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ECOLOGICAL SCALE AND HABITAT USE[1]

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Abstract. Population density can respond to habitat at different scales. If habitat selection occurs as a consequence of resource exploitation, the density of fine-grained consumers should reflect microhabitat variation. But if habitat use is controlled by a variety of selective pressures, it is no longer apparent whether density should respond to micro- or macrohabitat. These two alternatives can be tested simultaneously by multiple regression models where macrohabitats are represented by dummy variables. When the local densities of two Temperate Zone rodents were analyzed in this way, macrohabitat and temporal effects were consistent significant predictors of rodent density; microhabitat was not. This analysis suggests species whose patterns of resource and habitat use probably depart from classical interpretations of species coexistence. It is probably premature to assess the role of habitat selection in the structure of ecological systems until the results of further tests of habitat scaling are reported.

Key words: habitat selection; macrohabitat; microhabitat; Microtus; *Ontario;* Peromyscus; *regression; scale.*

INTRODUCTION

The fundamental rule of species distribution is that species are more abundant in some habitats than in others. Density-dependent habitat use is well documented and several explanatory theories have been proposed (Svärdson 1949, MacArthur and Levins 1964, 1967, Fretwell and Lucas 1970, Rosenzweig 1974, 1981, Grant 1975). Yet few tests of the relation between habitat and population density have been attempted (e.g., Whitham 1978, 1980, Fraser and Sise 1980), and even these are ambiguous (e.g., Rhomberg 1984). The ambiguity is in large part due to variation in the scale of habitat use, both in terms of species' responses and in the models themselves. Animals can perceive, and the densities of their populations respond to, habitat in two ways. Fine-grained species use subsets of the habitat mosaic in direct proportion to the abundance of those subsets, whereas coarse-grained species select some habitats preferentially over others (Levins 1968). Surely these distinctions are ones of degree. Every species' physiology, morphology, and behavior preclude fine-grained use of all resources, so each species is to some extent selective. Given that a species harvests a given subset of the available resources, it can harvest those chosen resources in proportion to their abundance, or some preferentially over others. Even the most selective of predators may proportionately allocate their foraging among certain classes of prey phenotypes, and so all species (and phenotypes within species) are likely both coarse- and fine-grained in resource use, and similarly in habitat. The outcome is that our inferences about causal forces of habitat selection related to resource extraction are at least partly contrived. Ultimate explanations for habitat use must also address alternative evolutionary explanations for the observed patterns (Price 1984). Then we have to ask, at what scale of habitat should we look for pattern and process? Should species select habitat based on microhabitat or macrohabitat?

How we approach studies of habitat use will depend on our relative interest in revealing ultimate as opposed to proximate mechanisms responsible for habitat selection. At one level of analysis, we need to know the habitat preference of species at each scale of habitat. Similar patterns should occur among species with similar foraging strategies (MacArthur and Levins 1964, MacArthur and Pianka 1966, Pyke et al. 1977, Krebs 1978). Individuals should forage in those habitats where the return in fitness is maximized. Species (or individuals) that exploit all habitat patches are likely specialized in diet (MacArthur and Levins 1964), whereas species that select some patches over others probably do so because the patches differ in the density of resources (Rosenzweig 1974). At another level of analysis, we need to know how a species' density responds to the different scales of habitat. Knowing the density response at different habitat scales allows us to evaluate the significance of habitat to patterns of coexistence of interacting species (Schoener 1974), and its possible importance as a templet for life history and other ecological strategies (Southwood 1977). A third level would document fitness rewards of individuals at alternative scales of habitat use. A fourth would evaluate the allocation of time and energy by individuals. Before any of these can be attempted, we must have clear and unambiguous rules for defining habitat scale.

