

**Is patch use determined by fine-scale microhabitat differences or
density-dependent habitat selection?**

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Abstract

If individuals base their patch and habitat choices on fine-scale differences in microhabitat, then their use of patches, defined by capture sites, should correspond with measures of microhabitat. But if individuals assess and respond to habitat at larger spatial scales, then site use should correspond with habitat selection at those scales. I tested these predictions by monitoring the distribution of meadow voles (*Microtus pennsylvanicus*) in 0.25ha old-field enclosures in northern Ontario, Canada (the Lakehead University Habitron). I varied the population density in two pairs of adjacent enclosures and tested for habitat selection with habitat isodars. Three of four isodars were statistically significant, but even so, meadow voles were vague density-dependent habitat selectors. The use of capture sites was related to microhabitat only in the one case where isodars failed to detect density-dependent habitat selection. Otherwise, site use was related to the number of animals living in paired enclosures. Site use by meadow voles was determined primarily by density-dependent habitat selection.

Introduction

Knowledge of the mechanisms that create local patterns of species' 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). Most models assume that individuals base their habitat use on microhabitat measured by physical and chemical variables which influence an individual's allocation of time and energy (Morris, 1987a).

Resource selection functions (RSF), for example, relate the probability of use of point locations to resources at those locations (Boyce *et al.*, 1994, 2002; Akçakaya & Atwood, 1997; Mladenoff, 1997; Mladenoff & Sickley, 1998; Boyce & McDonald, 1999; Manly *et al.*, 2002; Marzluff *et al.*, 2004). An alternative approach called Interaction Assessment (INTASS) assumes that animals equalize fitness at the microhabitat scale (Emlen *et al.*, 1989, 1992, 2003, 2006).

Empirical studies support both approaches. Many ecologists, nevertheless, caution against relying solely on animals' use of microhabitat when assessing patterns of abundance (Bowers, 1986; Morris, 1987a; Orrock *et al.*, 2000; Jorgensen, 2004). Although individuals may preferentially select among microhabitats (Bellows *et al.*, 2001; Bowman *et al.*, 2001; Martin & McComb, 2002), habitat measurements at larger scales are often better predictors of local abundance (Bowers, 1986; Morris, 1987a; Jorgensen & Demarais, 1999; Orrock *et al.*, 2000; Graf *et al.*, 2005; Coppeto *et al.*, 2006). It is therefore questionable whether studies emphasizing only the use of microhabitat successfully capture the mechanism driving species local abundance.

A third approach assumes that individuals equalize fitness at the habitat scale where density reduces mean fitness (Fretwell & 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), can thus reveal underlying density-dependent habitat selection (stream salmonoids, Rodriguez, 1995; deer mice and red-backed voles, Morris, 1996; two different species of gerbils, Abramsky *et al.*, 1997; birds living in urban parks, Fernández-Juricic, 2001; feral cats and dingoes, Edwards *et al.*, 2002; eastern grey kangaroos, Ramp & Coulson, 2002; prairie voles, Lin & Batzli, 2001; meadow voles, Pusenius & Schmidt, 2002; fleas, Krasnov *et al.*, 2003; and brown-headed cowbirds in tallgrass prairie, Jensen & Cully, 2005).

I therefore ask the question: Is the frequency of use of point locations by a density-dependent habitat-selecting species, the meadow vole (*Microtus pennsylvanicus*), driven primarily by small-scale differences in microhabitat or by larger-scale density-dependence?

I develop two models that predict the use of individual sites. One model is based solely on microhabitat. The second includes density-dependent habitat selection. I assess the models by first testing for density-dependent habitat selection with habitat isodars (Morris, 1988). I then test whether meadow voles' use of sites is determined at the microhabitat or habitat scale. Site use by meadow voles was primarily determined by larger-scale density dependence.

Theory

Imagine a population of ideal habitat selectors that choose between two adjacent habitats. Assume that individuals can be captured, and microhabitat quantified, at specific points in each habitat. Imagine further that (1) individuals maximize their reproductive success by choosing habitats which yield the greatest fitness, (2) fitness declines with increasing population density, and (3) individuals occupy habitats such that their expected fitness in each habitat is equal at any density (Fretwell & Lucas, 1969; Figure 1a).

If individuals are ideally distributed and have equal capture probabilities, then the frequency of captures at sites should reflect an individual's expected fitness at that site:

$$SU_i = f(W_i) \quad (1)$$

where SU_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).

