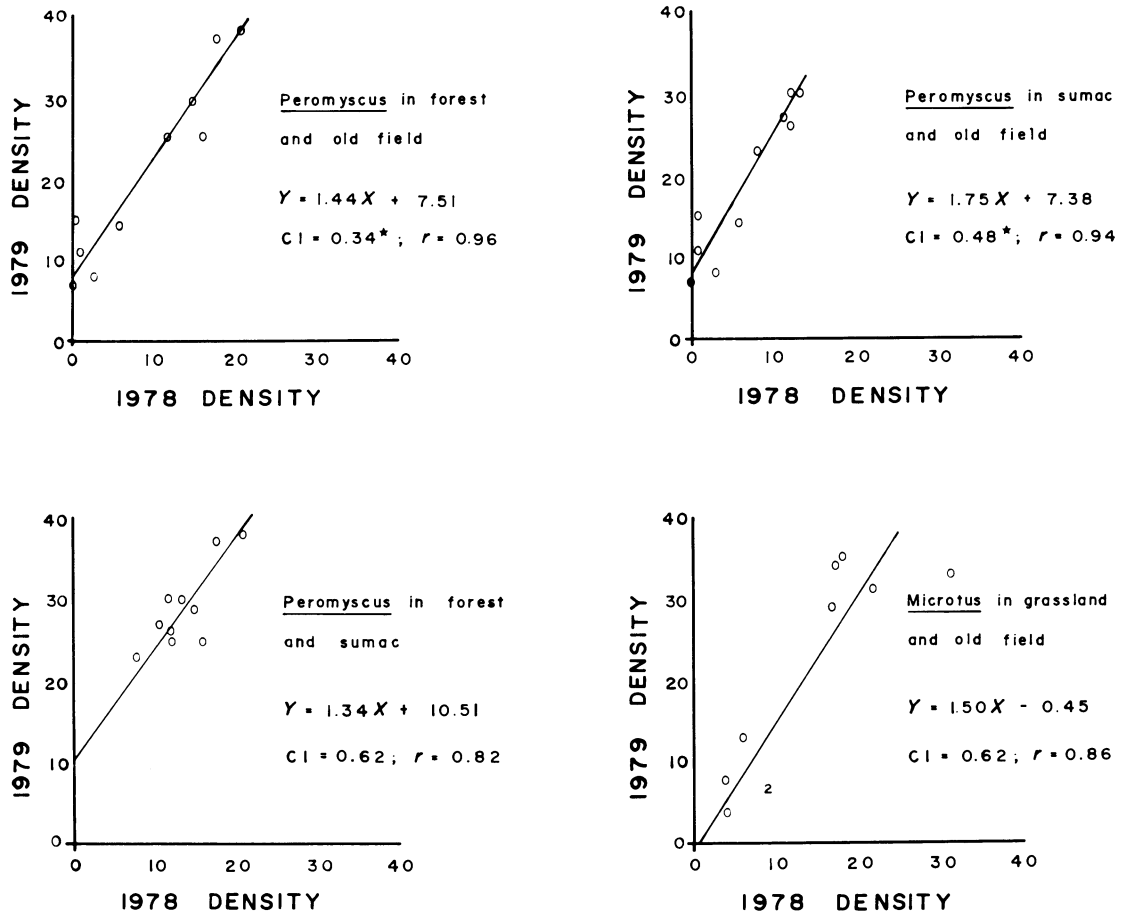
FIG. 7. Density regressions for two-habitat comparisons of rodent habitat selection in Point Pelee National Park. Densities in 1979 exceeded those in 1978. All regressions are highly significant ($P < .005$). Slopes for comparisons of *Peromyscus* density in the sumac × old field and forest × old field comparisons are significantly >1.0. CI = 95% confidence interval about the slope; $r$ = Pearson product-moment correlation coefficient. ★ = slope significantly different from 1.0.

stantial amount of the variation in population density (mean $R^2 = 0.77$; Fig. 7). Most regressions had a reasonable scatter of data points along both axes, and there was no strong indication of curvilinear responses over the range of densities reported here. Comparisons of 1978 and 1979 density estimates for *Peromyscus* in the two wooded habitats (forest and sumac) and for *Microtus* in the open (grassland and old field) demonstrated the similarity of density-dependent habitat selection in those habitats (slopes > 1.0 but not significantly different from 1.0). Comparisons between wooded and open habitats (*Peromyscus* density in the forest and sumac compared with that in the old field) showed a significant divergence in habitat suitability with density (slope significantly > 1.0). The intensity of density-dependent feedback on habitat choice appeared to be related to how similar the habitats were in structure and other ecological characters. It is interesting that suitability–density functions diverged from one another. The degree of density dependence was less severe in habitats with the greatest density. In

sharp contrast to the comparisons between habitats, none of the microhabitat (3 × 3 subplot) regressions was statistically significant.