Explicit biological definitions of spatial and temporal scales are essential if we are to resolve the influence of space and time on patterns, structure, process, and

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function in ecological systems. Unlike other approaches which impose human bias on ecological scale (Maurer 1985), biological definitions use the attributes of the organisms we study to define the organisms' perception of scale. We can measure geographical range, population density, generation time, migration and dispersal distances, territory or home range sizes and daily activity budgets, and use these to show us how the organisms perceive the spatial and temporal scaling of their environment. When we do that, we have effectively removed the influence of human perception from our interpretations of ecological scale.

While there is a continuous gradient of scales reflecting community, population, and individual perceptions of habitat, in practice we need define only a few of them. If we define habitat type as the spatial scale within which similar physical/chemical variables can be used to describe its variation, then different habitat types are described by different suites of physical/chemical variables. Within habitat types, we can define macrohabitats as distinguishable units whose minimum area corresponds to that within which an average individual performs all of its biological functions (home range) during a typical activity cycle. Microhabitat can be quantified by physical/chemical variables that influence the allocation of time and energy by an individual within its home range. An individual would be expected to encounter multiple microhabitat "patches" during a typical activity cycle. This paper describes the relationship between the different scales of habitat, proposes an analytical method to evaluate the relationship between habitat scale and population density, and documents that method with a worked-out example on two Temperate Zone small-mammal species.

A Model of Habitat Scaling

Within some particular habitat type, say forest, grassland, or marsh, microhabitat variation within and among homogeneous sampling units can be represented as an F ratio where

$$\text{MS } H_{\text{macro}}/\text{MS } H_{\text{micro}} = F.$$

The numerator represents the mean square of some measure of microhabitat among the homogeneous units (macrohabitats), and the denominator is the error variation in microhabitat within those units. Then different macrohabitats can, in theory, be rigorously discriminated as those homogeneous sampling sites greater than the average home range of the species of interest, where $F > F_{(\text{critical})}$ (Morris 1985). Having defined macrohabitat and microhabitat variation in this way, we can predict the specialization strategies of constituent species by similarly partitioning the variance in fitness. A species should be coarse-grained in macrohabitat use whenever

$$\text{MS } W_{\text{macro}}/\text{MS } W_{\text{micro}} > F_{\text{critical}}.$$

The terms represent mean squares of habitat suitability (fitness) for macro- and microhabitats, respectively. Otherwise, the species should be fine-grained in macrohabitat, and its grain size for microhabitat will depend upon its foraging strategy. Eventually, we should wish to evaluate these relations with fitness data of individuals within and among different macrohabitats. In the absence of such data, we can assume that population density covaries with reproductive success in a given macrohabitat. Of course, density-dependent feedback on fitness could mean that habitats with the greatest density reward individuals with the same or even less expected reproductive success than they may gain elsewhere (Fretwell and Lucas 1970, Rosenzweig 1981). The effect of density-dependent feedback is not crucial, because the same theories predict that population density will reflect the density-independent suitabilities of the different habitats.

The scaling of habitat use can be represented by a linear model of the form

$$N = a_0 + b_1F_1 + b_2F_2 \ldots + b_nF_n + b_{n+1}D_1 + b_{n+2}D_2 \ldots + b_{n+m}D_m + e,$$

where N is the predicted density, the F's represent microhabitat factors, the D's are dummy variables scored 0 and 1 representing $m + 1$ macrohabitats, and e is normally distributed error variation. To determine the scaling of habitat use by any particular species, we simply need to estimate population density and microhabitat variation within small plots nested among different macrohabitats, and evaluate the prediction equation by multiple regression. Similarly, the model can be extended to include effects of macrohabitat and temporal replication by the inclusion of suitable dummy variables, and can evaluate interspecific effects by including the densities of the interacting species (Schoener 1974, Crowell and Pimm 1976, Hallett and Pimm 1979). An alternative approach to quantifying the components of hierarchial scaling in habitat would be nested analysis of variance. A nested ANOVA may not be appropriate where additional factors such as interspecific densities, or temporal and spatial replication, are being simultaneously evaluated.

