Coexistence of Specialist and Generalist Rodents Via Habitat Selection

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COEXISTENCE OF SPECIALIST AND GENERALIST RODENTS VIA HABITAT SELECTION[1]

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Abstract. Habitat specialization is an effective mechanism of coexistence among competing species. But many communities also include generalized species whose habitat use overlaps that of the specialists. Two hypotheses seem most likely to account for the pattern: (1) Habitat generalists may coexist in competitively structured communities by exploiting habitats unused, or underused, by habitat specialists. (2) Population densities of the specialized species may be limited (e.g., by predation) below levels where the specialists can competitively exclude habitat generalists. I evaluated these ideas in a community of small mammals occupying mesic and xeric habitats at nine different locations in the Rocky Mountains of southern Alberta, Canada. A chipmunk generalist coexists with two specialists, one with a distinct preference for xeric habitat (deer mouse), and another with a similar preference for mesic habitat (red-backed vole). Habitat selection appeared to depend primarily on the density of conspecifics. The generalist coexisted by responding to habitat at a larger scale than did the specialists. Shared predators, whose habitat selection operates on a larger scale than that of their prey, may augment coexistence of all species by reinforcing habitat selection by the specialists.

Key words: Alberta; apparent competition; Clethrionomys; *coexistence; habitat selection; isodar; isoleg;* Peromyscus; *predators, shared;* Tamias.

INTRODUCTION

Most theories of habitat selection predict, at equilibrium, that evolution should tend to produce species that specialize on a subset of available habitats (Rosenzweig 1987, Brown and Pavlovic 1992, Holt and Gaines 1992; R. D. Holt, *in press*). The specialists competitively exclude less well-adapted phenotypes and species. But most natural assemblages appear to be composed of ostensibly competing species that vary from those with very narrow habitat requirements to others with more or less ubiquitous distributions. A recent theory demonstrates that widespread habitat generalists may coexist with competing habitat specialists if they exploit the shared environment at a larger spatial scale (J. S. Brown, *in press*; summary in *Discussion*). The generalist's strategy allows it to exploit whichever habitat(s) is unused or underused by more specialized species.

An alternative hypothesis is easily constructed where other interactions, most notably predation, allow coexistence if populations tend to be maintained below their equilibrium with resource supply. Competition may be at so low a level, or so infrequent, that generalists exploit all patches regardless of the density of specialists. A different version would allow generalists to simply avoid competing specialists by occupying whichever habitat contains the lowest density of specialist individuals.

Neither hypothesis must necessarily account for the

initial evolution of habitat preference. Many species, including small mammals such as those studied below, have relatively short histories of coexistence (e.g., Graham 1986). Habitat preferences for these species probably evolved independent of any current species interactions that, nevertheless, maintain the species' coexistence. Regardless which scenario one favors, resolution among the alternatives must turn on our ability to unambiguously measure the degree of habitat specialization among coexisting species. This paper illustrates one way of achieving that objective. It uses the results to test for competitive vs. predator-mediated coexistence. I begin by describing how habitat selection theory can be used to differentiate between habitat specialists and generalists, and how these strategies are related to spatial scale. I use the theory to define specialist rodents at the large scale of replicated sampling grids located in adjacent xeric and mesic habitats in the Rocky Mountains of southern Alberta, Canada. I follow this analysis with another at the scale of individual sampling stations to infer the spatial scale of habitat specialization. I search for competitive interactions among species by isoleg analysis (Rosenzweig 1974, 1981, 1991) and finish by discussing the role of habitat selection in the coexistence of boreal rodents.

Detecting habitat specialists and generalists: isodar theory

Morris (1992) and T. W. Knight and D. W. Morris (*in press*) demonstrated how scales of habitat selection can be inferred from isodars (plots of density in paired habitats such that the expected reproductive success of
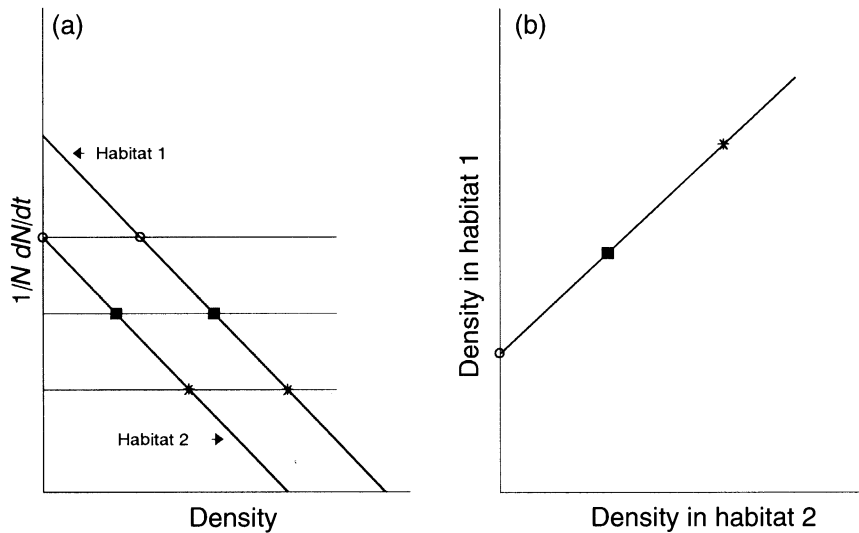
FIG. 1. Examples of fitness–density curves of a density-dependent ideal habitat selector (a) and the resulting isodar (b). Intersections of the fitness curves with horizontal lines correspond to the densities where fitness in the two habitats is identical (ideal habitat distribution). The isodar is a plot of these intersections across the entire range of fitness. Three example points are illustrated with symbols. The isodar intercept corresponds to the quantitative difference between habitats (different maximum fitness at low density); its slope is the ratio of the slopes of the fitness curves (a qualitative difference). After Morris (1988).

an individual habitat selector is the same in both). To draw an isodar, imagine that you know the relationship between population density and reproductive success in each habitat. Assume that individuals select habitat in a way that maximizes their expected fitness, then plot the densities where the expected fitness is equal in both habitats (Fig. 1: this need not correspond to an ideal free distribution).

Habitat isodars recast fitness-density curves from evolutionarily stable strategies of density-dependent habitat selection into a form that allows the theory to be tested with census data (D. W. Morris, in press). The isodar intercept reflects differences between habitats in the maximum fitness their occupants can attain at low density (a quantitative difference). Quantitative differences in habitat create shared habitat preferences among competing species (Rosenzweig 1979, 1981, Pimm and Rosenzweig 1981, Morris 1988). Qualitative differences that alter the slope or shape of fitness with density lead to distinct preferences and produce isodars with slopes greater than, or less than, one (Morris 1988). Thus, the isodar for a habitat-selecting species specializing on one habitat or the other would necessarily have an intercept >0 or a slope ≠0. Pairs of habitats perceived identical by a generalist would yield isodars that pass through the origin with slope =1. Isodars have most frequently been derived by regressing replicated measures of density in one habitat against paired samples from another (Morris 1988, 1989, 1992, 1994, 1995, Rodríguez 1995, Ovadia and Abramsky 1995). A problem with this approach is that it cannot be applied easily to autocorrelated temporal estimates of density that characterize many ecological

studies. Fortunately, isodars can frequently be inferred from temporal data by a form of "profile" analysis evaluating sets of interactions in analysis of variance (e.g., D. W. Morris, in press).

