

# Do animals select habitat at small or large scales? An experiment with meadow voles (*Microtus pennsylvanicus*)

M.L. Oatway and D.W. Morris

**Abstract:** Habitat and patch use are crucial to the dynamics of populations and the structure of ecological communities. But ecologists have not rigorously tested whether animals choose habitat at small or large scales. If individuals base their patch and habitat choices on fine-scale differences in habitat, then their use of different sites should correspond with measures of microhabitat at those sites. But if individuals use density to assess and respond to habitat at larger spatial scales, then site use should correspond with the scale of density-dependent habitat selection. We tested these predictions with experiments that measured microhabitat and monitored the use of capture sites by meadow voles (*Microtus pennsylvanicus* Ord, 1815) in 0.25 ha old-field enclosures. We varied the density of voles in pairs of adjacent enclosures and tested for density-dependent habitat selection. Then we assessed whether their frequency of captures at trapping stations was best predicted at the small scale of microhabitat or at the much larger scale of enclosures where density varied. The voles selected habitat at different scales. When the use of enclosures was predicted by density, the scale of density-dependent choice trumped the use of small-scale patches. And when voles selected amongst different small-scale patches, their use of enclosures was independent of density. These results suggest that assessments of spatial scale in habitat use must include tests for both scale- and density-dependent habitat choice.

**Résumé :** L'utilisation des habitats et des taches est d'importante cruciale pour la dynamique des populations et la structure des communautés écologiques. Les écologistes n'ont cependant pas vérifié de façon rigoureuse si les animaux choisissent leur habitat à petite ou à grande échelle. Si les individus fondent leur choix d'habitats et de taches sur des différences à échelle fine de l'habitat, leur utilisation des différents sites devrait alors correspondre à des mesures du microhabitat dans ces sites. Mais, si les individus utilisent la densité pour évaluer un habitat et pour y réagir à des échelles spatiales plus grandes, l'utilisation des sites devrait alors correspondre à l'échelle de la sélection d'habitat dépendante de la densité. Nous avons vérifié ces prédictions au moyen d'expériences qui mesurent le microhabitat et qui suivent l'utilisation des sites de capture chez des campagnols de Pennsylvanie (*Microtus pennsylvanicus* Ord, 1815) dans des enclos de 0,25 ha de champs abandonnés. Nous avons fait varier la densité des campagnols dans des paires d'enclos adjacents et avons vérifié l'existence de sélection d'habitat dépendante de la densité. Nous avons ensuite déterminé si les fréquences des captures aux sites de piégeage peuvent être mieux prédites à l'échelle réduite du microhabitat qu'à l'échelle beaucoup plus vaste de l'enclos à laquelle la densité varie. Les campagnols choisissent leur habitat à différentes échelles. Lorsque l'utilisation des enclos peut être prédite d'après la densité, l'échelle du choix dépendant de la densité l'emporte sur l'utilisation des taches à petite échelle. Lorsque les campagnols font leur choix parmi différentes taches à petite échelle, leur utilisation des enclos est indépendante de la densité. Ces résultats indiquent que l'évaluation de l'échelle spatiale dans l'utilisation de l'habitat doit comporter des tests de choix de l'habitat dépendant à la fois de l'échelle et de la densité.

[Traduit par la Rédaction]

## Introduction

Knowledge of the mechanisms that create local patterns of abundance is vital to understanding population dynamics and to wildlife conservation. But first, we must know the spatial scale at which animals make habitat decisions (Wiens et al. 1986; Morris 1987a; Levin 1992) and incorporate those scales into our models of habitat selection.

Most current models assume that individuals base their habitat use on microhabitat measured by the physical and chemical variables influencing an individual's allocation of time and energy (Morris 1987a). Resource selection func-

tions, for example, relate the probability of use of points in space to resources located at those points (Boyce and McDonald 1999; Boyce et al. 2002; Manly et al. 2002). An alternative approach, called interaction assessment, assumes that animals equalize fitness among microhabitats (Emlen et al. 1989, 1992, 2003, 2006). This ideal free distribution (Fretwell and Lucas 1969) can then be used to measure the effect of interacting species on habitat choice.

Empirical studies with several taxa support both approaches. Many ecologists nevertheless caution against relying solely on animals' use of microhabitat when assessing patterns of abundance (Morris 1984, 1987a; Bowers 1986;

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Orrock et al. 2000; Jorgensen 2004). Although individuals may preferentially select among microhabitats (Bellows et al. 2001; Bowman et al. 2001; Martin and McComb 2002), the type of habitat is often a better predictor of local abundance (Morris 1984, 1987a; Bowers 1986; Jorgensen and Demarais 1999; Orrock et al. 2000; Graf et al. 2005; Coppeto et al. 2006). For example forest type, a measure of macrohabitat (Morris 1987b), explained much more variation in small mammal abundance on trapping grids in the northern Sierra Nevada than did a series of microhabitat variables measured within 1 m of individual trapping stations (Coppeto et al. 2006). It is therefore questionable whether studies emphasizing only the use of microhabitat successfully capture the mechanism driving a species' local abundance.

A third approach assumes that individuals equalize fitness at the habitat scale where density reduces mean fitness (Fretwell and Lucas 1969; Rosenzweig 1974, 1981; Morris 1987b, 1988). The density in each habitat corresponds to the evolutionary stable strategy of habitat selection (Morris et al. 2001). Graphs of the density of individuals in one habitat versus the density in an adjacent habitat (habitat isodars, Morris 1988) reveal the underlying density-dependent habitat selection (e.g., stream salmonoids, Rodríguez 1995; gerbils, Abramsky et al. 1997; urban birds, Fernández-Juricic 2001; kangaroos, Ramp and Coulson 2002; meadow voles, Pusenius and Schmidt 2002; fleas, Krasnov et al. 2003; and brown-headed cowbirds, Jensen and Cully 2005). Thus, we ask the following question: Is the frequency of use of point locations by individuals of a density-dependent habitat selecting species driven primarily by small-scale differences in microhabitat or by larger scale density dependence?

We develop two models that predict the use of individual sites. One model is based solely on microhabitat. The second includes density-dependent habitat selection at a larger spatial scale. We then describe an experiment on meadow voles (*Microtus pennsylvanicus* Ord, 1815) designed to differentiate between these two alternatives. We first test for density-dependent habitat selection with habitat isodars (Morris 1988). We then evaluate whether meadow voles' use of capture sites was determined by microhabitat choice or density-dependent habitat selection.