In practice, the researcher will likely wish to keep the number of microhabitat variables to a minimum. Density estimates for many species represent time-consuming and logistically difficult activities. This usually means that the number of density estimates will be limited, and will restrict the regression analysis to a moderate number of independent variables. The number of dummy and density variables will be dictated by the variety of macrohabitats censused and the number of potentially interacting species, so that any reduction in the dimensionality of the model must occur through reduction in the number of microhabitat variables. This could be accomplished, in many instances, by data reduction using factor analytical procedures. Preliminary factoring of complex microhabitat data

TABLE 1. The number of different mice (*Peromyscus leucopus, P*) and voles (*Microtus pennsylvanicus, M*) captured in different subplots of four macrohabitats in Point Pelee National Park.

Subplot	Macrohabitat							
	Forest		Sumac		Old field		Grassland	
	P	*M*	*P*	*M*	*P*	*M*	*P*	*M*
				1978				
1	7	0	6	0	0	1	0	8
2	8	0	5	0	0	6	0	7
3	8	0	5	0	2	4	4	6
4	4	3	7	0	0	0	0	4
5	8	0	3	0	0	1	0	8
6	4	0	3	0	2	3	0	7
7	6	0	7	0	1	1	0	12
8	7	0	4	0	0	1	1	8
9	8	0	5	0	0	2	2	13
10	10	0	5	0	2	0	2	6
11	6	0	4	0	1	5	0	5
12	5	1	5	0	1	5	0	6
13	7	0	4	0	4	0	2	8
14	12	1	5	0	2	1	3	11
15	6	0	5	0	0	5	1	5
				1979				
1	7	0	11	0	8	2	0	9
2	9	0	10	0	1	3	1	13
3	12	0	14	0	9	4	3	14
4	5	2	8	0	7	0	0	15
5	10	0	13	0	1	7	0	8
6	14	0	11	0	4	2	1	13
7	10	0	16	0	4	2	0	11
8	12	0	9	0	3	0	0	10
9	12	0	10	0	2	2	0	15
10	15	0	14	0	4	2	0	11
11	12	0	8	0	2	2	0	9
12	17	0	12	0	3	3	2	10
13	13	0	9	0	10	0	0	12
14	15	0	11	0	5	2	4	12
15	16	0	12	0	2	12	1	11

structures also has desirable properties for subsequent data analysis (Green and Vascotto 1978, Green 1979).

METHODS

Protocol

I used the following protocol to study the scale of density-dependent habitat use by *Peromyscus* and *Microtus* in southern Ontario.

1) Select homogeneous macrohabitats within one habitat type for analysis.

2) Subsample these habitats in such a way as to be able to estimate microhabitat variation and the density response to that variation (these units will usually be smaller than average home range size).

3) Collect single estimates of microhabitat and population density within the subsamples.

4) Scrutinize the microhabitat variables for those that are at least close to having a multivariate normal distribution, and discard the others.

5) Screen the remaining variables for redundancy and reduce the number of selected variables by some form of factor or principal components analysis.

6) Reconfirm the macrohabitat designations by multivariate analysis of variance (e.g., multiple discriminant functions analysis) on the extracted factor scores among macrohabitats.

7) Select some reference macrohabitat and construct *m* dummy variables to represent the remaining macrohabitats.

8) Repeat (7) for temporal or spatial replicates.

9) Include density estimates for interacting species (not applied in this study).

10) Screen bivariate scatterplots of all pairwise variables for nonlinear responses.

11) Evaluate the model by multiple regression.

12) Examine the residuals to determine the goodness of fit of the prediction equation.

An analogous design based on log-linear models could be used for categorical data, for example, where microhabitats are represented by discrete classes instead of by continuous variables.

