

THE EFFECT OF SPATIAL SCALE ON PATTERNS
OF HABITAT USE: RED-BACKED VOLES AS
AN EMPIRICAL MODEL OF LOCAL ABUNDANCE
FOR NORTHERN MAMMALS

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ABSTRACT—The scaling of habitat use by *Clethrionomys gapperi* was evaluated in southern Alberta and central Labrador. In both geographic locations, *Clethrionomys* density was significantly related to macrohabitat and not to microhabitat variation. These results are similar to those reported for temperate-zone small mammals in Ontario. Density responses to macrohabitat suggest that these rodents are coarse-grained foragers, the abundance of which responds to overall resource productivity. Microhabitat selection may not evolve in such a system, and detecting differences in microhabitat use between species may do little to reveal the factors responsible for patterns of distribution and abundance. This is opposite to conventional models that recognize differences among species, but suggest that interference competition for space should lead to habitat selection.

Our interpretations of structural processes in ecological communities are directly related to the scale of investigation (Wiens, 1986), and our progress at making correct inferences regarding process depends on asking questions appropriate to the scale of our analysis (Wiens *et al.*, 1986). Analyses of distributional patterns at a local level are appropriate for addressing questions about the influence of ecological interactions on population dynamics. Regional and larger scale biogeographical studies outline the ecological constraints to adaptation and the environmental contexts within which local interactions operate. Local populations do not exist within an ecological vacuum, conveniently defined by study site boundaries, and any complete analysis of general processes structuring ecological communities has to incorporate regional and biogeographical patterns. In the same way, patterns do not exist in a vacuum either, and there is a logical dependency between patterns we observe, regardless of scale, and underlying ecological processes. Observations of the relationship between relative abundance and geographical distribution led Brown (1984) to propose a causal link between those patterns, and their dependence upon the local use of multidimensional and covarying resources by similar species with similar ecological requirements.

The scaling patterns we observe tell us at least as much about how biological species respond to their perceived scaling of the environment as they tell us about the limits of our own perception. To interpret the structure of local communities, we must understand how species respond to, or at least perceive, the scaling of their resources. A profitable first beginning would be to choose an environmental dimension known to be important in the structuring of a particular community, or group of

communities, and evaluate how species respond to changes in the scale of that dimension. Such studies will play a pivotal role in ecology because they are at the crucial interface between life history, population and genetic processes, the behavioral and evolutionary mechanisms of foraging, and community structure.

Distributional patterns of north-temperate small mammals depend in large part on differential habitat use (Hirth, 1959; Pearson, 1959; Wirtz and Pearson, 1960; Shure, 1970; M'Closkey, 1975; M'Closkey and Fieldwick, 1975; M'Closkey and Lajoie, 1975; Krebs and Wingate, 1976; Sly, 1976; Brown, 1978; Dueser and Shugart, 1978; Hansen and Warnock, 1978; Morris, 1979, 1983, 1984a, 1984b; Vickery, 1981; Hansson, 1982). Species interactions also may be important (Koplin and Hoffmann, 1968; Murie 1971; Grant, 1972; Crowell and Pimm, 1976, Rowley and Christina, 1976; Henttonen *et al.*, 1977; Master, 1977; Redfield *et al.*, 1977; Dueser and Hallett, 1980; Hallett *et al.*, 1983), but the overall influence of competition is probably subsidiary to habitat preference (Morris, 1983; Galindo and Krebs, 1985; Wolff and Dueser, 1986). Habitat can exert its influence over patterns of distribution and abundance at different scales (Morris, 1985), and habitat selection in northern small mammals provides a convenient system to evaluate how animals respond to environmental scaling.

There are no general rules on how to measure habitat, nor is there any consensus on what spatial scales habitat use should be monitored. In practice, ecologists have identified two alternatives—between- and within-habitat components (for example, Cody, 1974), more recently termed macro- and microhabitat. There are no standard operational rules on how to differentiate between them. Morris (1987) has suggested the following working definitions: define habitat type as the spatial scale within which similar physical or chemical variables, or both can be used to describe its variation. Different habitat types are described by different suites of physical or chemical variables. Within habitat types, define macrohabitat 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 or chemical variables that influence the allocation of time and energy by an individual within its home range. When viewed in this way, habitat variation becomes a continuous process that can be partitioned into separate components, and analyzed statistically by analysis of variance and its analogues.