Imagine a sampling protocol applied to a seasonally reproducing species where replicated estimates of population density are accumulated at two periods during the reproductive season. Samples are collected across a series of paired habitats (A and B) occurring in three different locations. Assume, initially, that the two habitats differ only in the maximum fitness that can be achieved at low density. One habitat would support a higher density than the other (the isodar slope would be 1, the intercept would be ≠0). The challenge is to devise an analysis that can expose the underlying relationship in relative population density and reveal how that pattern varies with time and through space. To see how this can be done, imagine that the replicated density estimates are plotted as isodars (Fig. 2).

Different sets of interactions among habitats, samples, and locations signify different patterns in the data (different isodars). In the first case imagine, as above, fitness differences where one habitat has a higher constant density of the species than does the other. Further imagine that density in the two habitats varies among locations but that relative differences in density between habitats and between sample periods are constant. A repeated-measures analysis of variance would reveal expected differences in density among locations, between habitats, and between sampling periods with no interaction among them (Fig. 2a). Now imagine, in addition, that the change in density between samples is greater in one location than that of at least one other
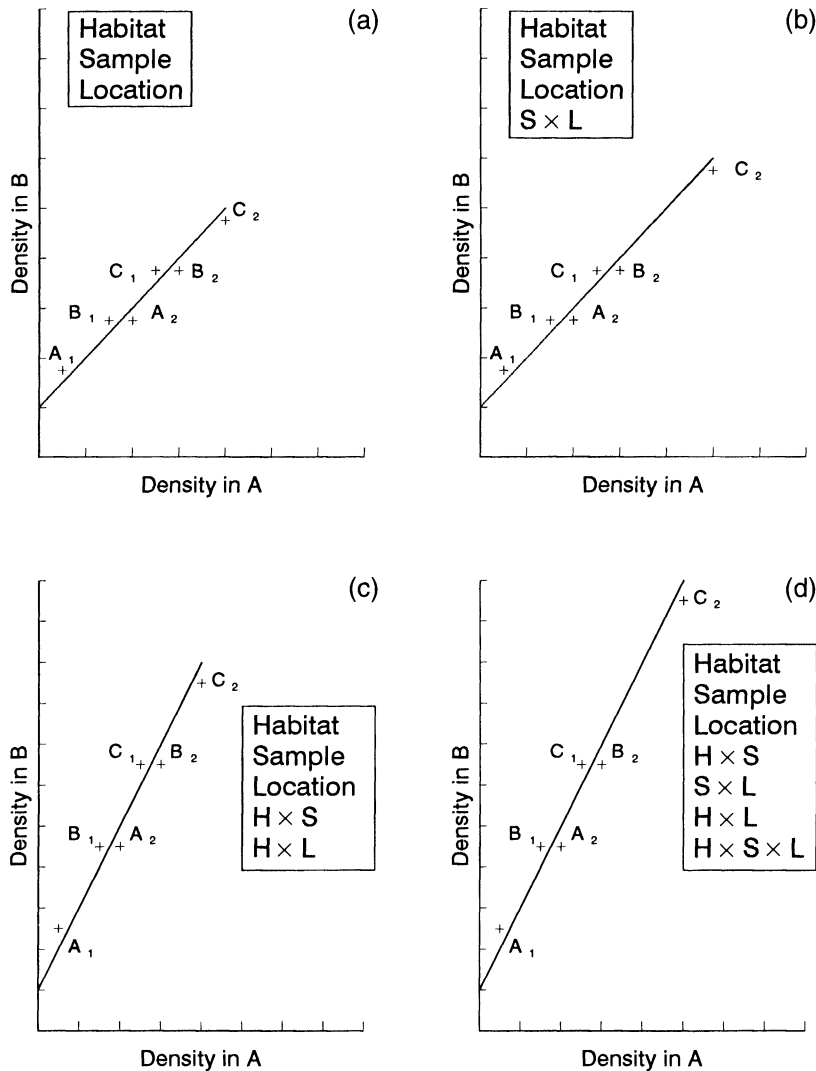
FIG. 2. Examples of linear isodars and their expected significant effects on density that would be revealed by repeated-measures ANOVA (listed in boxes). Curvilinear or nonlinear effects can be inferred by plotting the data. Small capital letters with subscript numbers 1 or 2 correspond to estimates of density collected in different locations and at different times, respectively. Interactions among main effects are denoted in the boxes by large capital letters (H = habitat, L = location, S = sample period). In graph (c), for example, density in the two habitats depends upon (interacts with) sample and location even after the mean effects of habitat, sample, and location have been removed (the slope of the curve is >1).

(location C, Fig. 2b). The sample × location interaction would be significant as would the three main effects. Next, imagine both quantitative and qualitative differences between habitats (an isodar slope ≠1). The difference in density in the two habitats varies with sample period and location (habitat × sample, habitat × location interactions, Fig. 2c). Finally, imagine the same habitats where the change in density between samples varies among locations (location C again, all effects significant, Fig. 2d). The pattern of significant main effects and interactions allows one to infer whether the isodar intercept is different from zero or if the slope may be different from one. Sets of analyses conducted on different species allow one to contrast the isodars,

and to determine each species' response to habitat and higher spatial scales (location).

I use the pattern of interactions to infer the isodars of three coexisting boreal rodents living in two habitats. Significant interactions between habitat and density suggest specialists, but the method, like all others, is imperfect and demands careful design and interpretation. It is possible to generate some of the interactions I use to infer isodars by means other than density-dependent habitat selection, and by patterns additional to those I highlight in Fig. 2. Habitat × location interactions could, for example, indicate different isodars in different locations rather than the same repeated isodar with a slope ≠1. This problem can be reduced by

the judicious selection of replicated habitats occurring at each location. One could then test for multiple isodars by searching for differences in the isodar regressions among locations by analysis of covariance. But if one had enough replicates for this test there would be no need for the interaction shorthand I outline above. Multiple isodars can be more simply detected by searching for telltale residuals that consistently depart from an isodar regression including data from all locations. I guard against multiple isodars, and visually appraise the data, by plotting all of the density estimates used in the interaction analyses.

Scale-dependent coexistence of specialists and generalists

Isodars, and our interpretation of specialist vs. generalist strategies, are likely to depend on how closely our sampling scale matches scales of habitat selection. One way of dealing with this problem is to identify an appropriate scale where specialists use patches preferentially (coarse-grained exploitation, Levins 1968). Generalists, at the same scale, would show no habitat preference.