Rodent densities fluctuate not only between years, but also within years. To check for possible seasonal biases in abundance, I repeated the analyses separately for spring (May–July) and autumn (August–October) density estimates. The results were not as clean as those

TABLE 3. Movement of individual *Peromyscus* among four habitats in Point Pelee National Park.

| Habitat of first capture | Habitat of subsequent capture(s)* | | | | |
|---|---|---|---|---|---|
| | Grass-land | Sumac | Old field | Forest | Total |
| Grassland | ··· | 5 | 0 | 1 | 6 |
| Sumac | 4 | ··· | 2 | 3 | 9 |
| Old field | 0 | 5 | ··· | 2 | 7 |
| Forest | 0 | 1 | 2 | ··· | 3 |
| Total | 4 | 11 | 4 | 6 | 25 |

* Two animals moved twice.

TABLE 4. *Peromyscus* demography in three habitats in Point Pelee National Park. Data are mean values calculated for the seven trap intervals after *Peromyscus* became firmly established in the old field.

| Habitat | Demographic variable* | | | | | | |
|---|---|---|---|---|---|---|---|
| | TD | AD | JD | JM | TR | AR | JR† |
| Old field | 55.4 | 23.3 | 25.0 | 64.7 | 45.1 | 17.9 | 37.1[b] |
| Forest | 42.1 | 26.9 | 9.4 | 50.1 | 45.9 | 21.4 | 21.0[a] |
| Sumac | 38.0 | 23.7 | 10.6 | 75.9 | 43.3 | 19.1 | 24.0[a,b] |
| $\chi^2$ | 5.43 | 1.14 | 5.21 | 2.00 | 1.93 | 1.50 | 6.00 |
| $P$ | .07 | .56 | .07 | .37 | .38 | .47 | .05 |

* TD = total disappearance: % of known population disappearing from the trapped population between subsequent intervals; AD = adult disappearance: % of known population disappearing as adults; JD = juvenile disappearance: % of known population disappearing while juveniles or subadults; JM = juvenile mortality: % of juveniles or subadults recruited in interval *t* that disappeared during interval *t* + 1; TR = total recruitment: % of known population recruited between subsequent trap intervals; AR = adult recruitment: % of known population recruited as adults; and JR = juvenile recruitment: % of known population recruited as juveniles or subadults.

Ages were determined by pelage characteristics.

† Habitats with the same superscript letter were not significantly different (*P* > .05) from one another. For all the other variables there were no significant differences.

combining seasons but were in the same direction (five of eight macrohabitat regressions were statistically significant, all significant slopes were positive, only the contrast between spring densities in the forest and old field were significantly different [greater] from the predicted slope of 1.0; seven of eight microhabitat regressions were not statistically significant).

The densities of *Peromyscus* in the forest and sumac both exceeded the estimated density in the old field; consequently the ordering of habitat quality for *P. leucopus* would appear to be forest > sumac > old field. Or is it? The increase in population densities across habitats was unequal. The ranking of proportional increase in densities from 1978 to 1979 was old field > sumac > forest (the actual numerical changes are given in Table 2). Even though the density-dependent feedback on habitat quality was shown to be more intense in the old field than in either of the wooded habitats, there was incomplete compensation and population growth rates were unequal. If these density changes reflected reproductive performance in the different habitats, then the fitness rewards of mice in the old field were higher than they were in the sumac and forest. Movement of marked animals from habitat to habitat was uncommon (23 of 354 marked animals in the entire study area), even though the trapping grids were adjacent to one another. There was no obvious preference of migrants for one habitat over another (Table 3). It seems possible that the fitness rewards in 1978 for *P. leucopus* in the old field exceeded those of their relatives in the two wooded habitats.