For comparisons among co-occurring species, habitat scaling can be evaluated by multidimensional contingency tables among habitats and their replicates, followed by discriminant functions analyses of microhabitat differences within plots (Morris, 1984a). This approach answers questions about differential habitat use among species, but cannot be used to evaluate possible density responses within species. Morris (1987) suggested multiple regression analysis, using dummy variables to represent habitat treatments

and their spatio-temporal replicates, as one method to reveal patterns of habitat scaling within species. The scaling of habitat use can be represented by a linear model of the form

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

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 the normally distributed error variation. I used the regression method to look for scaling patterns of density-dependent habitat selection in two subspecies of the red-backed vole—(*Clethrionomys gapperi athabascae*) in the Rocky Mountains of southern Alberta and (*Clethrionomys gapperi proteus*) in the boreal forest of central Labrador. My objectives were to (1) reveal the scaling of habitat use by this important northern herbivore, and (2) interpret this scaling in terms of its importance to the structure of boreal small mammal assemblies.

STUDY AREAS

Red-backed voles were live-trapped, individually marked and released in each of two 0.81-hectare replicates of six habitats in the Kananaskis Valley of Alberta, and in four 0.03-hectare hexagonal plots spaced 150 meters apart in three forest habitats replicated in each of the Churchill and Goose River valleys of Labrador. Single Longworth live-traps baited with oatmeal and peanut butter, apple or potato slices (for moisture), and mattress stuffing (for insulation) were placed at permanently marked trap stations located at 15-meter intervals. In Alberta, traps were set on alternate trap lines in the evening, checked at first light and mid-evening the next day, and collected at first light on the second day. Each station was monitored three times from 16 May to 31 August 1977. In Labrador, traps were set in the morning, checked that evening, and first light and mid-evening the second and third days, and collected at first light on the fourth day. Each Labrador station was monitored twice from 16 July to 2 August 1984.

In Labrador, each hexagon represented a sampling subplot. In Alberta, subplots were created as three by three trap grids at each of the four corners of the seven by seven habitat replicates. Forested habitats only are used in the regression analyses. In Labrador, these were: mixed forest—black and white spruce (*Picea mariana*, *P. glauca*), balsam fir (*Abies balsamea*), poplar (*Populus balsamifera*), paper birch (*Betula papyrifera*) with an understory of alder (*Alnus crispa*), mountain maple (*Acer spicatum*), Labrador tea (*Ledum groenlandicum*), and pin cherry (*Prunus pennsylvanicus*); mature spruce-fir—black spruce and balsam fir, with an alder, Labrador tea and blueberry (*Vaccinium* spp.) understory on a deep carpet of mosses; and spruce-lichen woodland—interpersed black spruce, with clumps of blueberries, Labrador tea, sheep laurel (*Kalmia angustifolia*), and dwarf birch

TABLE 1.—Variables used to quantify microhabitat across five forest habitats in the Kananaskis Valley of Alberta. Other forest variables measured included tree and shrub diversity and biomass, but they and their transformations failed to meet the statistical criteria for inclusion in the analysis.

Variable	Description
Q1	Amount of vegetation from 0 to 0.25 meters
SUMQ	Total vegetation below 1.75 meters
API	Arcsin proportion of vegetation from 0 to 0.25 meters
VERT	Vertical vegetation density from 1.75 meters
DVERT	Vertical density diversity
LMAT	Log ₁₀ mat depth
CMAT	Coefficient of variation of LMAT
CDIV	Diversity of cover types
DEBRIS	Square root of logs, fallen trees, and other debris within 3 meters

(*Betula* sp.) on a rich lichen tapestry (*Cladonia rangiferina*). Complete descriptions of the Kananaskis habitats can be found in Morris (1984a).

Red-backed voles occurred with variable densities in all habitats, and their abundances were estimated as the number of different individuals captured per subplot. In Alberta, microhabitat was quantified at every station. Arithmetic means of each variable were calculated over all nine stations per subplot (Table 1). In Labrador, microhabitat variables were recorded only at the central stations of each hexagon (Table 2). Microhabitat data complexity was reduced by principal axis factoring (PAF method, SPSS^s) with varimax rotation. The generated microhabitat factors and appropriate dummy variables representing alternate habitats and replicates were entered as independent variables into a stepwise regression (STEPWISE method, SPSS^s) predicting *Clethrionomys* density. In both locations, the dummy variables for macrohabitat were contrasted against the standard of mature coniferous forest.