I illustrate an example of this effect in Fig. 3. Solid horizontal lines correspond to a spatial scale where patches are recognized as distinct by a habitat specialist and similarly correspond to the scale of habitat sampling. Dotted lines in the upper panel (part "a") represent the larger scale where patches are recognized as distinct by a generalist. For this example, the quality of (fitness obtained from) the habitat for the generalist is the mean of adjacent pairs of sampling plots. The top panel depicts a hypothetical transect of patches, and of sampling plots, across a heterogeneous landscape. There is a slight trend of declining habitat quality along the spatial gradient. Sampling plots are ranked by quality in panel b, which has been arbitrarily split into two habitats. The plot rankings demonstrate a marked gradient for the habitat specialist that has a clear advantage in habitat A. Dotted lines in panel b correspond to the expected habitat quality of the generalist if one uses the same order *and scale* of sample plots as for the specialist. With the exception of two sample plots (numbers 13 and 14), the quality of the two habitats would appear similar for the generalist species. This occurs even though this example ranks habitat quality equally for the two species; if one were to increase the scale of sample plots to twice their initial size (equal to the minimum scale of habitat preference exhibited by the generalist) both species would appear to have the same preference for habitat.

Two points emerge from the example. (1) Our interpretation of generalist species can be an artifact of sampling. We can test for such artifacts by collecting data at multiple scales. We need not be too concerned, however, because many generalists are likely to rank their large patches differently from the average of smaller-scale patches used by specialists (contrary to
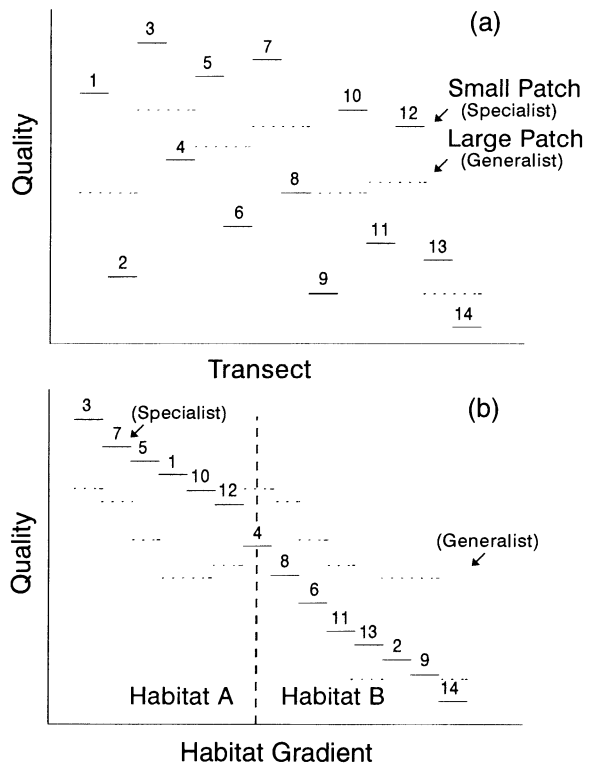

FIG. 3. An example of how the scale of sampling can influence interpretations about habitat preference. Solid horizontal lines represent the scale of sample plots that also correspond to a scale at which specialists recognize differences in habitat patches. Dotted horizontal lines in panel (a) correspond to a larger patch size where generalists can recognize differences among patches. Numbers identify individual samples. Samples 1 and 2 would reveal large differences in habitat quality for the specialist. The same samples would yield identical habitat quality for the generalist because it cannot recognize habitat differences at the small scale. Panel (a) illustrates an example of samples collected along a transect in a heterogeneous landscape; panel (b) ranks them by their quality. The two habitats correspond to an arbitrary higher scale that could be inferred by an experienced naturalist. Habitat A is of higher quality than is habitat B.

my example). (2) A species that is coarse grained in habitat use at one spatial scale will also be coarse grained at many larger scales. Thus, an isodar analysis that identifies both specialists and generalists can be assumed to have captured an important dichotomy in scale, but not necessarily the smallest scale at which specialists recognize differences among habitat patches.

STUDY SITES AND METHODS

South and west exposures in Alberta's southern Rocky Mountains tend to support different plant communities than those found on north-, and to a lesser extent, east-facing slopes. At elevations below the tree line, xeric exposures range from open grass and forb-covered meadows (*Elymus innovatus, Calamagrostis canadensis, Poa* spp., *Zygadenus elegans, Astragalus*

spp., *Castilleja miniata, Anemone multifida*) with sparse tree cover (mostly lodgepole pine, *Pinus contorta*) and interspersed shrubs (buffalo-berry, *Shepherdia canadensis*; wild rose, *Rosa acicularis*; shrubby cinquefoil, *Potentilla fruticosa*, and juniper, *Juniperus communis* and *J. horizontalis*) to dense lodgepole pine forest with an understory dominated by *Shepherdia*, bearberry (*Arctostaphylos uva-ursi*), and alder (*Alnus viridis*) with a litter layer of slowly decaying pine needles. Mesic exposures tend to be dominated by fir (*Abies lasiocarpa*) and spruce (*Picea glauca*) with abundant ericaceous and other shrubs (e.g., *Vaccinium* spp., *Ledum groenlandicum, Menziesia ferruginea, Salix* spp., *Ribes* spp.) on deep feather-moss floors (*Pleurozium shreberi, Hylacomnium splendens, Ptilium crista-castrensus*) containing a typical boreal flora (*Linnea borealis, Cornus canadensis, Pyrola* spp., *Equisetum* spp., *Streptopus amplexifolius*). The boundaries are not discrete. Some northern exposures are dominated by pine forest, particularly following fire, and some southern exposures are covered by plant communities that resemble those on north-facing slopes. Transitions between north- and south-facing slopes may be on the scale of a few metres along sharp ridges and valleys and plants from each community frequently occur, at low abundance and of depauperate form, in the other.

I located 40 3 × 3 live-trap grids (20-m spacing between traps) paired across nine mesic/xeric boundaries in an area of ≈500 km² along ridges and valleys in the Kananaskis, Powderface, and Spray Valleys of southwestern Alberta (50°38′–51°05′ N, 114°57′–115°12′ W, elevations ranged from 1525 to 2010 m). All locations contained two "xeric" grids paired with two nearby "mesic" grids. Distance between grid pairs was on the order of 200 m (except for one site, "Fortress," where the distance between xeric and mesic pairs was 1 km). The minimum distance between replicate grids within each habitat was 100 m. Two locations contained six grids; in each case, two of the six grids represented atypical conditions (avalanche slopes and ground squirrel [*Spermophilus columbianus*] colonies) and were excluded from all analyses.