The analysis of demographic data tended to confirm the suspicion of greater fitness for field-dwelling *Peromyscus*. Supporting the migration data, disappearance and both total and adult recruitment were similar among the three habitats (Table 4). Juvenile disappearance tended to be greater in the old field than in the other habitats. The juvenile recruitment rate relative to the minimum number of total animals known alive in that habitat was significantly higher in the field than in the

forest. In contrast, juvenile mortality as a percent of those recruited in the previous trapping interval was not significantly different among habitats. Analysis of the reproductive data showed significant differences in the proportion of females in reproductive condition that was higher than expected in both the field and forest and lower than expected in the sumac (Table 5). There were no significant differences among habitats in the proportion of breeding males.

Demographic differences between habitats were not clear-cut, but were suggestive of the following explanation of differences in population growth rates. High population growth in the old field appeared to be the result of a greater recruitment of young animals, which in turn reflected the high proportion of breeding females in that habitat. The total number of animals added to the field population was, nevertheless, much less than in either of the wooded habitats. Similarly, the high growth rate in the sumac seemed to be mediated by high juvenile recruitment rates and not by directional and very low dispersal, which was more or less constant among habitats.

There were modest differences in *Microtus* demog-

TABLE 5. Reproductive status (NR: nonreproductive; RE: reproductive) of adult male and female *Peromyscus* captured in three habitats in Point Pelee National Park (pooled data for 1978 and 1979*). Expected values are in parentheses.

| | Sex | | | |
|---|---|---|---|---|
| | Male | | Female | |
| Habitat | NR | RE | NR | RE |
| Old field | 5 (4.2) | 23 (23.8) | 2 (4.1) | 14 (11.9) |
| Forest | 29 (23.7) | 127 (132.3) | 27 (33.8) | 104 (97.2) |
| Sumac | 10 (16.1) | 96 (89.9) | 29 (20.1) | 49 (57.9) |
| | $\chi^2 = 4.28$; $P = .12$ | | $\chi^2 = 8.6$; $P = .01$ | |

* Comparisons within years were similar except that the old field had too few animals in 1978 for statistical analysis.

TABLE 6. *Microtus* demography in two habitats in Point Pelee National Park. Variables as in Table 4, except ages based on body mass: <30 g = juvenile, >30 g = adult. Data are mean values over all trap intervals.

| Habitat | Demographic variable | | | | | |
|---|---|---|---|---|---|---|
| | TD | AD | JD | TR | AR | JR |
| Grassland | 61.5 | 42.5 | 15.9 | 68.7 | 50.4 | 14.4 |
| Old field | 57.4 | 31.4 | 28.4 | 51.7 | 27.9 | 23.6 |
| Z | −0.45 | −1.96 | −1.17 | −2.40 | −2.59 | −1.53 |
| P | .66 | .05 | .24 | .02 | .01 | .13 |

TABLE 8. Reproductive status of adult male and female *Microtus* (NR: nonreproductive; RE: reproductive) captured in two habitats in Point Pelee National Park (pooled data for 1978 and 1979*). Expected values are in parentheses.

| Habitat | Sex | | | |
|---|---|---|---|---|
| | Male | | Female | |
| | NR | RE | NR | RE |
| Grassland | 18 (17.3) | 121 (121.7) | 118 (114.4) | 79 (82.6) |
| Old field | 5 (5.7) | 41 (40.3) | 26 (29.6) | 25 (21.4) |
| | $\chi^2 = 0.01; P = .91$ | | $\chi^2 = 0.98; P = .32$ | |

\* Comparisons within years were similar.

raphy between habitats. Total disappearance, juvenile disappearance, and juvenile recruitment were not different between habitats (Table 6). Adult disappearance, total recruitment, and adult recruitment were significantly greater in the grassland than in the old field. This corresponds to a higher rate of adult turnover in the grassland.

I was unable to analyze for differences in juvenile mortality by the same technique as for *Peromyscus* because recruitment was more seasonal for *Microtus*. Instead, I summed the total number of juveniles captured in only one interval, or in more than one, and analyzed the results by contingency analysis. Juvenile survival was similar in both habitats (Table 7). Analysis of reproductive data found no significant differences in the proportion of breeding males and females in the two habitats (Table 8).

High adult turnover of *Microtus* in the grassland could represent reduced adult survival, movement into and out of my study plot, and sporadic trapability of individual animals. I am unable to differentiate among these alternatives, but I suspect that voles were much more likely to move into and out of the grassland plot, which was contiguous with adjacent grassland, than they were to move from the old field, which was surrounded by trees and shrubs. Regardless, *Microtus* population growth rates in the two habitats were similar. No marked *Microtus* moved between the grassland and old field.