Field methods

Small mammals were live-trapped for six consecutive months during 1978 and 1979 in adjacent wooded and open habitats in Point Pelee National Park, located on the northwestern shore of Lake Erie (Morris 1984*a*) (Table 1). White-footed mice (*Peromyscus leucopus*) were abundant in two wooded macrohabitats (forest and sumac), whereas meadow voles (*Microtus pennsylvanicus*) were abundant in grassland. Intermediate densities of both species were recorded in a fourth macrohabitat, an abandoned old field.

TABLE 2. Microhabitat variables included in the final factor solutions of microhabitat structure.

Variable	Description*	Habitat type
Q1	Amount of vegetation from 0 to 0.25 m height	both
Q2	Amount of vegetation from 0.25 to 1 m height	wooded
SUMQ	Total vegetation below 1.75 m height	wooded
DIV	Vegetation profile diversity	wooded
VERT	Vertical vegetation density from 1.75 m	wooded
DVERT	Diversity of vertical vegetation density	both
LMAT	Log_{10} litter (mat) depth	open
CMAT	Coefficient of variation of LMAT	both
SBDEN	Square root of distance to nearest shrub	open
SSDEN	Square root of distance to nearest sapling	open
STDEN	Square root of distance to nearest tree	wooded

* Q1 measures vegetation density in the ground layer; Q2 quantifies the density of tall herbs and shrubs; SUMQ (horizontal plane) and VERT (vertical plane) integrate total understory cover. DIV is at a maximum when the layering of vegetation is evenly distributed among layers; DVERT specifies the degree of patchiness in plant cover. LMAT estimates litter depth; CMAT is an indicator of horizontal variation in litter depth. SBDEN, SSDEN, and STDEN are negatively related to the density of shrubs, saplings, and trees, respectively.

Each plot consisted of a 9 × 15 array of sampling points spaced at 15-m intervals. Microhabitat was quantified at every station. Variables used in the final factor solutions included estimates of shrub and tree density (SBDEN, SSDEN, STDEN), horizontal profiles (Q1, Q2, SUMQ), profile diversity (DIV), vertical density (VERT, DVERT), accumulated litter and its variability (LMAT, CMAT) (Table 2). Profiles and litter depth were re-measured in the open macrohabitats in 1979 to control for possible successional changes in microhabitat structure. Variables used in the analyses were those measurement variables or their transformations that gave a more or less symmetrical and unimodal distribution of scores within a particular habitat type (Table 2).

To create subplots for the density-dependent analyses, I grouped sampling stations into square 3 × 3 grids (15 grids per macrohabitat per year). Rodent density was estimated as the number of different individuals captured per grid. Microhabitat structure for a given subplot was calculated as the arithmetic mean of each structural variable for that subset of nine stations. Averaging microhabitat variation in subplots may reduce the magnitude of microhabitat variation relative to that among macrohabitats, and would bias the analysis toward significant macrohabitat effects. When the process being evaluated is variation in population density, sampling plots must be large enough to obtain reliable population estimates. An inevitable trade-off occurs between the accuracy of the estimates for population density and those for microhabitat variation. The key to making correct inferences about the influence of scale on ecological patterns is to choose scales that reflect the processes being studied. An analysis of small-mammal behavioral responses to microhabitat should be conducted among patches substantially smaller than the patches I use here to evaluate scaling effects in density-dependent habitat selection.

TABLE 3. Varimax-rotated factor loadings of microhabitat variables in mature forest and sumac macrohabitats in Point Pelee National Park. The magnitudes of the loading coefficients are used to interpret their respective microhabitat factors.

	Microhabitat factor	
Variable	Forest floor and shrub density (57%)*	Understory development and forest patchiness (21%)
Q1	0.88	−0.07
Q2	0.66	0.63
SUMQ	0.78	0.57
DIV	0.23	0.92
VERT	0.81	0.44
DVERT	0.90	0.18
CMAT	−0.27	0.18
STDEN	−0.08	0.69

* Percent of total variance accounted for.

TABLE 4. Varimax-rotated factor loadings of microhabitat variables in grassland and old-field macrohabitats in Point Pelee National Park. The magnitudes of the loading coefficients are used to interpret their respective microhabitat factors.