Plant communities and habitat structure were quantified at different scales during early-mid summer (20 June–4 August). Four square 0.05-m² cover plots were randomly located in each of the four quadrants of a 10-m² square superimposed on each of the nine stations in each sample grid. The biomass of forest-floor species was estimated by their respective percent cover. Percent cover by substrate type (litter, wood, rock, soil) was recorded in each 2.5-m² quadrant. The depth of the forest mat (mosses, litter, humus) was measured at the northeast corner of every forest-floor cover plot. Shrub and tree (minimum diameter at breast height [dbh] = 5 mm) biomass was estimated for each species using the point-quarter technique (Smith 1990). Shrub heights and diameters were used to estimate shrub vol-

ume (assuming a cylindrical shape). Importance values for each forest-floor species were calculated as (relative dominance + relative frequency)/2. Similar values were calculated for trees and shrubs (importance value = (relative dominance + relative density + relative frequency)/3 (Smith 1990). Substrate "abundances" were calculated as (mean cover + frequency)/2. Slope, measured with a clinometer, elevation to 3-m accuracy, and aspect were recorded at every station. Mean slope and elevation were calculated for each grid. Aspect (to the nearest degree) was transformed ($\sin[\theta/2]$, Abramsky et al. 1985) before calculating the grid mean.

Small mammal communities were censused in each grid during three 72-h live-trapping periods during early, mid, and late summer of 1989 (20 June–7 July, 1–16 August, and 21 August–26 September, respectively). Additional censuses were carried out in grids free of snow, but those data produced an unbalanced design and were excluded from all isodar analyses. Single Longworth traps were checked at sunrise and sunset each day. Soiled traps were replaced with clean ones that had been washed in detergent, rinsed, and baited before being reset. All rodents were identified to species, individually marked with ear tags, and released at the point of capture.

Population density of each species was estimated as the number of different animals captured on replicated grids during each trapping interval. I did not use mark-recapture estimates accumulated among sampling intervals because they may often yield inflated values as individuals alter their habitat choice from one interval to the next. Unbiased estimates may best be achieved by counting the number of different individuals captured during short but intense sampling pulses. Treated this way, one can reasonably assume that the repeated measures of density are independent of a temporal sampling bias (e.g., individuals using one habitat at time i, and $i + 2$, and another at time $i + 1$). In any case, estimates of absolute density are irrelevant to the analyses, which are based entirely on relative differences.

ANALYSIS

Habitat selection: large scale

Plant and habitat variables were calculated for each grid and summarized by principal components analysis (PCA, Norušis 1992a). The analysis was intended only to provide estimates of habitat variation experienced by rodents, not to summarize the overall plant community. Despite intense sampling (36 0.05-m² cover plots in each live-trap grid), many plant species were absent from all samples in a substantial number of grids. Plant species with frequencies of occurrence <5% were deleted prior to analysis. Only those variables, or their transforms, that were more or less unimodal and symmetrical were retained. Variables with low values of Kaiser-Meyer-Olkin (KMO, Norušis 1992a) measures of sampling adequacy were deleted

TABLE 1. Two principal components contained 61.2% of the common variation among 8 habitat variables describing 36 rodent live-trap grids in the Rocky Mountains of southern Alberta.

Variable	Rotated loadings	
	PC1	PC2
Total cover by forest-floor species	0.79	0.11
Importance value of *Pyrola secunda*	0.75	−0.09
Importance value of mosses	0.72	0.38
Importance value of *Elymus innovatus*	−0.70	−0.39
Log_{10} mat depth	0.62	0.05
Abundance of litter	−0.11	−0.84
Mean elevation	−0.04	0.76
$\sqrt{(\text{number of saplings} + 0.5)}$	0.47	0.68

one at a time in sequential principal components analyses until a final solution with an overall KMO of 0.75 was attained (see Table 1). Components with eigenvalues >1 were extracted and used as covariates in the analyses of rodent densities to control for grid-to-grid variation in habitat. I used stepwise discriminant function analysis (Norušis 1992*a*) to confirm that the components could, in fact, differentiate between habitats.

I used repeated-measures MANOVAs (Norušis 1992*b*, von Ende 1993) for each rodent species to assess density-dependent habitat use. The first analyses contrasted densities in xeric vs. mesic habitats by location (between-subject effects) with temporal estimates of density (samples) treated as repeated measures (within-subject effects). Habitat principal components were added as covariates. As noted above, seasonal increases in population density would be reflected in a significant sample (density) main effect. Deviations in mean density between mesic and xeric grids would be revealed by a significant habitat effect. Differences in isodar slopes through time would be identified by a significant interaction between sample and habitat (any interaction that does not include habitat cannot alter the relative densities in different habitats). Differences in the relationship of density to habitat between locations and time would be revealed by a significant three-way interaction term. I deleted nonsignificant covariates and repeated the analysis to generate the final significance tests and MANOVA coefficients.

I used the MANOVA coefficients (mean difference in density of each species in the two habitats) to estimate the isodar intercept. A positive coefficient corresponds to greatest density in the mesic habitat, a negative coefficient to greatest density in the xeric habitat. The intercept estimate may be biased when the isodar slope departs from unity but it will, nevertheless, correctly identify habitat preference. I estimated isodar slopes by geometric mean regression of density estimates (Sokal and Rohlf 1981:550; both variables were estimated with error) for those comparisons where both habitats were occupied. The regressions are biased by the lack of spatial-temporal independence in the data (tested by the MANOVAs). Spatial-temporal effects

will, in general, add substantial noise to the data and make it even more difficult to detect significant habitat covariance in density. Significant isodar regressions will, therefore, tend to confirm the importance of consistent habitat covariation in density among the nine sampling locations.

Habitat selection: fine scale

Contrasts between mesic vs. xeric habitats are appropriate for my tests of density-dependent habitat selection. It is possible, nevertheless, that habitat selection may be operating at a finer scale of habitat variation. I complemented the large-scale analyses with a separate analysis at the scale of individual trap stations. The analysis was designed to demonstrate any differences among species in their response to small-scale variation in habitat. I used the habitat variables from the first PCA (except mean elevation, which would bias analyses toward the larger scale of differences among grids) to generate new principal components. I changed the acceptance level for the KMO measure to 0.7 because the effective variance in habitat is greater when variables are calculated for individual stations as compared to the first analysis where the variance was modeled by averaging values for each grid. I used the final selection of variables from the PCA to search for significant differences in habitat use among rodent species by stepwise discriminant functions analysis (Norušis 1992*a*). Analyses were conducted separately for xeric and mesic habitats to avoid mixing scales of habitat use. All stations received equal weighting in the analysis.

The primary purpose of this fine-scale analysis was to determine how well rodent densities in the two habitats corresponded to differences in microhabitat between pairs of grids. I calculated the difference in rodent density between pairs and plotted it against the Euclidean distances of the mean principal component scores for pairs of habitats at each location. This analysis, if significant, would demonstrate that differences in density were strongly linked to the relative differences in habitat. The analysis was necessary because relative differences in habitat at different locations, and corresponding differences in density, could create significant interactions between density, habitat, and location (different isodars at different locations). A nonsignificant outcome would suggest a single isodar.

Caveat

My analyses implicitly assumed that my large-scale census data corresponded with scales of habitat selection of the three common rodent species analyzed here. Otherwise, differences in density between habitats could represent a variety of artifacts that modify population density. Such artifacts were possible for a small number of my grids, most notably those at Fortress Mountain, where distances between mesic and xeric plots exceeded the probable effective distance of hab-

TABLE 2. Number of different individuals known alive over three sampling periods during 1989 in replicated grids in two habitats at nine different locations in the Rocky Mountains of southern Alberta (means ± 1 SE). Standard errors ($n = 6$) include variation in estimates between replicates and through time.