## Theory

Imagine a population of ideal habitat selectors that choose between two adjacent habitats. Assume that individuals can be captured and microhabitat quantified at predetermined points in each habitat. Imagine further that (i) individuals choose habitats to maximize their evolutionary fitness, (ii) fitness declines with increasing population density, and (iii) individuals are free to occupy the habitat they choose. Individuals will move among habitats until their expected fitness is the same in each one (ideal habitat selection; Fretwell and Lucas 1969).

Now imagine that we determine habitat use by capturing individuals at different sites in the occupied habitats. If these ideally distributed individuals have similar capture probabilities, then the frequency of captures at sites should reflect their expected fitness:

$$[1] \quad U_i = f(W_i)$$

where  $U_i$  is the frequency of use of site  $i$ , and  $W_i$  is a

measure of fitness at site  $i$ . Thus, sites that yield higher fitness receive more use (Emlen et al. 1992). Typically, the expected fitness at a site depends on habitat characteristics (Emlen et al. 1992):

$$[2] \quad W_i = g(Z_i) + \varepsilon$$

where  $Z_i$  is some (usually linear) combination of microhabitat variables measured at site  $i$  and  $\varepsilon$  is the variation in fitness not represented by microhabitat. Ignoring the residual variation and substituting eq. 2 into eq. 1:

$$[3] \quad U_i = f[\alpha g(Z_i)]$$

where  $\alpha$  is a scaling constant. Equation 3 is thus a reliable predictor of site use if animals base their use of sites solely on microhabitat. The density-dependent pattern of habitat use emerges from the ideal-free distribution at individual capture sites.

However, if ideal habitat selection occurs at a larger scale (Fretwell and Lucas 1969), then the fitness at any site will depend on the population density in the surrounding habitat:

$$[4] \quad W_{ij} = h(N_j) + e$$

where  $W_{ij}$  is the expected fitness at site  $i$  in habitat  $j$ ,  $h$  defines the relationship between fitness and density,  $N_j$  is the population density in habitat  $j$ , and  $e$  is the variation in fitness not explained by population density. Furthermore, the density of ideal habitat selectors in one habitat reflects that of neighbouring habitats (Fretwell and Lucas 1969). We can reveal the underlying habitat selection by plotting the densities of individuals in two adjacent habitats such that expected fitness is equal in each (the habitat isodar; Morris 1988). If fitness declines linearly with population density, the isodar is given by

$$[5] \quad N_j = C + bN_L$$

where the intercept  $C$  represents habitat differences in resource abundance, the slope  $b$  represents habitat differences in structure and resource quality, and  $N_L$  is the population density in an adjacent habitat  $L$  (Morris 1988).

Substituting the isodar into the model of site use:

$$[6] \quad U_{ij} = f[\alpha g(Z_i) + \beta h(C + bN_L) + \text{err}]$$

where  $\text{err}$  is the variation in site use unexplained by the isodar and microhabitat. Equation 6 thus relates the use of individual sites to both site quality and density-dependent habitat selection.

In most cases, the scaling constant ( $\beta$ ) and fitness function ( $h$ ) will be unknown. We can nevertheless include the effect of density-dependent habitat selection at this large scale by substituting a binary habitat identifier for the actual isodar. The identifier,  $I$ , is scored 0 for habitat  $j$  and 1 for habitat  $L$ :

$$[7] \quad U_{ij} = f[\alpha g(Z_i) + I + \text{err}]$$

Equation 7 thus summarizes the scale of habitat use that will depend on such things as the spatial pattern in the landscape; the ability of individuals to sample different habitats; whether they have exclusive or shared access to resources; the number, quality, size, and the spatial distribution of resource patches; and of course, the spatial extent of the study.

The pattern of habitat use revealed by this analysis at different scales is preparatory to a detailed understanding of the underlying mechanisms of habitat choice. Habitat use by migratory songbirds, for example, may represent a hierarchy of selection decisions whereby individuals first choose among alternative macrohabitats before selecting breeding sites or territories (Orians and Wittenberger 1991). Other species may simply choose the best available site (Pulliam 1988; Rodenhouse et al. 1997). Habitat selection in both of these models is, nevertheless, driven by density. An analysis of site use within and between adjacent habitats will be able to detect the relative roles of microhabitat and density in habitat choice. Thus, if one has measures of site use, microhabitat, and population density in adjacent habitats, it is easy to determine whether the frequency of site use is caused by microhabitat choice (eq. 3) or density-dependent habitat selection at a larger scale (eqs. 5 and 7).

## Materials and methods

### Study species and study site

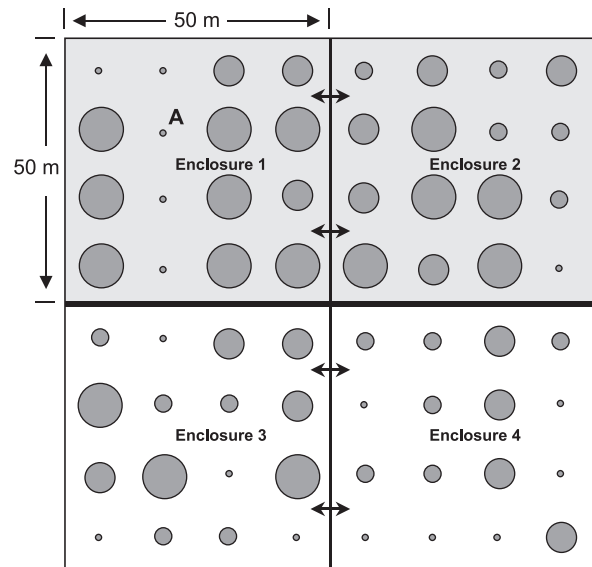
We used the meadow vole (*M. pennsylvanicus*), a widespread, herbivorous rodent that lives in a variety of open habitats (Getz 1985), as a model to test the theory. Meadow voles are ideal-free habitat selectors (Pusenius and Schmidt 2002; Lin and Batzli 2004), except at very high densities where habitat selection may be related to dominance (ideal-dominant distribution; Pusenius and Schmidt 2002).