	Microhabitat factor		
Variable	Shrub/herb density (20%)*	Litter layer (18%)	Field openings (16%)
Q1	0.39	0.10	−0.12
DVERT	−0.06	0.12	−0.49
LMAT	−0.01	0.69	0.18
CMAT	−0.03	−0.23	0.08
STDEN	−0.10	0.07	0.29
SSDEN	0.62	0.15	0.32
SBDEN	−0.28	0.13	0.07

* Percent of total variance accounted for.

Data analysis

Data reduction was accomplished by principal axis factoring (PAF method, SPSS-X) with varimax rotation. The resulting factors were used as input variables for two-group discriminant function analysis of microhabitat differences between macrohabitats (WILKS method, SPSS-X) and for the multiple regression analyses of density-dependent responses in habitat use (STEPWISE method, SPSS-X).

RESULTS

Two microhabitat factors together explained 78% of the microhabitat variation in the forest and sumac macrohabitats (Table 3). The first described a gradient in density of vegetation in the low understory and forest floor; the second defined a cline from a dense and complex profile in open areas to sparse and less structured profiles in sites with greater tree density.

Three factors were generated in the grassland and old-field macrohabitats and together they accounted for 54% of the accumulated microhabitat variation (Table 4). Factor interpretations were more difficult to assign than in the wooded habitats, but probably corresponded to underlying relationships of shrub and herb density, litter composition, and habitat "openness."

Nevertheless, the usefulness of these factors as macrohabitat descriptors was confirmed in the analyses of macrohabitat differences by discriminant function analysis. Both the sumac and forest ($\chi^2 = 44.86$; $P < .0001$), as well as the grassland and old field ($\chi^2 = 24.79$; $P < .0001$), were highly significantly different from each other in microhabitat structure.

Both stepwise multiple regression analyses, jointly assessing the influence of microhabitat, macrohabitat, and yearly effects on rodent density, were highly significant (Table 5). In both cases, year and macrohabitat effects alone were significant predictors of rodent density. I repeated the analysis using the original microhabitat variables instead of the generated factors and

TABLE 5. The relationship of *Peromyscus* and *Microtus* density with macrohabitat. Analysis was by stepwise multiple regression of rodent density with microhabitat factors, and with macrohabitat and yearly differences represented by dummy variables.

A) *Peromyscus* density in the forest and sumac

Regression summary

Step	Variable	b	Partial r
1	Density in 1979	5.60	0.77
2	Density in sumac	−1.47	−0.30

ANOVA table

Source	df	Mean square	P	R^2
Regression	2	251.33	<.001	0.61
Residual	57	5.65		

B) *Microtus* density in the grassland and old field

Regression summary

Step	Variable	b	Partial r
1	Density in old field	−6.97	−0.80
2	Density in 1979	2.23	0.40

ANOVA table

Source	df	Mean square	P	R^2
Regression	2	401.42	<.001	0.67
Residual	57	7.01		

obtained equivalent results. When macrohabitat and yearly variation in density was accounted for, microhabitat was incapable of significantly reducing residual variation in rodent density.