RESULTS

Three microhabitat factors explained 77.8 percent of the estimated microhabitat variation in the Kananaskis Valley (Table 3). All of these factors described various components of understory and forest floor physiognomy and composition. Forest and shrub structure also could be viewed as suitable components of microhabitat, but variables representing tree and shrub biomass, density and diversity did not meet data screening requirements of the factor analysis. Nevertheless, for forest-floor rodents like *Clethrionomys*, the three factors are likely good estimates of microhabitat variation experienced by these animals.

In Labrador, four factors explained 78.7 percent of the estimated microhabitat variation (Table 4). Two of these were related to understory and forest floor characteristics, one to "shrub density" and the other to "tree-shrub structure". Again, the microhabitat factors should provide good estimates of microhabitat variation experienced by *Clethrionomys*.

TABLE 2.—Variables used to quantify microhabitat in three forest habitats along the Goose and Churchill River valleys of Labrador.

Variable	Description
MAT	Mean of four estimates of mat depth
VERT	Mean of four estimates of vertical density
DVERT	Vertical density diversity
HEIGHT	Understory height
CDIV	Cover diversity
SQTREES	Square root number of tree species within 3 meters
SQDISTT	Square root of distance to nearest tree
LPBASAL	Log ₁₀ basal area of nearest trees in four quadrats
SQSHRUBS	Square root number of shrub species within 3 meters
LOGSHRUB	Log ₁₀ total shrub surface area within 3 meters
SQDISTS	Square root of distance to nearest shrub
ACOVER	Arcsin proportion of moss and lichen cover

In both geographic locations, stepwise multiple regression analysis revealed the dependence of *Clethrionomys* density on macrohabitat (Table 5). In Alberta, *Clethrionomys* density per subplot was significantly related to the rarity of red-backed voles in the two aspen replicates. No other single variable significantly contributed to the pattern of density variation. *Clethrionomys* density in replicate plots was marginally significant for inclusion in the overall regression equation ($P = 0.09$). A two-variable model containing the effects of replicate plots was significant ($F = 5.21$; $P = 0.01$), but accounted for only an additional six percent of the residual variation in population density ($r = 0.469$). No other variable was close to statistical significance for inclusion in the equation ($P \geq 0.21$). Similarly, in Labrador, *Clethrionomys* density was significantly related to vole density in the mixed macrohabitats. Again, only one dummy variable and no microhabitat factors were significant ($P \geq 0.22$ for all remaining variables).

TABLE 3.—Varimax rotated factor loadings of microhabitat variables in the Kananskis study sites. The magnitude of the loading coefficients are used to interpret their respective microhabitat factors.

Variable	Factor		
	Understory density	Understory and forest floor structure	Mat heterogeneity
SUMQ	.94	.14	.12
VERT	.85	.00	-.24
QI	.81	.48	.04
DVERT	.64	.31	-.04
API	-.07	.96	-.08
LMAT	-.20	-.70	-.15
DEBRIS	-.01	-.55	-.48
CDIV	.34	.47	.15
CMAT	-.08	.07	.91

TABLE 4.—Varimax rotated factor loadings of microhabitat variables in the Labrador study sites. The magnitude of the loading coefficients are used to interpret their respective microhabitat factors.

Variable	Factor			
	Tree-shrub structure	Shrub density	Understory structure	Forest-floor structure
SQTREES	-.84	-.10	-.25	-.02
SQDISTT	.82	-.07	.07	.06
LOGSHRUB	.75	-.02	.41	.11
ACOVER	-.34	.88	-.09	-.03
SQSHRUBS	.12	.84	.06	-.13
SQDISTS	-.39	-.77	-.34	.17
VERT	.19	.07	.84	.06
DVERT	.23	.09	.80	-.07
LPBASAL	-.22	.04	-.34	.73
CDIV	.14	-.22	.19	.58
HEIGHT	.50	-.05	.41	.56
MAT	-.20	.29	.04	-.34

DISCUSSION

The effect of habitat on local abundance of red-backed voles in two disparate geographical locations depended upon habitat scaling. In both locations, the local abundance of voles depended upon macrohabitat identity and not microhabitat preference. Morris (1987) reported similar results for the abundance of *Microtus pennsylvanicus* and *Peromyscus leucopus* in southern Ontario. Microhabitat selection consistently disappears when macrohabitat effects are included in analyses of density-dependent habitat selection (see also Morris, 1984b, 1985).