We monitored the distribution of meadow voles and their use of trapping stations in two pairs of 50 m × 50 m galvanized metal enclosures at the Lakehead University Habitatron (Morris 2003) located near Thunder Bay, Ontario, Canada, from May 2005 to September 2005. The enclosures were situated in an abandoned hayfield planted with red pine (*Pinus resinosa* Ait.) saplings. Each enclosure had 16 trapping stations spaced 6.25 m from the fences and 12.5 m from each other. Animals were incapable of moving between enclosures except when two 9.25 cm diameter gates at ground level were opened. The gates were located equidistant along enclosure fences. Common plant species in the four enclosures included red clover (*Trifolium pratense* L.), strawberry (*Fragaria virginiana* Duchesne), dandelion (*Taraxacum* spp.), yarrow (*Achillea millefolium* L.), as well as the red pine saplings 1–2 m tall.

### Experimental design

We tested the scale of site use by meadow voles with experiments that manipulated density and evaluated the voles' choice of habitat between pairs of experimental enclosures (Fig. 1). Pairings were determined by a random draw. We removed voles from the four enclosures prior to each experiment by live-trapping for 3 days and nights. We cannot exclude the possibility that one or more untrappable voles remained in the enclosures. Only one vole was known to persist from the first to the second experiment. We removed it as soon as it was captured (see Results). On 12 June 2005, we selected 22 voles of similar body size at random (10 males and 12 females) from animals held in two smaller (25 m × 25 m) old-field enclosures and placed them in an enclosure chosen at random from the two pairs. We closed the gates for 2 nights while the animals familiarized them-

**Fig. 1.** The spatial arrangement of enclosures and microhabitat variation in two pairs of enclosures used to assess meadow vole (*Microtus pennsylvanicus*) habitat selection in northern Ontario, Canada. Circles correspond to quartile scores of the first principal component summarizing microhabitat (scores increase with increasing diameter). Gates (arrows) were located at ground level to either allow (open) or inhibit movement between enclosures. (See Discussion for an explanation of movement among microhabitats at site A in enclosure 1.)



selves with the enclosure and each other. We then opened the gates on the third day for 2 consecutive days and nights. We closed the gates at dusk on day five, placed traps at each trapping station, and checked traps three times the following day (0630, 1200, and 1600). We placed two traps at each station whenever the number of voles exceeded the number of trapping stations in a single enclosure. We moved two randomly chosen voles from the first enclosure pair to a randomly chosen enclosure from the second pair. We opened the gates for 2 more days and nights before closing them and resuming live-trapping. We repeated the 3-day cycle 11 times. Thus, the design reduced density in the first enclosure pair from 22 to 2 animals, while it increased the density in the second enclosure pair from 2 to 22 animals. Each of these 11 density treatments served to replicate vole habitat use through time. This "spring experiment" ended on 15 July 2005.

Did our 3-day cycles provide enough time for voles to make their habitat choices? Our analysis incorporates an indirect test of this assumption. Given our random removal and addition of voles, the habitat isodars will be statistically significant ( $P < 0.05$ ) only if the voles actually moved from one enclosure to another (habitat selection, Morris 1988).

We replicated the entire experiment in the summer (27 July to 29 August) using different animals. We added 250 mL of rabbit chow (e.g., Lin and Batzli 2001) to each of 28 ABS (acrylonitrile butadiene styrene) tubes (30 cm long, 3 cm diameter) placed horizontally in one randomly selected enclosure in each pair. We reasoned that the extra food would change the relative habitat quality between enclosures and enhance the value of habitat selection. But the voles ate, on average, less than 0.02 L of the 7.0 L of food added during each 3-day cycle. So we used the summer experiment as a temporal replicate in our test for the scale of habitat selection.



Some readers may be concerned that our assessment of the scale of habitat use is biased if our populations are well below the habitats' carrying capacities (Lin and Batzli 2001, for example, reported maximum densities much higher than ours). However, it is crucial to note that true habitat preference, especially for a species with density-dependent habitat selection, can be determined only at small population sizes (Rosenzweig 1981). We return to this point in the Discussion.

We trapped animals with Sherman and Tomahawk small-mammal live traps protected from the sun and rain by aluminium trap-covers. We supplied traps with a potato wedge and cotton mattress stuffing and baited the traps with oats and peanut butter mixed with flour. We identified each trapped animal by ear tag, confirmed its sex and sexual condition, and subsequently moved or released the animal at the point of capture. We attempted to equalize capture probabilities by replacing all soiled traps with fresh ones that had been washed, sanitized, rinsed, and dried. Our samples were too small to evaluate whether these procedures equalized trappability among animals. Our randomization procedures should ensure that any residual bias does not unduly influence the results. All animal procedures were in accordance with the Animal Utilization Protocol approved by Lakehead University's Animal Care Committee (A10 05-06).

We measured 28 site characteristics (microhabitat variables) corresponding to those known to influence habitat selection by small mammals (e.g., Morris 1979, 1984) at each of the Habitrón's 240 trapping stations in midsummer when we judged vegetation cover to be maximum (Appendix A). We reasoned that this large sample would yield the most accurate description of local habitat variation. We eliminated all variables occurring in less than 5% of the samples, those lacking variance (Morris 1984), any with little correlation with other variables ( $<0.25$ ), as well as those with highly skewed distributions. We calculated the mean values of the remaining variables for each trap station and then used arcsine square root and square root transformations to improve their fit to a normal distribution (Appendix A). We summarized the common variation among the 17 remaining variables with principal components analysis (PCA, Varimax rotation, SPSS version 13, SPSS Inc., Chicago). We retained PC's based on the scree plot (Cattell and Vogelmann 1977) and then confirmed their retention with that expected from a broken-stick distribution (Jackson 1993).

We used forward stepwise discriminant functions analysis (DFA, SPSS version 13) on the retained PC scores to verify that our measures of microhabitat could reveal differences among enclosures. If at least two of the paired enclosures were significantly different, we assumed that there was sufficient microhabitat variance within all enclosures to provide the voles with a choice between scales. A significant habitat identifier would then imply that the voles responded to the scale of enclosures rather than the finer scale of microhabitat within them. If no enclosures were different, however, we could not exclude the possibility that voles' apparent choice between enclosures was actually caused by selection, at a fine scale, of unmeasured microhabitat variation.

### Habitat selection

We used isodar analysis (Morris 1987b, 1988) to verify density-dependent habitat selection by calculating geometric

mean regressions of the number of animals caught in one enclosure versus the number of animals caught in its paired enclosure at each population density (eq. 5). We then used forward stepwise multiple linear regression (SPSS version 13) to determine the scale of site use by meadow voles (eqs. 3 and 7). We regressed the number of accumulated vole captures ( $U_{ij}$ ) at each station against the PC scores ( $Z_{ij}$ ) and a binary identifier variable ( $I$ ), scored 0 and 1, to differentiate enclosures within each pair. By accumulating vole captures in each experiment, we assessed the relative roles of density dependence and microhabitat on vole site use, but not their interactions.