## DISCUSSION

The empirical study is best viewed as a demonstration that the regression method can provide new insights into density-dependent habitat selection. It should not be overinterpreted as a definitive test of habitat-dependent population regulation by temperate-zone

TABLE 7. Juvenile survival of *Microtus* living in two habitats in Point Pelee National Park. Expected values are in parentheses.

| Habitat | Number captured once | Number captured in >1 interval |
|---|---|---|
| Grassland | 45 (42.8) | 24 (26.1) |
| Old field | 14 (16.1) | 12 (9.8) |
| | $\chi^2 = 1.04; .1 < P < .5$ | |

rodents. Regardless, the regression tests of density-dependent habitat selection give a provocative first look at how mechanisms of population regulation vary with habitat. Structurally similar habitats also appear similar in the degree of density-dependent regulation by the populations exploiting those habitats. Density dependence in population regulation by *Peromyscus* inhabiting the forest was indistinguishable (parallel) from that of *Peromyscus* in the sumac. The same was true for *Microtus* in the grassland and old field. By way of contrast, the old field added far fewer *Peromyscus* between years than did either of the wooded habitats (divergence), yet there was incomplete compensation. The population growth rate in the old field exceeded that of the wooded habitats, and appeared to be due to differential reproduction.

In any event, the old field supported relatively more white-footed mice in 1979 compared with 1978, than did either of the wooded habitats. Unless there was an instantaneous adjustment of population density to habitat quality by migration, a most unlikely scenario given the low observed rate of migration, individuals that overwintered in the old field may have reaped sweepstake fitness rewards relative to animals in the adjacent wooded habitats.

This is a complication not dealt with in the current theory of density-dependent habitat selection. If the relative ordering of habitat quality changes independently of population density, as it could with successional changes in the 8-yr-old field, occasional fitness bonanzas may outweigh the apparent disadvantages of colonizing, or remaining in, temporarily suboptimal habitat. The same would be true whenever the relative population increase in one habitat exceeds that of others. Of course, during population decline, individuals remaining in these boom and bust habitats would be faced with greater fitness losses than those individuals in populations whose rate of decline is more gradual. Genotypes that speculate in this way on the ecological futures market walk an evolutionary tightrope between windfall profits and reproductive bankruptcy.

The severity of density dependence appeared to decline with increased carrying capacity. The "best" habitats appear to be those that not only have high levels of resources, but that also have high renewal rates for

those resources when they are being exploited. This in turn would imply a positive covariance between resource turnover rates and consumer biomass. On a local scale, where resource species are similar between habitats, those habitats that can maintain large populations of resource species are also likely to be able to sustain high population growth rates of those resources when they are being cropped below their carrying capacity. As habitats diverge in structure, substrate, proximity, and history, they are likely also to diverge in the similarity of resources for consuming species. We might expect a transition of density-dependent feedback on consumer fitness from parallel to divergent regulation as habitats become qualitatively less similar.

The apparent existence of different forms of population regulation among habitats sheds new light on the evolution of dispersal and its role in population regulation. In a mosaic of qualitatively similar habitats (parallel regulation), dispersing individuals should frequently be at a selective advantage. Successful emigrants to low-density habitats will achieve increased reproductive rewards relative to those remaining in high-density habitats because per capita population growth rates are unequal. As habitats become qualitatively less similar, the intensity of density-dependent regulation increases in the low-density habitats and dispersal is relatively less rewarding (per capita population growth rates are similar).

How do we reconcile this argument with Holt's (1985) prediction that, with optimal habitat selection, dispersal should evolve toward zero? According to Holt, optimal habitat selection may lock a species into habitat specialization, reducing the value of dispersal while simultaneously increasing risks of extinction. Holt's model assumes that dispersal is passive and proportional to population density. If, however, the rate of dispersal is itself density dependent, there is no longer an anomaly between optimal strategies of dispersal and habitat selection. Holt's extinction trap is unable to capture species for which dispersal is density dependent. Species occupying a wide range of different habitats have little to gain by density-dependent dispersal because dissimilar habitats should frequently differ in quality, and likewise in the intensity of population regulation. In such a mosaic, dispersers will frequently land in a habitat with a lower quality than the one they came from. Lack of dispersal leads to habitat specialization where all occupied habitats become more similar (parallel regulation), and where density-dependent dispersal is, again, selectively advantageous. Some dispersers will find themselves in vastly different habitats, and as long as they can establish and replace themselves, the range of habitats used will expand. This could lead to cycles of generalized and specialized habitat use analogous to (and perhaps driving) the taxon cycle of island biogeography (Wilson 1961).