For temperate-zone rodents, it now appears that macrohabitat and not microhabitat is differentially selected by coexisting species. At the local scale, it is difficult to speculate on the possible importance of microhabitat structure to patterns of species coexistence. I wonder what our perception of small mammal interactions would be if early studies of "microhabitat selection" had clearly distinguished between micro- and macrohabitat effects?

The density responses to macrohabitat suggest foragers with densities that respond primarily to overall resource abundance within macrohabitats, not to local variation in resources among microhabitats (Morris, 1987). In temperate and boreal forests, macrohabitat is probably a more reliable indicator of resource abundance than is microhabitat structure (Morris, 1987). Fundamentally different patterns of habitat selection may occur in other mammal faunas where variation in resource abundance occurs at smaller scales. As an example, desert rodent habitat use and abundance responds to local and ephemeral patches of high seed production (M'Closkey, 1983). Patterns of local distribution and abundance may be

TABLE 5.—The relationship of *Clethrionomys density* with macrohabitat. Analysis was by stepwise multiple regression of *Clethrionomys density* with microhabitat factors and macrohabitat dummy variables. Only one variable was statistically significant in each location ($P < 0.05$).

ALBERTA			
Regression Summary			
Step	Variable	b	r
1	Density in aspen	-1.59	-.397
ANOVA Table			
Source	df	Mean Square	P
Regression	1	16.28	0.011
Residual	38	2.28	
LABRADOR			
Regression Summary			
Step	Variable	b	r
1	Density in mixed forest	-2.75	-.585
ANOVA Table			
Source	df	Mean Square	P
Regression	1	40.33	.003
Residual	22	3.52	

understood only in the context of the environment to which the organisms are exposed. I suggest that a central feature of these environmental comparisons or classifications will depend upon the spatial and temporal scaling of resources. We should be surprised only if the habitat selection and life history strategies of the organisms we study do not respond to the scaling of their environments.

Resource depletion and competition at the macrohabitat level is unlikely to lead to the typical scenario of ecological segregation by microhabitat divergence, but would instead result in reduced population density. This may explain anomalies in competition studies on northern small mammals. Species removal and introduction experiments frequently have shown a depressive effect on population density by putative competitors (Koplin and Hoffmann, 1968; Crowell and Pimm, 1976; Redfield *et al.*, 1977), whereas carefully investigated patterns of spatial overlap do not (Morris, 1983; Wolff and Dueser, 1986). Even slight differences in diet and foraging could allow the coexistence of macrohabitat "selectors" with densities that fluctuate primarily in response to overall resource or microhabitat abundance. Among macrohabitats, they may exhibit complementary densities in response to resource differences among those habitats. Alternatively, their densities could be positively or neutrally correlated with one another depending upon the availability of covarying resources in specified macrohabitats. In this latter case, correlation analysis of their joint densities across suitable macrohabitats would indicate no competition because both are determined by overall habitat quality. But removal of one or the other species could reveal interaction as the density of the remaining species

responded to the overall increase in resources, or to the artificial increase in jointly consumed resources. Coarse-grained foraging with overall resource depletion also may account for my failure to capture *Peromyscus* in the relatively unproductive forests of Labrador, despite the co-occurrence of *Peromyscus* and *Clethrionomys* throughout most of the geographic range of red-backed voles. In resource poor environments, *Clethrionomys* simply may deplete resources below that which can sustain both species.

As ecologists begin to abandon purely deterministic models of species coexistence, the effects of spatial and temporal scales on our perception of ecological events, and the influence of scaling patterns on ecological communities, must be addressed. One way to do that would seem to be to acknowledge the influence of scale on our observations, decide upon which scale we are going to ask questions, work at that scale, and leave it at that. If only nature were so simple. Ecological processes have a profound influence on local and regional biogeography and evolution. These ecological interactions are as much a pawn to past evolutionary and geographical events as is our perception of them. All spatial and temporal scales interact in complex ways to feed back onto each other. The fundamental question is not how our perception of ecological processes is limited by the scale of our inquiry, but is, instead, how do biological organisms perceive and respond to the temporal and spatial scaling of their environment? One of the big challenges facing evolutionary biology is to describe that complex mapping.

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