We reasoned that if two or more variables were statistically significant in our multiple regressions, then each variable alone or in combination could represent a potentially competing model for site use. It would then be appropriate to use model selection procedures (e.g., Akaike's information criterion; Burnham and Anderson 2002) to evaluate which model(s) best described site use for meadow voles. All stepwise regressions included only one variable, so there were no competing models to select.

We differentiated four a priori predictions:

H<sub>1</sub>: If density-dependent habitat selection by meadow voles occurs at the scale of habitat enclosures, then their habitat preference will be revealed by a statistically significant isodar.

H<sub>2</sub>: If the voles use only fine-scale microhabitat variation to choose sites, then some sites will be used more than others and the regression predicting site use will include only one or more of the principal components ( $Z_{ij}$ ; eq. 3).

H<sub>3</sub>: If site use by voles is redundant with their use of enclosures, then the regression of site use will include only the binary identifier variable ( $I$ ; eq. 7).

H<sub>0</sub>: If meadow voles use enclosures independent of density and do not choose some sites over others, then the regression will not be significant.

## Results

### Microhabitat varied along three principal dimensions

Three PCs, accounting for 56% of the common variation in 17 habitat variables, summarized microhabitat (Appendix A). PC1 described a gradient ranging from stations with several pine saplings growing in open areas dominated by forbs to stations with fewer pine and much taller vegetation. PC2 defined a cline from sites with alder (*Alnus* B. Ehrh.) and goldenrod (*Solidago* L.) to those with short forbs with deep litter. PC3 reflected a succession gradient from overgrown alder thickets to abandoned hayfield.

### Enclosures differed in microhabitat

The first PC was the only variable retained in the stepwise DFA (Table 1,  $F_{[3,60]} = 3.77$ ,  $P = 0.015$ ). Enclosure 4 was composed of a more open microhabitat with somewhat shorter vegetation than were the other enclosures (mean PC1 for enclosure 4 = 0.04, mean PCs of all other enclosures = 0.87).

### Meadow vole captures were similar in the spring and summer replicates

We recorded 287 vole captures in the spring and 328 in the summer. All animals caught during spring were *M. pennsylvanicus*. Two deer mice (*Peromyscus maniculatus* (Wagner,

**Table 1.** Pairwise comparisons of the differences in habitat structure revealed by stepwise discriminant functions analysis (DFA) among four small-mammal enclosures in northern Ontario, Canada.

Enclosure	Statistic	1	2	3
2	<i>F</i>	0.01		
	<i>P</i>	0.939	—	
3	<i>F</i>	1.18	1.35	
	<i>P</i>	0.281	0.249	—
4	<i>F</i>	8.24	8.68	3.18
	<i>P</i>	0.006	0.005	0.080

**Note:** Analysis based on principal component (PC) scores. The first PC only was included in the stepwise solution.

1845)) and one southern red-backed vole (*Myodes gapperi* (Vigors, 1830)) entered the enclosures and were removed in the summer. None of the meadow voles escaped from their respective enclosures. Many females gave birth during the experiments. We removed their offspring at first capture (28 juveniles during spring and 19 during summer). We caught only one adult nonexperimental animal (in summer). We used only captures of the adult experimental animals to calculate the isodar and evaluate the scale of site use.

### Meadow voles were vague density-dependent habitat selectors

We calculated isodars for each of the two paired enclosures in spring and summer. The density of meadow voles in one enclosure depended on the density in its adjacent paired enclosure in three of the four comparisons (i.e., accept  $H_1$ : meadow voles are density-dependent habitat selectors; Fig. 2). Meadow voles preferred one enclosure over another in only one experiment (slope 95% CI = 1.28 to 2.91, intercept 95% CI = -2.22 to 2.97; Fig. 2). Otherwise, the significant meadow vole isodars revealed an equal preference for both enclosures (Fig. 2).

We were concerned that variation in trap success could bias the isodar analysis, so we searched for data where trap success fell one or more standard deviations below the mean of 75%. Trap success was low on very hot, sunny days and when nights were clear. We identified these residuals on each isodar. Periods with low trap success did not bias the isodars (Fig. 2).

We were also concerned that the nonsignificant isodar (Fig. 2) may have been caused by a bias in sex or weight classes among enclosures. So we tested for each effect.

The sex ratio of trapped animals during spring was not different from the starting ratio of 10 males and 12 females ( $\chi^2 = 1.41$ ,  $P = 0.23$ ). We did catch more males than expected in the summer treatment ( $\chi^2 = 21.51$ ,  $P < 0.001$ ). But the sex bias in the summer could not have caused the nonsignificant spring isodar.

Animals caught in enclosure 1 (mean = 30.8 g) weighed, on average, 2 g more than those caught in enclosure 2 (mean = 28.8 g) in spring ( $F_{[1,65]} = 4.39$ ,  $P = 0.04$ ). Vole body size thus correlated with habitat preference in that experiment. There was no weight bias in any of the other three comparisons.

### Site use by meadow voles was best predicted by density-dependent habitat selection

All four experiments yielded significant regressions of site use. The use of capture sites by meadow voles was related only to the habitat identifier in three of the four analyses (Table 2). And for each of these, the isodar was also significant (Fig. 2; accept  $H_1$  and  $H_3$ : meadow voles choose sites at the scale corresponding to their density-dependent habitat selection).

There was a single and revealing exception. Site use in one spring experiment was independent of density (reject  $H_1$ ) and was related only to microhabitat (Table 2; accept  $H_2$ : meadow voles used microhabitat to choose sites).