DISCUSSION

The dependence of small-mammal density upon macrohabitat is contrary to a long history of past associations of small mammals with microhabitat selection (Pearson 1959, Wirtz and Pearson 1960, Rosenzweig and Winakur 1969, M'Closkey 1975*a*, *b*, 1976*a*, *b*, 1978, M'Closkey and Fieldwick 1975, M'Closkey and Lajoie 1975, Price 1978, Dueser and Shugart 1978, Morris 1979, Vickery 1981, and many more). These past results may have been confounded due to a mixing of macrohabitat and microhabitat effects (Morris 1984*a*, *b*). Nevertheless, the current results suggest either consistent biases in my research protocol, or the need to pursue new directions in the study of density-dependent habitat selection. I will first look for biases in my own research. Perhaps, for example, my choice of microhabitat variables has consistently excluded microhabitat features important to the distribution and reproductive potential of the animals I have studied. This is entirely possible, but it is a criticism that applies to all studies of microhabitat, not just mine. I have attempted to minimize this effect by summarizing microhabitat complexity in terms of underlying microhabitat factors that are undoubtedly related to a host of unmeasured variation in microhabitat. Furthermore, I have shown that macrohabitats can be distinguished on the basis of my choice of microhabitat factors, and have shown elsewhere that putative examples of microhabitat preference were instead outcomes of macrohabitat differences (Morris 1984*b*). I have also replicated the analyses on this fauna and on others (Morris 1987) using the raw microhabitat measures as independent variables in the regression analyses, and have in all cases obtained identical results as when microhabitat factors are used to describe microhabitat variation.

A second alternative is that my subplots fail to represent microhabitat variability adequately. Perhaps microhabitats should be distinguished on the basis of objective variation in vegetation structure. This could be accomplished by partitioning factor scores into discrete classes and then designating each class as a different microhabitat. This would lead to microhabitat "plots" of variable size, and could introduce statistical bias and logistical difficulties in the sampling of rare microhabitat classes. With different plot sizes, a simple regression using density as the dependent variable is not valid because the sample effort for the density estimates is unequal. Prior to regression, the density response, if it can be called that, would have to be weighted by the intensity of use of the different microhabitats. Such a procedure will likely capture more of the variation in microhabitat than does my subplot design. My interest, however, is not to evaluate rodent activity; it is instead an attempt to evaluate population dynamics in response to habitat variation. I suspect that can be best addressed by nested and uniform partitions of spatial scale.

A third possibility is that my observations of macrohabitat preference are tainted by experience with abnormal systems. This too is possible, but if true, I have studied the same abnormal situation in southern Ontario, the Rocky Mountains of Alberta, and the boreal forests of central Labrador (Morris 1987).

The remaining alternative is that the density of Temperate Zone and northern small mammals does indeed respond to macrohabitat. It also appears that this response is not related to microhabitat preference. Elsewhere, I suggested that such a pattern could be consistent with fine-grained foraging and patchy distribution (Morris 1984*a*). This scenario is supported by M'Closkey's (1975*b*, 1976*a*) observations that the frequency of use of different microhabitats by *P. leucopus* was related to structural complexity. White-footed mice seem to encounter different patches of microhabitat with equal frequency (M'Closkey 1976*a*). After encountering those patches, if they forage in some more than others, they would seem to obey Rosenzweig's (1974) specifications for a habitat selector that encounters patches in the proportion in which they occur, but exploits them differentially.

Foraging may occur only in the most rewarding patches, whereas population density responds to overall resource abundance. Density patterns also reflect social and other selective pressures which are unlikely

to have strict microhabitat correlates. The abundance of suitable prey may be determined more by macrohabitat than by microhabitat. Seed and mast production available to omnivores like *Peromyscus* will likely vary more among macrohabitats with different plant species compositions and forest age-structure than among sites within macrohabitats. Likewise, the production of palatable forage for herbivores like *Microtus* is probably linked to the species composition and successional status of alternative macrohabitats. As a consequence, population density should respond more at the macrohabitat level than at the scale of microhabitat.

Even if there are local patches of abundant resources within macrohabitats, when patch size is less than the home range size of the forager, it is unlikely to lead to predictable changes in local abundance at that patch. Such patches may also be ephemeral, and again mitigate against consistent microhabitat trends in abundance. Nevertheless, the summed abundances of prey should show reliable patterns among macrohabitats, and consumer abundance should reflect that variation. I suggest that this is the case for Temperate Zone and northern small mammals.