	Species					
	Clethrionomys		Peromyscus		Tamias	
Location	Mesic	Xeric	Mesic	Xeric	Mesic	Xeric
Elpoca	2 ± 1.06	0	0	0	0.5 ± 0.22	1 ± 0.26
Fortress	4 ± 0.58	4.5 ± 0.5	1.2 ± 0.65	6.8 ± 1.38	4 ± 0.58	2 ± 0.78
Hood	1 ± 0.26	0.2 ± 0.17	0	0.8 ± 0.54	3.8 ± 0.95	4 ± 0.36
Kent	6.2 ± 1.25	5.8 ± 0.7	2.8 ± 1.01	0	1.5 ± 0.5	1 ± 0.36
Lusk	6.7 ± 2.01	2.5 ± 0.62	0	0.8 ± 0.4	2.3 ± 0.56	0.5 ± 0.22
Sibbald	4.5 ± 1.15	5.2 ± 1.78	1.5 ± 0.22	1.2 ± 0.48	1.8 ± 0.7	4.2 ± 0.48
Seismic	4.3 ± 0.84	4.8 ± 1.51	0	1.8 ± 0.79	0	0
Wedge	3.3 ± 0.72	0	6.2 ± 0.7	10.7 ± 1.89	7 ± 0.36	3.2 ± 0.79
Wintour	1.5 ± 0.76	0	0	1.2 ± 0.6	2.8 ± 0.7	4.3 ± 1.82

itat selection by individual rodents. The problem was minimized by a patchy landscape where distances between a grid in a single habitat and its corresponding alternative habitat were less than the distance between replicate grids in the same habitat. Distances between sample locations were orders of magnitude greater. It was thus reasonable to assume that the isodar and isoleg analyses reflected the scale of habitat choice in this system. This interpretation was confirmed by results from the fine-scale analyses.

Competitive coexistence

I searched for potential competitive interactions, as well as potential positive covariance in density between species (two specialists, Peromyscus maniculatus and Clethrionomys gapperi, and one generalist, Tamias amoenus), by calculating pairwise correlations of their seasonal density estimates. I calculated the difference in combined density of the two specialist species (total number of Clethrionomys plus Peromyscus; data were insufficient for separate tests during each sampling interval) between habitats at each location to generate two classes of joint abundance (combined density greatest in xeric habitat, combined density greatest in mesic habitat). I calculated differences in abundance for the generalist chipmunk similarly and searched for significant differences among species by contingency analysis (Fisher's exact test). A significant result would illustrate adaptive habitat selection by chipmunks in response to the relative density of specialists in the alternative habitat.

I completed my analysis of habitat selection and coexistence by plotting isolegs (lines of equal habitat choice, Rosenzweig 1974, 1979, 1981, 1989, 1991) for the two specialist species. Isolegs are plotted in the same state space as isoclines and have been successfully used to evaluate the role of habitat in promoting the stable coexistence of competing species (e.g., Rosenzweig 1981, 1991, Pimm et al. 1985, Rosenzweig and Abramsky 1986). The isoleg intercept reflects only intraspecific density-dependent habitat selection, its

slope reflects the competitive effect of interacting species. Isolegs can thus be used to infer the likelihood that pairs of density-dependent habitat selectors interact competitively.

RESULTS

Habitat selection at the scale of grids and sampling locations: mesic and xeric habitats

Two principal components accounted for 61% of the common variation in habitat (Table 1). The first specified a gradient from abundant forb cover on sites covered with deep mosses to grass-covered sites with a shallow litter layer. The second component corresponded to a cline ranging from high-elevation sites with many saplings and mosses to lower-elevation locations with abundant litter interspersed with grasses.

The result of stepwise discriminant-function analysis contrasting xeric and mesic habitats was highly significant ($\chi_2^2 = 13.8$, $P = 0.001$), confirming that they represent two more or less distinct habitats suitable for my analyses of habitat selection. Both principal components contributed to the significant discrimination between habitats (PC1, Wilks' $\lambda_{1,34} = 0.76$, $P = 0.003$; PC2, Wilks' $\lambda_{1,34} = 0.66$, $P = 0.03$).

Three rodent species (red-backed vole, Clethrionomys gapperi; deer mouse, Peromyscus maniculatus; and pine chipmunk, Tamias amoenus) dominated all communities (Table 2). Clethrionomys occurred in at least one grid at each location; Peromyscus and Tamias were absent from one location each. Phenacomys intermedius, Zapus princeps, and Microtus longicaudus were sparsely distributed among the 36 sampling grids (Phenacomys were present in nine grids, Zapus in four, and Microtus in one only).

The rodent isodars: two specialists and one generalist

The densities of the three common rodent species increased throughout the summer (significant sample effect, Tables 3–5). Each species seemed to respond to

TABLE 3. Habitat and location differences in sequential samples estimating density of *Clethrionomys gapperi* in mesic and xeric habitats at nine different locations in the Rocky Mountains of southern Alberta (repeated-measures MANOVA).

Source†	ss	df	F	P
Between grids				
Constant	1064.1	1	298.5	<0.001
Habitat	36.8	1	10.3	0.005
Location	425.3	8	14.9	<0.001
Habitat × Location	72.7	8	2.6	0.047
Error	64.2	18		
Within grids				
Sample	117.7	2	18.2	<0.001
Habitat × Sample	2.1	2	0.3	0.73
Sample × Location	147.6	16	2.8	0.004
Habitat × Sample × Location	58.3	16	1.1	0.4
Error	116.3	36		

† No covariates were statistically significant, $F = 0.2$, $P = 0.8$.

TABLE 4. Habitat and location differences in sequential samples estimating density of *Peromyscus maniculatus* in mesic and xeric habitats at eight different locations in the Rocky Mountains of southern Alberta (repeated-measures MANOVA).

Source†	ss	df	F	P
Between grids				
Constant	459.4	1	188.5	<0.001
Habitat	51.0	1	20.9	<0.001
Location	646.5	7	37.9	<0.001
Habitat × Location	148.8	7	8.7	<0.001
Error	39.0	16		
Within grids				
Sample	60.8	2	19.5	<0.001
Habitat × Sample	9.6	2	3.1	0.6
Sample × Location	68.4	14	3.1	0.004
Habitat × Sample × Location	46.5	14	2.1	0.04
Error	50.0	32		

† No covariates were statistically significant, $F = 1.9$, $P = 0.2$.

similar large-scale differences in habitat (principal component covariates were uncorrelated with the density of any rodent).