### Discussion

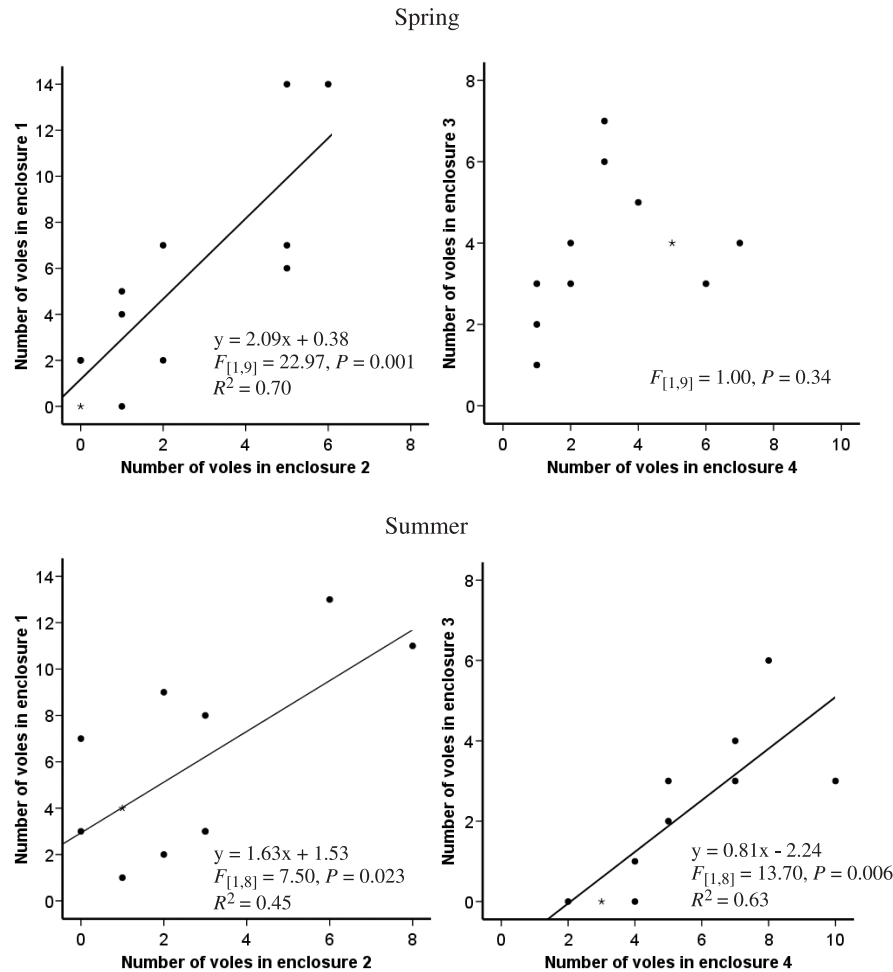
Whenever isodars were significant, vole captures were predicted only by the habitat identifier. And when density did not determine habitat selection, vole captures were predicted only by microhabitat. These crucial results confirm the logic of our theory. When isodars were significant, they were detected with a single binary variable. And, when the use of enclosures was independent of density, microhabitat was the best predictor of site use. Voles thus appear capable of assessing and responding to fine scale variation in microhabitat, but their use of sites may be better associated with density-dependent habitat choice at larger scales.

How can we explain this pattern? One possibility is that the pattern itself depends on density. Imagine two environments in which paired habitats have the same maximum fitness values, but different carrying capacities (Fig. 3). In environments where carrying capacity is low, the change in fitness with population growth or decline is great. Movement to a different habitat could reward dispersing individuals with large fitness dividends. The density in each habitat will be finely tuned with the density-dependent decline in fitness (a well-fitted isodar). In environments with high carrying capacity, the change in fitness for an equivalent growth or decline in population size is small. The costs of habitat selection may not outweigh its advantages, and individuals may not even be able to detect the slight difference in fitness between habitats. The resulting vague isodar would have substantially more variance than one generated in an environment with lower carrying capacities.

We manipulated the density of meadow voles in paired enclosures from 2 to 22 animals (1 to 11 animals/ha). Populations of meadow voles in other old-field enclosures in Illinois have been observed as high as 300 voles/ha (Lin and Batzli 2001) and even higher in upper New York State (100–800 voles/ha; Pusenius and Schmidt 2002). So the carrying capacities in our enclosures were probably much higher than the low experimental densities, and the fitness gains and penalties for habitat choice were likely negligible. It is hardly surprising, therefore, that our experiments revealed rather substantial variation in meadow vole habitat selection. Even so, the three significant isodars imply that voles can usually detect relatively small differences in fitness potential.

Some readers may be concerned that, because we eliminated a subset of uncorrelated and poorly distributed microhabitat variables, the PCA did not reflect site characteristics

**Fig. 2.** Isodars comparing meadow vole densities between adjacent 0.25 ha enclosures. Asterisks (\*) correspond to density estimates obtained when trap success was one or more standard deviations below the mean.



**Table 2.** Summary of four multiple linear regressions assessing habitat selection by meadow voles in northern Ontario, Canada.

Source						
Experiment	Enclosure comparison	Model	$N^*$	Adj. $R^{2\dagger}$	$F$	$P$
Spring	1 vs. 2	$U_{ij} = 6.13 - 3.31I$	32 (143)	0.27	12.41	0.001
	3 vs. 4	$U_{ij} = 4.04 + 0.98PC2$	32 (117)	0.11	4.66	0.039
Summer	1 vs. 2	$U_{ij} = 4.94 - 2.56I$	32 (121)	0.26	12.06	0.002
	3 vs. 4	$U_{ij} = 2.25 + 3.75I$	32 (132)	0.23	10.45	0.003

\*Sample size is the number of capture sites in each pair of enclosures. The total numbers of captures are in parentheses.

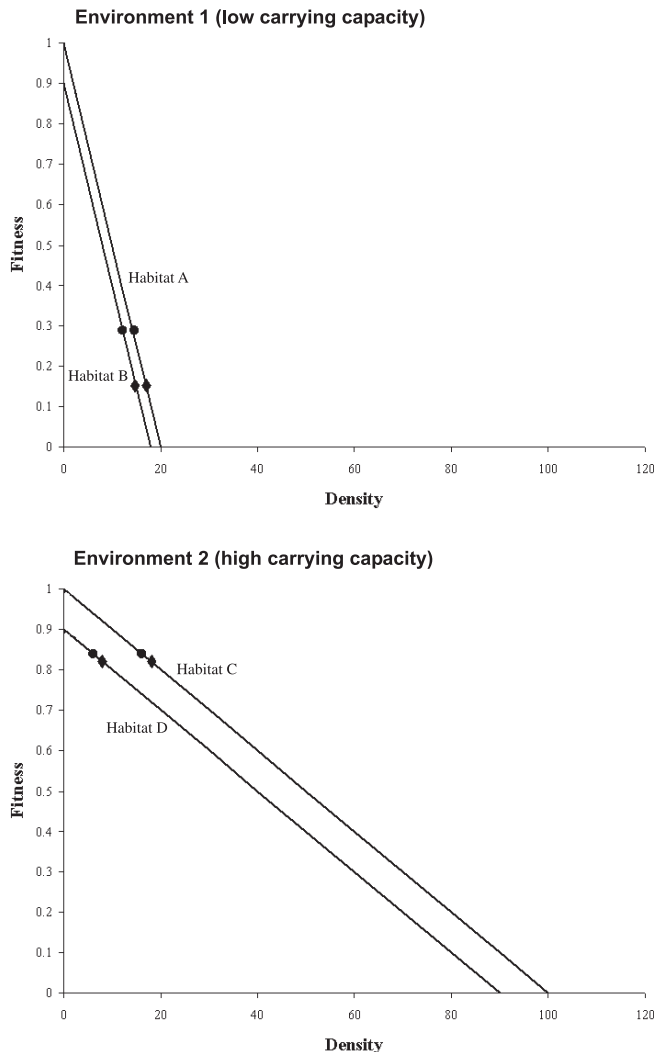
<sup>†</sup>Degrees of freedom was reduced to exclude variance explained by chance alone.