If this view is correct, then manipulations of resource abundance should be reflected in the population dynamics and life histories of consumers. Several such studies have been performed, where small-mammal food resources have been supplemented by the addition of artificial and natural foods (Bendell 1959, Fordham 1971, Flowerdew 1972, 1976, Cole and Batzli 1978, Hansen and Batzli 1978, 1979, Abramsky et al. 1979, Gilbert and Krebs 1981, Taitt 1981*a, b,* Ford and Pitelka 1984). In all cases, small-mammal species have responded by increasing population size, and/or by changes in reproductive and survival traits. Both fine- and coarse-grained foragers would be expected to show similar responses. Thus future studies of the effects of resource manipulation should control for microhabitat variation in resources, or search for shifts in microhabitat preference with overall resource availability.

Another interpretation is that population density is more closely related to the relative abundances of different microhabitat patches among macrohabitats than it is to their absolute values for physical/chemical properties. Macrohabitat would appear to be a better predictor of population density than microhabitat, but due now to differences in the abundances of microhabitats of variable quality. This in turn would reflect the allocation of time and energy among microhabitats (a major component of an individual's overall reproductive success) and would also necessarily reflect population density. More realistically, macrohabitats probably differ in the relative abundance of their component microhabitats as well as the magnitude of physical/chemical variables. In both instances, analysis of variance techniques may confound the relative influences of habitat scale on population density. Part of the density relation to macrohabitat will be determined by microhabitat variation, which is operationally removed from the microhabitat component. This is a potential problem with all analyses of variance and is not restricted to scaling studies of habitat. If macrohabitats differ in other ways, such as productivity, this effect would appear to be reduced, though it is difficult to imagine very many such differences which would not be associated in some way with microhabitat. In all cases it is still of fundamental interest to investigate the relative magnitudes of variation in population density between macro- and microhabitat. The strength of the method (and ANOVA in general) lies in its ability to detect significant additive variation in population density among different habitat scales. The analysis of habitat scale should not be used to suggest that one scale is more important than the other; that would be an abuse of the method and of analysis of variance. Rather, it suggests that for a particular process like population dynamics, one scale is more suitable to understanding that process than is another. Population dynamics of Temperate Zone rodents appears to be an effect of factors operating at the macrohabitat scale.

The story on patterns of habitat use by Temperate Zone and northern small mammals is incomplete. At the moment, small-mammal density responses to macrohabitat suggest a proximate explanation of relatively selective foragers whose densities reflect overall resource abundance. This hypothesis awaits experimental confirmation. Vertebrates in other ecosystems may or may not show similar relationships between population density and habitat scaling. The local abundance of heteromyid rodents, for example, responds to local and ephemeral patches of high seed production (M'Closkey 1983), and these animals are legendary in their differential exploitation of microhabitat (e.g., Rosenzweig and Winakur 1969, Brown and Lieberman 1973, Rosenzweig et al. 1975, M'Closkey 1976*b,* Price 1978, Price and Kramer 1984). An analysis relating desert rodent density to macro- and microhabitat would be a valuable contribution to the continuing effort to come to grips with spatial and temporal scale.

Macrohabitat selection still leaves much of the variation in small-mammal abundance unaccounted for. That in itself is not surprising. Resource abundance must be highly variable among replicates of any one particular macrohabitat, and among mutually acceptable macrohabitats. Similarly, autocorrelations of past abundance at any one site are bound to explain much of the residual variation in population density as they account for the past influences of history, differential colonization and dispersal, as well as the vicissitudes of temporal environmental variation. Some biologists will be interested in reducing that variation. Nonetheless, the present results are unequivocal. Population density of Temperate Zone small mammals depends upon the scaling of habitat.

Careful separation of macrohabitat and microhabitat effects on the population density of small mammals has revealed unexpected patterns of habitat use, which nevertheless suggest testable alternatives for what may be determining patterns of local distribution and abundance of these animals. Application of the technique to other systems may generate similar rewards. At the very least, it would do much to eliminate the current ambiguity about the roles of scale and habitat selection in the structure of ecological systems.

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