The density of each species was higher in some locations than in others (location main effect). The relative densities of *Clethrionomys* and *Tamias* in the two habitats did not vary with the period of sampling (the habitat × sample interaction was nonsignificant for each species). *Clethrionomys* density increased at different rates in different locations (sample × location interaction, Table 3), but, for *Peromyscus* only, the interaction between habitat and location varied with density (the habitat × sample × location interaction, Table 4). This three-way interaction proves that the isodar slope is significantly different from unity (Fig. 2). *Peromyscus* consistently preferred the xeric habitat (isodar slope >1, Fig. 4). The three species responded differently to mesic and xeric habitats. Significant habitat main effects for voles and mice correspond to isodars with intercepts significantly different from zero. Red-backed voles preferred the mesic habitat, deer mice preferred xeric (Fig. 4; *Clethrionomys*' MANOVA coefficient for habitat = 1.01 [mesic had greater density, $t = 3.2$, $P = 0.005$] and *Peromyscus* coefficient for habitat = −1.26 [xeric had greater density, $t = -4.6$, $P < 0.001$]. The signs of the coefficients correspond to my coding in the MANOVA; the signs for the isodar intercepts [opposite the MANOVA coefficients in this case] depend upon which habitat is used as the ordinate).

Despite the significant interaction between habitat and location, chipmunks had no preference for either habitat (Fig. 4). The significant habitat × location interaction was caused, instead, by frequent reversals in apparent habitat preference by chipmunks at different locations (e.g., Table 2), not by a consistent difference in density between habitats as suggested by the model in Fig. 2.

A similar pattern occurred for *Clethrionomys*, whose isodar slope was not different from one (Fig. 4).

Would mark-recapture estimates of population density within intervals produce different patterns? I computed the correlation between my estimates and the jackknife estimator of population density (capture probabilities assumed to vary among individuals [program CAPTURE]; Otis et al. 1978, Rexstad and Burnham 1991, Manning et al. 1995). The predicted jackknife densities were highly correlated with my estimates (*Clethrionomys*, $r = 0.93$; *Peromyscus*, $r = 0.97$; *Tamias*, $r = 0.93$). Standard errors of the jackknife estimates were not heterogeneous among sampling locations ($F_{8,146} = 1.56$, $P = 0.14$, all species combined; analyses for individual species were similar but compromised by small samples at some locations). These results demonstrate a very high correspondence be-

TABLE 5. Habitat and location differences in sequential samples estimating density of *Tamias amoenus* in mesic and xeric habitats at eight different locations in the Rocky Mountains of southern Alberta (repeated-measures MANOVA).

Source†	ss	df	F	P
Between grids				
Constant	726.0	1	169.2	<0.001
Habitat	5.0	1	1.2	0.3
Location	187.8	7	6.2	0.001
Habitat × Location	85.8	7	2.9	0.04
Error	68.7	16		
Within grids				
Sample	18.8	2	3.9	0.03
Habitat × Sample	10.0	2	2.1	0.1
Sample × Location	35.4	14	1.1	0.4
Habitat × Sample × Location	34.2	14	1.0	0.4
Error	76.3	32		

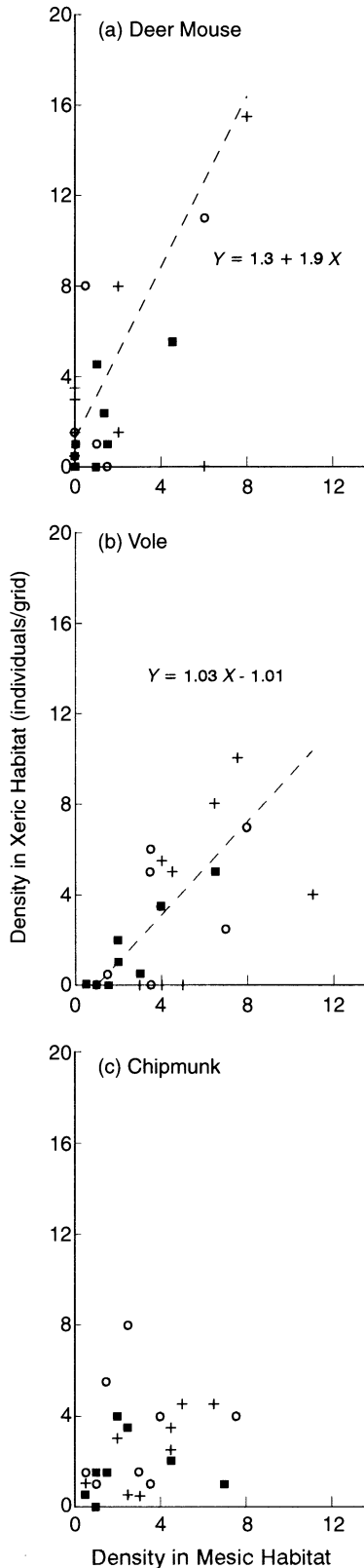† No covariates were statistically significant, $F = 1.4$, $P = 0.3$.

tween alternative density estimates with no obvious bias among species or sampling locations. The results also imply that my sampling intensity was sufficient to assess densities and to obtain representative samples of the small mammal community. An analysis based on mark-recapture estimates would produce the same pattern as the one I report here.

To briefly summarize, *Peromyscus* specialized on the xeric habitat. Deer mice not only preferred the xeric habitat at low density (isodar intercept $\neq 0$), their preference for the xeric habitat actually increased with density (isodar slope > 0). *Clethrionomys* specialized on the alternative mesic habitat. Voles preferred the mesic habitat at all densities (isodar intercept $\neq 0$, slope not different from 1). *Tamias* was an opportunist with no preference for either habitat and had no isodar.

Habitat selection at the scale of trap stations: one isodar for each specialist

Principal components analysis at the scale of individual trapping stations also identified two gradients (Table 6). The first varied from grassy stations with abundant litter to stations with numerous saplings and forbs. The second defined a gradient from deep mossy mats to a shallow litter layer in grass-covered areas.

Stepwise discriminant function analysis contrasting stations where each of the three species was captured was highly significant in the xeric habitat ($\chi^2_2 = 10.0$, $P = 0.007$). The first principal component, only, contributed to significant separation. Stations where *Clethrionomys* were captured had significantly higher mean scores on the discriminant function (0.30, abundant forbs and saplings) than did either *Peromyscus* (-0.23, grass-covered sites with abundant litter, $F_{1,235} = 9.77$, $P = 0.002$) or *Tamias* (-0.05, midway on the gradient, $F_{1,235} = 4.95$, $P = 0.03$). Stations occupied by *Peromyscus* and *Tamias* were not significantly different from one another ($F_{1,235} = 1.27$, $P = 0.26$). Neither principal component was capable of discriminating rodent capture points in the mesic habitat ($F_{2,263} = 2.08$, $P = 0.13$, and $F_{2,263} = 0.30$, $P = 0.74$, for PC1 and PC2, respectively). Despite differences in the xeric habitat, microhabitat separation is unlikely to play a major role in ecological separation of the three rodent species.

There was no significant correlation between the difference in rodent density between paired grids and the mean difference in habitat (Euclidean distances between mean PC scores, $P \geq 0.19$ for all comparisons). Differences in rodent density did not appear to be linked to differences in microhabitat. It is as if rodent densities corresponded to gross differences between

FIG. 4. The abundance of three rodent species occupying mesic and xeric boreal forest habitats in the Rocky Mountains of southern Alberta. Densities correspond to the mean number

←

of individuals caught in replicated 3 × 3 live-trap grids (each 0.16 ha) in each habitat. Isodars are illustrated by dashed lines. Symbols correspond to different 72-h trapping sessions (session 1, ■; session 2, ○; session 3, +).