important to meadow voles. Meadow vole habitat selection may respond more to total cover, for example (Lin and Batzli 2001; Pusenius and Schmidt 2002; Lin and Batzli 2004), rather than to our somewhat more refined estimates of microhabitat. So we summed cover separately for all herbaceous and woody plants and repeated all analyses. The PCA summarizing the combined variables was significant with two PCs accounting for 60% of the variance in habitat. There was no difference in habitat among enclosures (no discriminant function was significant). Nevertheless, the main results were unchanged. Whenever the isodar was significant (Fig. 2), the habitat identifier was the only signifi-

cant variable in the site use regression. When habitat selection did not depend on density (Fig. 2), however, no variable was associated with site use.

It is important to note, even when we reanalyzed the site characteristics at a different resolution by combining cover variables, that the key result was the same. The frequency of site use by meadow voles was best revealed at the scale of enclosures. It is interesting that site characteristics predicted site use only when analyzed at a fine resolution (i.e., no lumping of variables). As well, contrary to the original DFA, there was no significant habitat difference between enclosures when cover variables were lumped together. We

**Fig. 3.** Hypothetical fitness functions in pairs of habitats located in environments with the same maximum fitness, but different carrying capacities. The increase in density from lower (●) to higher (◆) population size is the same in both environments. But the reduction in fitness is much more extreme in the low carrying capacity environment (top) than it is in the environment with a high carrying capacity.



interpret these results as evidence that enclosures actually did differ in site characteristics (Table 2) that were obscured at a more coarse resolution of microhabitat.

Habitat selection by meadow voles creates patterns of abundance that are strong and undeniable and implicate an interaction between scale and density in vole habitat choice. We can detect the density-dependent signal by an appropriate scale identifier in assays of microhabitat selection. Although we advocate the use of indicator variables in both theoretical and applied studies of animal habitat selection, it is crucial to ponder their statistical meaning. A significant habitat identification variable emerges in our form of site use regressions only when mean site use is greater in one habitat (enclosure) than in another. This outcome can be caused by greater density in one habitat (our significant spring isodar) or by different capture probabilities in habitats with similar densities (our summer isodars).

Differences in capture probabilities are particularly inter-

esting because they imply, if only the indicator variable is significant, that the difference in site use is not associated with differences in microhabitat quality. Poor quality sites may be used more often than expected. Such undermatching of site use can occur when individuals have limited knowledge of site quality (Abrahams 1986; Ranta et al. 1999) or when there is strong interference that forces subordinate individuals to use otherwise suboptimal sites (ideal-despotic distribution; Fretwell and Lucas 1969; Sutherland 1983).

But it is also possible that meadow voles underused high-quality sites because the grain size of the Habitron environment is large. When the environment is fine-grained (neighbouring patches vary greatly), but has high spatial correlation, foragers tend to match patch quality no matter how limited their knowledge may be (Ranta et al. 2000). But in coarse-grained environments where the quality of neighbouring patches changes only slightly or has little spatial correlation, individuals tend to undermatch site quality (Ranta et al. 2000). The undermatching will occur even when individuals are familiar with large areas (Ranta et al. 2000).

We illustrate spatial variation in microhabitat with quartiles of PC1 scores at the 64 trapping stations used in our experiments (Fig. 1). Scores increase with increasing circle diameter. Imagine an individual at site A (Fig. 1, Enclosure 1). Any movement in a northward or southward direction places the animal in the same microhabitat (positive correlation). Easterly or westerly movements, however, place the animal in a different microhabitat (negative correlation). In such a predictable fine-grained environment, foragers should match site use with microhabitat (Ranta et al. 2000). The spatial distribution of microhabitat in the Habitron, however, varies from enclosure to enclosure (Fig. 1). Unless voles have clearly directed movements that also vary by enclosure, their knowledge of the spatial variation among microhabitats will be relatively low. Site use will undermatch site quality (Ranta et al. 2000), and voles will be captured more often at poor-quality sites than expected.

Individuals' habitat choice affects the abundance and distribution of species (Fretwell and Lucas 1969; Rosenzweig 1974, 1981; Morris 1988), intra- and inter-specific interactions (Rosenzweig 1974, 1981; Morris 1988; Danielson 1992; Abramsky et al. 1997), resource distributions (Morris and Knight 1996), and species' persistence through space and time (Guisan and Zimmermann 2000; Fahrig 2001; Jonzén et al. 2005). But the scale of habitat choice is seldom assessed in the context of density dependence. Patterns of microhabitat use are frequently more apparent than real (Morris 1984, 1987a) and often reflect, as in meadow voles, density-dependent habitat selection at larger spatial scales. Ecologists must determine the appropriate scales driving habitat choice to successfully understand the intricate dynamics and spatial distribution of animal populations.