Successional habitats represent a special case where

the degree of density dependence shifts in response to the accumulation (or loss) of resource species, their biomasses, and their growth potential. Early in succession, accumulation of resources may allow high population growth rates of consumer species with little incentive for dispersal to other habitats. At the peak of the successional history of a particular habitat, resource renewal rates are high, and the density-dependent stimulus for emigration remains low. Beyond this peak, renewal rates decline, density-dependent feedback on fitness intensifies, there is increased pressure for migration, and successful dispersers may colonize other sites to begin the process anew. Such a scenario would lead to a complicated habitat selection strategy simultaneously evaluating speculative and conservative dispersal alternatives, and may lead to cyclical dispersal episodes reflecting the underlying mode of population regulation.

The regression test has also provided insights into the effect of spatial scale on habitat use. At the microhabitat scale, the general result was an absence of significant covariation in rodent density. This could be caused by an inverse relationship between a microhabitat's quality and its carrying capacity. At low density, microhabitat $a$ with a higher basic suitability would achieve a greater animal density than $b$. With increasing overall density, $b$ would support more animals than $a$ (cross-overs). Such an inverse relationship between $r$ and $K$ could occur through a similar inverse relation between resource abundance and resource renewal, the opposite of what I have argued for macrohabitats. Unless all of the cross-overs occurred at about the same density, some of the paired regression points could lie above the intersection (curves converging; $b < 1.0$), some below (curves diverging; $b > 1.0$), and some above and below ($b$ is negative). The one significant regression had a negative slope, suggesting that such an inverse relation may operate at the microhabitat scale.

A more parsimonious alternative is that habitat selection theory is scale dependent. Fine-grained consumers (those that harvest resources in the proportions in which they occur) should habitat select (MacArthur and Levins 1964, Rosenzweig 1974, 1981). Foraging distinctions are arbitrary, and all species are both fine- and coarse-grained. Their expected fitness rewards in alternative habitats may not be density dependent, and other selective forces in addition to resource exploitation must ultimately determine habitat-related fitness rewards (Price 1984, Morris 1987a). Patterns of density-dependent habitat use would no longer be obvious at the microhabitat scale. Densities of these species may respond instead to overall habitat quality, with the result that local abundances within small subplots could fluctuate with little predictability. For such species, intraspecific competition may be more of a scramble for resources (Nicholson 1954) resulting in fitness rewards that show little predictable variation within any one macrohabitat.

The confirmation of density dependence at the scale of macrohabitat supports an emerging documentation that the abundances of northern mammals are effected primarily by macrohabitat processes. Several possibilities can account for this scaling pattern. One of the most likely is that population density responds to overall resource abundance, which in northern mammals should be correlated more with macro- than with microhabitat (Morris 1987a, b). Similarly, other selective forces related to predation rates, physiological tolerances, and social interactions are unlikely to depend mainly on microhabitat. Individual foraging behavior may depend upon microhabitat, but not population density. These limitations suggest that future tests of habitat selection theory should emphasize scale-dependent experimental manipulations of resource abundance and population density.

The regression test showed that population regulation is habitat dependent. It is a useful empirical tool, and opens new doors to the field biologist interested in how environmental variation, behavior, and life histories interact to influence population dynamics, and ultimately, patterns of distribution. To the theorist it poses several questions. Is habitat speculation an evolutionarily stable life history strategy? What is the relationship between habitat quality and population regulation? Is there some fundamental reason why the intensity of density-dependent feedback on fitness appears inversely related to carrying capacity? What are the expected shapes of suitability–density functions? What is the relationship between density-dependent dispersal and habitat heterogeneity? What are the implications of temporal patchiness on dispersal and population dynamics?

The consequences of variation in density-dependent habitat choice should be contemplated carefully by anyone interested in the evolution of density-dependent reproductive and behavioral strategies. Even so, we must not dismiss the possibility of a high positive covariance between population density and resources that would minimize density-dependent depression of reproductive success.

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