TABLE 6. Two principal components contained 53.7% of the common variation among six habitat variables describing 324 rodent live-trap stations in the Rocky Mountains of southern Alberta.

Variable†	Rotated loadings	
	PC1	PC2
Abundance of litter	−0.78	0.08
$\sqrt{(\text{number of saplings} + 0.5)}$	0.70	0.15
Total cover by forest-floor species	0.56	0.25
Log_{10} mat depth	−0.16	0.81
Importance value of *Elymus innovatus*	−0.44	−0.62
Importance value of mosses	0.39	0.54

† Variables are the same as those in the gridwise analysis but were calculated at a smaller scale (mean elevation was excluded, and the importance value of *Pyrola secunda* did not pass the inclusion criterion for the KMO test).

mesic and xeric habitats, not to the relative differences between any adjacent pair of those habitats (all of the density estimates for a species fall along a single isodar). The general absence of fine-scale differences confirms that the mesic/xeric dichotomy was an appropriate scale for the analysis of habitat selection among the three rodent species.

Tests for competitive coexistence

Differences in density-dependent habitat selection between voles and deer mice revealed distinct habitat preferences with little potential for competitive interactions. The suspected lack of competition was confirmed by the absence of significant correlations in all pairwise seasonal density estimates (absolute values of all correlations ≤ 0.29, $n = 36$ estimates) and by predominantly noninteracting isolegs. Similarly, *Tamias*

did not avoid habitats where the combined numbers of *Clethrionomys* and *Peromyscus* were greatest (one-tailed Fisher's exact test, $P = 0.29$).

Clethrionomys' isoleg was nearly vertical, that for *Peromyscus* nearly horizontal (Fig. 5). The density of *Peromyscus* had a small effect on the choice of habitat by *Clethrionomys* and vice versa.

DISCUSSION

The mix of mesic and xeric habitats in Canada's southern Rocky Mountains has dramatically different effects on habitat preferences and spatial regulation of the three rodent species (Fig. 5). *Tamias* appeared to have no preference for either habitat and represents a fine-grained generalist at the grid scale used in this study. *Clethrionomys* demonstrated a preference for mesic habitat (the proportion of the population in mesic habitat declined with increased density, isodar intercept < 0). *Peromyscus* preferred the alternative xeric habitat (isodar intercept > 1, slope > 1). The isodar intercepts were significant even though the habitats varied along a moisture gradient that had no apparent effect on the population density of any rodent (no significant relationship with the habitat PCs). Thus, at the scale of mesic vs. xeric habitats, the two specialist rodents appeared to recognize only that the habitats were different rather than the absolute position on the mesic-xeric gradient.

The pattern changed somewhat at the scale of individual trapping stations. In xeric habitat, *Peromyscus* and *Tamias* preferentially used different sites than *Clethrionomys*. In mesic habitat, there was no difference among the three species. These results appear to confirm the assertion of the "scale theory" that species
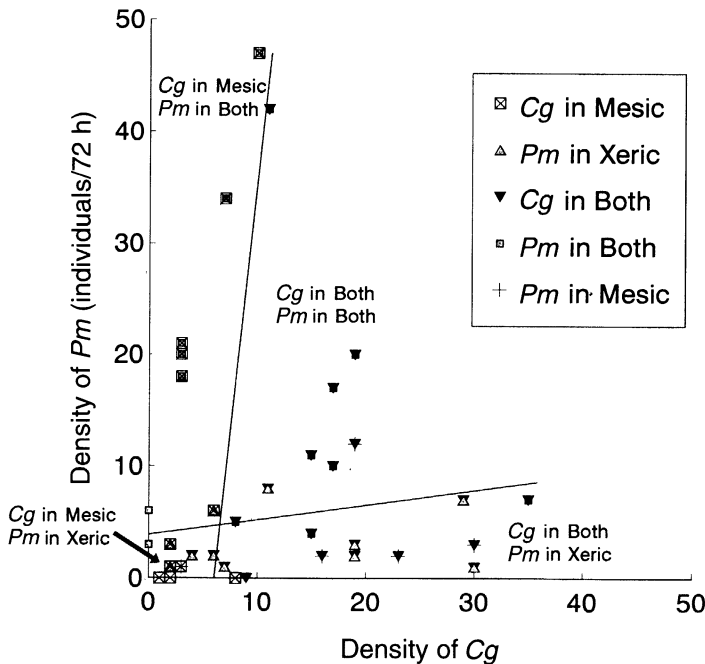

FIG. 5. Isolegs (fitted by eye) for two common density-dependent habitat-selecting rodents occupying mesic and xeric habitats in the Rocky Mountains of southern Alberta. The isoleg for *Peromyscus* (*Pm*) is nearly horizontal and is crossed by the nearly vertical isoleg of *Clethrionomys* (*Cg*). Densities for the isolegs are the number of different rodents captured during 72-h trapping sessions summed across four mesic and xeric habitat trapping grids (each 0.16 ha) at each of nine sampling locations. Chipmunks had no habitat preference and thereby lack an isoleg.

FIG. 6. An example of stable apparently competitive isoclines that could apply to *Clethrionomys* and *Peromyscus* occupying mesic and xeric habitats (as in Fig. 5). Straight lines are the isolegs for the habitat-selecting prey (distinct habitat preferences). Curved lines are the species' isoclines (ZNGIs). The intercepts of the isoclines are the result of preferential habitat use by shared fine-grained predators. When *Clethrionomys* is rare it occupies one habitat only (mesic). When *Peromyscus* is abundant, it occupies both habitats, but is always more abundant in its preferred habitat (xeric). Predators preferentially exploiting the richest habitat (xeric in this example) have a greater negative effect on *Peromyscus* than on *Clethrionomys*. The *Peromyscus* isocline will intersect the *Peromyscus* axis at a lower density than the *Clethrionomys* isocline. The opposite scenario applies when *Peromyscus* is rare. Intraspecific density-dependence is greater than that caused by interspecific effects, and both species coexist around a stable equilibrium. The exact shapes and locations of the isoclines are uncertain.
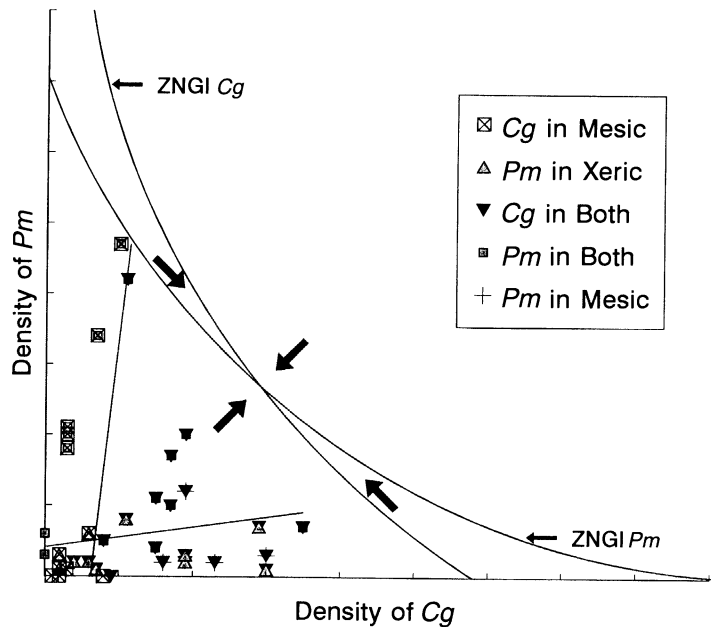
that are coarse grained in habitat use at one spatial scale will often be coarse grained at larger spatial scales. More generally, the fine-scale results confirm the choice of mesic/xeric contrasts for the analyses of density-dependent habitat selection.