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## References

- Abrahams, M.V. 1986. Patch choice under perceptual constraints: a cause for departures from an ideal free distribution. *Behav. Ecol. Sociobiol.* **19**: 409–415. doi:10.1007/BF00300543.
- Abramsky, Z., Rosenzweig, M.L., and Subach, A. 1997. Gerbils under threat of owl predators: isoclines and isodars. *Oikos*, **78**: 81–90. doi:10.2307/3545803.
- Bellows, A.S., Pagels, J.F., and Mitchell, J.C. 2001. Macrohabitat and microhabitat affinities of small mammals in a fragmented landscape on the upper coastal plain of Virginia. *Am. Midl. Nat.* **146**: 345–360. doi:10.1674/0003-0031(2001)146[0345:MAMAOS]2.0.CO;2.
- Bowers, M.A. 1986. Geographic comparison of microhabitats used by three heteromyids in response to rarefaction. *J. Mammal.* **67**: 46–52. doi:10.2307/1381000.
- Bowman, J., Forbes, G.J., and Dilworth, T.G. 2001. The spatial component of variation in small-mammal abundance measured at three scales. *Can. J. Zool.* **79**: 137–144. doi:10.1139/cjz-79-1-137.
- Boyce, M.S., and McDonald, L.L. 1999. Relating populations to habitats using resource selection functions. *Trends Ecol. Evol.* **14**: 268–272. doi:10.1016/S0169-5347(99)01593-1. PMID:10370262.
- Boyce, M.S., Vernier, P.R., Nielson, S.E., and Schmiegelow, F.K.A. 2002. Evaluating resource selection functions. *Ecol. Model.* **157**: 281–300. doi:10.1016/S0304-3800(02)00200-4.
- Burnham, K.P., and Anderson, D.R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. 2nd ed. Springer-Verlag, New York.
- Cattell, R.B., and Vogelmann, S. 1977. A comprehensive trial of the scree and KG criteria for determining the number of factors. *Multivariate Behav. Res.* **12**: 289–325. doi:10.1207/s15327906mbr1203\_2.
- Coppeto, S.A., Kelt, D.A., Van Vuren, D.H., Wilson, J.A., and Bigelow, S. 2006. Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. *J. Mammal.* **87**: 402–413. doi:10.1644/05-MAMM-A-086R1.1.
- Danielson, B.J. 1992. Habitat selection, interspecific interactions and landscape composition. *Evol. Ecol.* **6**: 399–411. doi:10.1007/BF02270700.
- Emlen, J.M., Freeman, D.C., and Wagstaff, F. 1989. Interaction assessment: rationale and a test using desert plants. *Evol. Ecol.* **3**: 115–149. doi:10.1007/BF02270916.
- Emlen, J.M., Freeman, D.C., Bain, M.B., and Li, J. 1992. Interaction assessment. II. A tool for population and community management. *J. Wildl. Manag.* **56**: 708–717.
- Emlen, J.M., Freeman, D.C., Kirchoff, M.D., Alados, C.L., and Duda, J.J. 2003. Fitting population models from field data. *Ecol. Model.* **162**: 119–143. doi:10.1016/S0304-3800(02)00390-3.
- Emlen, J.M., Duda, J.J., Kirchoff, M.D., and Freeman, D.C. 2006. Interaction assessment: a modeling tool for predicting population dynamics from field data. *Ecol. Model.* **192**: 557–570. doi:10.1016/j.ecolmodel.2005.07.012.
- Fahrig, L. 2001. How much habitat is enough? *Biol. Conserv.* **100**: 65–74. doi:10.1016/S0006-3207(00)00208-1.
- Fernández-Juricic, E. 2001. Density-dependent habitat selection of corridors in a fragmented landscape. *Ibis*, **143**: 278–287.
- Fretwell, S.D., and Lucas, H.L., Jr. 1969. On the territorial behaviour and other factors influencing habitat distribution in birds. *Acta Biotheor.* **14**: 16–36.
- Getz, L.L. 1985. Habitats. In *Biology of New World *Microtus**. Edited by R.H. Tamarin. Spec. Publ. No. 8. The American Society of Mammalogists. pp. 286–309.
- Graf, R.F., Bollmann, K., Suter, W., and Bugmann, H. 2005. The importance of spatial scale in habitat models: capercaillie in the Swiss Alps. *Landsc. Ecol.* **20**: 703–717. doi:10.1007/s10980-005-0063-7.
- Guisan, A., and Zimmermann, N.E. 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* **135**: 147–186. doi:10.1016/S0304-3800(00)00354-9.
- Jackson, D.D. 1993. Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecol. Monogr.* **74**: 2204–2214. doi:10.2307/1939574.
- Jensen, W.E., and Cully, J.F. 2005. Density-dependent habitat selection by brown-headed cowbirds (*Molothrus ater*) in tallgrass prairie. *Oecologia (Berl.)*, **142**: 136–149. doi:10.1007/s00442-004-1709-x. PMID:15375686.
- Jonzén, N., Rhodes, J.R., and Possingham, H.P. 2005. Trend detection in source-sink systems: when should sink habitats be monitored? *Ecol. Appl.* **15**: 326–334.
- Jorgensen, E.E. 2004. Small mammal use of microhabitat reviewed. *J. Mammal.* **85**: 531–539. doi:10.1644/BER-019.
- Jorgensen, E.E., and Demarais, S. 1999. Spatial scale dependence of rodent habitat use. *J. Mammal.* **80**: 421–429. doi:10.2307/1383290.
- Kingston, S.R., and Morris, D.W. 2000. Voles looking for an edge: habitat selection across forest ecotones. *Can. J. Zool.* **78**: 2174–2183. doi:10.1139/cjz-78-12-2174.
- Krasnov, B.R., Khoklova, I.S., and Shenbrot, G.I. 2003. Density-dependent host selection in ectoparasites: an application of isodar theory to fleas parasitizing rodents. *Oecologia (Berl.)*, **134**: 365–372. PMID:12647144.
- Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology*, **73**: 1943–1967. doi:10.2307/1941447.
- Lin, Y.K., and Batzli, G.O. 2001. The influence of habitat quality on dispersal, demography, and population dynamics of voles. *Ecol. Monogr.* **71**: 245–275. doi:10.2307/2657218.
- Lin, Y.K., and Batzli, G.O. 2004. Movement of voles across habitat boundaries: effects of food and cover. *J. Mammal.* **85**: 216–224. doi:10.1644/1545-1542(2004)085<0216:MOVAHB>2.0.CO;2.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., and Erickson, W.P. 2002. *Resource selection by animals: statistical design and analysis for field studies*. 2nd ed. Kluwer Academic Publishers, The Netherlands.
- Martin, K.J., and McComb, W.C. 2002. Small mammal habitat associations at patch and landscape scales in Oregon. *For. Sci. Monogr.* **48**: 255–264.
- Morris, D.W. 1979. Microhabitat utilization and species distribution of sympatric small mammals in southwestern Ontario. *Am. Midl. Nat.* **101**: 373–384. doi:10.2307/2424603.
- Morris, D.W. 1984. Patterns and scale of habitat use in two temperate-zone small mammal faunas. *Can. J. Zool.* **62**: 1540–1547.
- Morris, D.W. 1987a. Ecological scale and habitat use. *Ecology*, **68**: 362–369. doi:10.2307/1939267.
- Morris, D.W. 1987b. Tests of density-dependent habitat selection in a patchy environment. *Ecol. Monogr.* **57**: 269–281. doi:10.2307/2937087.
- Morris, D.W. 1988. Habitat-dependent population regulation and community structure. *Evol. Ecol.* **2**: 253–269. doi:10.1007/BF02214286.
- Morris, D.W. 2003. How can we apply theories of habitat selection



- to wildlife conservation and management? *Wildl. Res.* **30**: 303–319. doi:10.1071/WR02028.
- Morris, D.W., and Knight, T.W. 1996. Can consumer–resource dynamics explain patterns of guild assembly? *Am. Nat.* **147**: 558–575. doi:10.1086/285866.
- Morris, D.W., Lundberg, P., and Ripa, J. 2001. Hamilton's rule confronts ideal free habitat selection. *Proc. R. Soc. Lond. B Biol. Sci.* **268**: 921–924.
- Orians, G.H., and Wittenberger, J.F. 1991. Spatial and temporal scales in habitat selection. *Am. Nat.* **137**: S29–S49. doi:10.1086/285138.
- Orrock, J.L., Pagels, J.F., McShea, W.J., and Harper, E.K. 2000. Predicting presence and abundance of a small mammal species: the effect of scale and resolution. *Ecol. Appl.* **10**: 1356–1366. doi:10.2307/2641291.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.* **132**: 652–661. doi:10.1086/284880.
- Pusenius, J., and Schmidt, K.A. 2002. The effects of habitat manipulation on population distribution and foraging behavior in meadow voles. *Oikos*, **98**: 251–262. doi:10.1034/j.1600-0706.2002.980207.x.
- Ramp, D., and Coulson, G. 2002. Density dependence in foraging habitat preference of eastern grey kangaroos. *Oikos*, **98**: 393–402. doi:10.1034/j.1600-0706.2002.980304.x.
- Ranta, E., Lundberg, P., and Kaitala, V. 1999. Resource matching with limited knowledge. *Oikos*, **86**: 383–385. doi:10.2307/3546456.
- Ranta, E., Lundberg, P., and Kaitala, V. 2000. Size of environmental grain and resource matching. *Oikos*, **89**: 573–576. doi:10.1034/j.1600-0706.2000.890317.x.
- Rodenhouse, N.L., Sherry, T.W., and Holmes, R.T. 1997. Site-dependent regulation of population size: a new synthesis. *Ecology*, **78**: 2025–2042. doi:10.2307/2265942.
- Rodríguez, M.A. 1995. Habitat-specific estimates of competition in stream salmonoids: a field test of the isodar model of habitat selection. *Evol. Ecol.* **9**: 169–184. doi:10.1007/BF01237755.
- Rosenzweig, M.L. 1974. On the evolution of habitat selection. *In* Proceedings of the First International Congress of Ecology. Centre for Agricultural Publishing and Documentation, The Hague. pp. 401–404.
- Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology*, **62**: 327–335. doi:10.2307/1936707.
- Sutherland, W.J. 1983. Aggregation and the 'ideal free' distribution. *J. Anim. Ecol.* **52**: 821–828.
- Wiens, J.A., Addicott, J.F., Case, T.J., and Diamond, J. 1986. Overview of the importance of spatial and temporal scale in ecological investigations. *In* Community ecology. Edited by J. Diamond and T.J. Case. Harper & Row, New York. pp. 145–153.

## Appendix A

**Table A1.** Microhabitat variables measured between 29 July and 7 August 2005 at 240 trapping stations in the Lakehead University Habitron, northern Ontario, Canada, and their summary by principal components analysis (PCA).

Variable	Description	Correlation		
		PC1	PC2	PC3
H5*	Percent horizontal cover at 1.00 m	<b>0.867</b>	–0.049	–0.112
H4*	Percent horizontal cover at 0.75 m	<b>0.853</b>	0.170	0.001
H6*	Percent horizontal cover at 1.25 m	<b>0.779</b>	–0.162	–0.287
H7*	Percent horizontal cover at 1.50 m	<b>0.678</b>	–0.290	–0.261
H3*	Percent horizontal cover at 0.50 m	<b>0.670</b>	<b>0.417</b>	0.260
AlVi <sup>†</sup>	Percent cover by <i>Alnus viridis</i>	<b>0.591</b>	<b>–0.486</b>	<b>–0.386</b>
SoSp <sup>‡</sup>	Percent cover by <i>Solidago</i> spp.	<b>0.588</b>	–0.383	0.102
Mat <sup>§</sup>	Litter depth (cm)	0.134	<b>0.534</b>	0.039
TaSp <sup>‡</sup>	Percent cover by <i>Taraxacum</i> spp.	0.066	0.172	<b>0.650</b>
H2*	Percent horizontal cover at 0.25 m	0.051	<b>0.769</b>	0.147
GrSe <sup>‡</sup>	Percent cover by grasses–sedges	0.013	0.149	<b>0.803</b>
AcMi <sup>‡</sup>	Percent cover by <i>Achillea millefolium</i>	–0.224	<b>0.626</b>	0.170
TrPr <sup>‡</sup>	Percent cover by <i>Trifolium pratense</i>	–0.247	0.253	<b>0.724</b>
H1*	Percent horizontal cover at 0.125 m	–0.250	<b>0.777</b>	0.076
TrRe <sup>‡</sup>	Percent cover by <i>Trifolium repens</i>	–0.263	0.271	0.211
FrVi <sup>‡</sup>	Percent cover by <i>Fragaria virginiana</i>	<b>–0.364</b>	0.389	–0.042
PiRe <sup>†</sup>	Percent cover by <i>Pinus resinosa</i>	<b>–0.399</b>	0.205	<b>0.418</b>

**Note:** Bold type identifies variables with high correlations on each component.

\*Square root of mean percent cover of 10 cm × 20 cm checkered boards measured on both east and west sides of the north–south trapping lines at each station from a distance of 1 m on a five-point scale (1, 0%–20%; 5, 80%–100%; Morris 1979; Kingston and Morris 2000).

<sup>†</sup>Arcsine square root of mean percent cover of shrubs and trees in four 2 m × 2 m quadrats centered at each trap station.

<sup>‡</sup>Arcsine square root of mean percent cover of sedges, grasses, and herbaceous plants in 25 cm × 50 cm quadrats placed east and west of the trap lines within 1 m at each station.

<sup>§</sup>Square root mean depth of plant litter measured in each corner of the 25 cm × 50 cm quadrats.