The isodar differences between *Peromyscus* and *Clethrionomys* suggest distinct habitat preferences, a result confirmed by the isolegs for the two habitat-selecting specialists. The crossed and near-perpendicular isolegs illustrate that habitat choice is determined predominantly by intraspecific density.

The isolegs should not be interpreted to imply that coexistence of the two specialist species is necessarily unpredictable or unstable. Boreal rodents share numerous predators (several studies implicate the ability of predators to regulate small mammal prey in boreal ecosystems [e.g., Erlinge et al. 1984, Hansson and Henttonen 1988, Hanski et al. 1993]). The influences of these predators can be mapped as isoclines (Holt et al. 1994) onto the isoleg graphs (Fig. 6). Fine-grained predators should preferentially exploit the habitat with the higher energy return, assumed to be related to prey density. Thus, when deer mice are rare and voles abundant, predators should forage predominantly in mesic habitat. When voles are rare, and deer mice abundant, predators should switch to the xeric habitat. This model agrees with the habitat use of stoats (*Mustela erminea*), which restrict their activity to prey-rich patches when microtines are rare (Oksanen et al. 1992). When both rodent species are rare, each occupies its preferred habitat only, and predators may be forced to forage in alternative habitats (mustelid habitat preferences may disappear during microtine crashes, Oksanen et al. 1992) or switch to alternative prey (as in southern Sweden, Erlinge et al. 1984). The result is a predator-me-

diated equilibrium allowing the coexistence of the two prey species (Fig. 6).

Could the predators, in addition to their control of prey density, actually be responsible for distinct habitat preferences? Do numerical responses of predators to one prey species reinforce habitat selection by the second (apparent competition, Holt 1977, Holt 1984, Holt and Kotler 1987, Holt and Lawton 1994)? Perhaps, but relative habitat preferences of *Peromyscus* and *Clethrionomys* are likely to have as much to do with the species' independent evolutionary origins and generally noncompetitive coexistence (e.g., Grant 1972, Morris 1983, Wolff and Dueser 1986) as they do with the density of predators. Yet it is intriguing that the best evidence for competitive interactions between *Clethrionomys* and *Peromyscus* involves density-dependent habitat shifts on small islands that lack a full complement of predators (Crowell and Pimm 1976). Divergent habitat use between these two rodent species may be maintained, at least in part, by apparent competition. But I was unable to detect any competition, apparent or otherwise. The responses and consequences of shared predators may be richer that we imagined, promoting, in this case, apparently noncompetitive coexistence via habitat selection.

Regardless, there is considerable variation in abundance within and between habitats (Fig. 5) that casts doubt on the existence of a single, stable, predator-mediated equilibrium. If an "equilibrium" occurs it is likely to vary among locations and to certainly vary through time, as both predator and prey populations reproduce seasonally in this environment. Future studies will need, therefore, to evaluate more critically how shared predators modify prey isoclines in heterogeneous landscapes.

The coexistence of the specialists with *Tamias* may appear more problematical. One can explain *Tamias'* independence from the other two rodents on the basis of differences in diet, in diel activity, and in *Tamias'* ability to avoid competition by hibernation. Each mechanism has been shown to account for patterns of coexistence in desert rodents (Brown 1989*a, b*). Yet, one can use theories of habitat selection to argue that *Tamias,* being a generalist, coexists with the two specialists by exploiting the margins of their preference. This mechanism of coexistence depends upon density-dependent habitat selection operating at different spatial scales for specialists and generalists. The mechanism can be augmented by apparent competition driving the specialists into separate habitats, thereby creating opportunity for habitat generalists.

The data suggest, at least at the scales of the analyses reported here, that *Tamias* may have occupied the xeric and mesic habitats independently of any patterns in its own density or that of its putative competitors. *Tamias* had no isodar and no isoleg. It must, at these scales, have represented either a non-habitat selector, a species that selects habitat independent of density, or one whose density never reached the point where its habitat selection was expressed.

Communities composed of a generalist and two one-habitat specialist species may represent one example of novel mixtures of community organizations (J. S. Brown, *in press*). In Brown's theory, habitat strategies depend upon the relative costs and benefits of habitat selection. Costs are high in a fine-grained environment because individuals must move through relatively poor patches in order to exploit rich ones (Rosenzweig 1974, 1981). For habitat selection to be an evolutionarily stable strategy, the costs must be balanced by benefits obtained from the selected habitats. Opportunist species are favored when the grain size of the patches is small (costs of specialization are high) and habitat productivities are similar (profits from each habitat are about the same). Specialists emerge when the habitats are relatively more coarse grained; costs of habitat selection are reduced.

A generalist can coexist with two specialists as long as it perceives the environment as relatively fine-grained, and as long as at least one habitat is unused or underused by the specialists (J. S. Brown, *in press*). Grain is a function not only of the environment, but also of the activity scale of the consumer. Even if the environment is constant, differences among species in activity scale can create variation in grain size among the three habitats in Brown's model. Relatively large-bodied chipmunks appear to perceive the environment at a different grain size than do the smaller deer mice and red-backed voles (three species, three habitats). Both processes likely lead to a startling array of possible community organizations. It is somewhat surprising, therefore, that the dominant deer mouse, vole,

chipmunk community is so common throughout the boreal forest.

Another common feature of boreal-forest rodent communities is a relatively large number of sparse species (e.g., Krebs and Wingate 1976, 1985, Martell and Radvanyi 1977, Nagorsen and Peterson 1981, Morris 1983, 1984, Martell 1984, Vickery et al. 1987). Could these represent the less robust assemblies alluded to by Brown? Increasing the number of habitats increases species diversity and the potential kinds of community organization. But in multiple habitat systems, slight changes in the scale and productivity of habitat can have profound effects on the overall community assembly (J. S. Brown, *in press*). Dominant species may always be present because they are inextricably linked to abundant habitats with predictable grain sizes. Their community organization will also be predictable and robust. Rare and sparse species may key on different habitats, and represent a variety of forms of community organization that thwart attempts to categorize their structure.

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