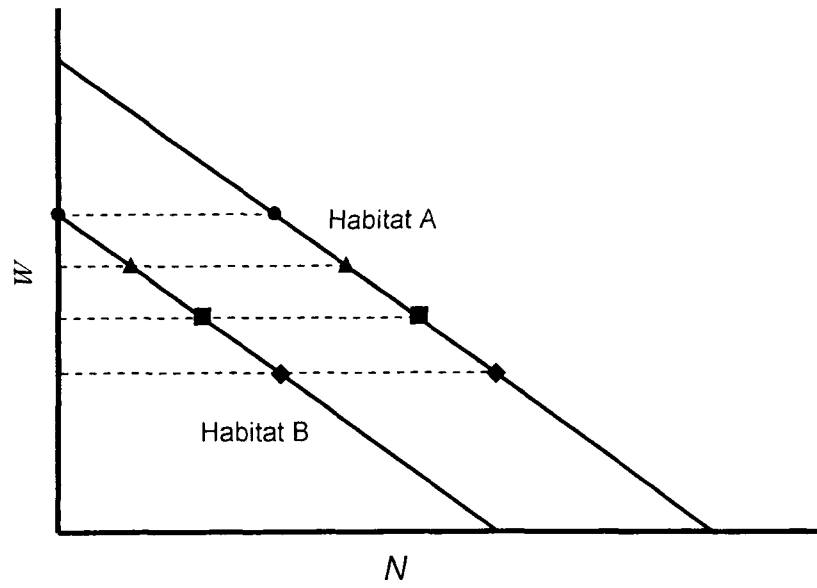
Typically, the expected fitness at a site depends on habitat characteristics (Emlen *et al.*, 1992):

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

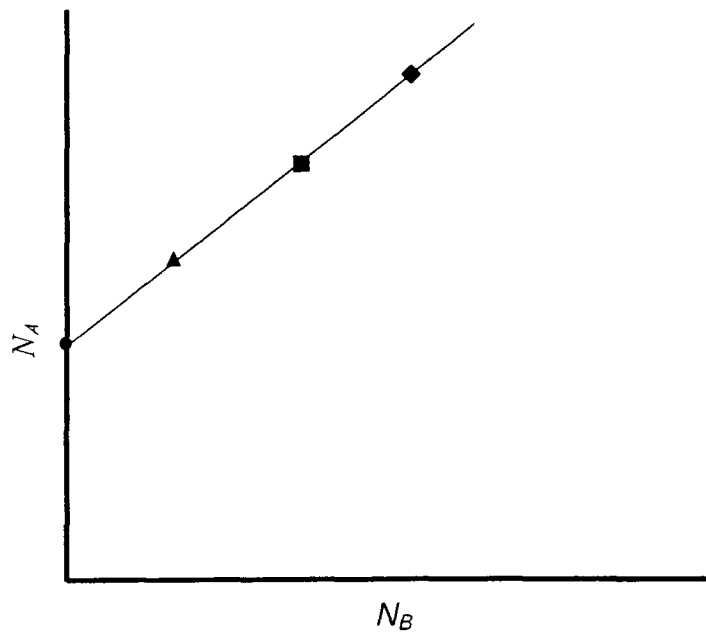
where Z_i is some (usually linear) combination of habitat variables at site i and ε is the variation in fitness not represented by microhabitat variation.

FIGURE 1. An illustration of how isodars reveal density-dependent habitat selection (Morris, 1988). (a) Fitness functions for two habitats (A and B) illustrating a linear decline in fitness (W) with increasing population density (N). The horizontal dashed lines connect densities where fitness in both habitats is equal (ideal-free distribution (IFD); Fretwell & Lucas, 1969). (b) The habitat isodar produced from the IFD in part (a). Subscripts correspond to the two habitats and symbols reflect the different population densities illustrated in (a).

(a)



(b)



Ignoring the residual variation and substituting equation (2) into equation (1):

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

where α is a scaling constant. Equation (3) is thus a reliable predictor of site use if animals base their use of sites solely on fine-scale microhabitat.

But with ideal habitat selection (Fretwell & Lucas, 1969), the fitness at any site depends on the population density in the surrounding habitat:

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

where W_{ij} is the expected fitness at site i in habitat j , N_j is the population density in habitat j , and e represents the variation in fitness not explained by population density. The function “ h ” defines how fitness declines with increasing population density.

Combining equations (4) and (2) and again ignoring the error variance:

$$W_{ij} = g(Z_i) + h(N_j) \quad (5)$$

then, substituting the variables for fitness (5) into the site-use equation (1), we obtain:

$$SU_{ij} = f[\alpha g(Z_i) + \beta h(N_j)] \quad (6)$$

where β is a scaling constant and site use (SU_{ij}) depends on both the microhabitat at site i and density in the surrounding habitat j .

Recall that if individuals are ideal habitat selectors, then the population density in one habitat will reflect that of neighbouring habitats (Fretwell & Lucas, 1969). We can reveal the underlying habitat selection by plotting the densities of individuals in two habitats such that expected fitness is equal (the habitat isodar; Morris, 1988; Figure 1b). If fitness declines linearly with population density, the isodar is given by:

$$N_j = C + b N_k \quad (7)$$

where C is the intercept corresponding to differences in resource abundance between habitats, b is the slope of the isodar corresponding to habitat differences in structure and resource quality, and N_k is the density in an adjacent habitat k (Morris, 1988). Habitat isodars, however, need not be linear (Morris, 1994).

Substituting the isodar into the site-use model:

$$SU_{ij} = f[\alpha g(Z_i) + \beta h(C + b N_k) + err] \quad (8)$$

where “*err*” represents variation in site use unexplained by the isodar and microhabitat. Equation (8) thus relates the use of individual sites to both microhabitat and density-dependent habitat selection.

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

$$SU_{ij} = f[\alpha g(Z_i) + I + err] \quad (9)$$

The scale of habitat use 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. 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 & 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.

Hypotheses

H₁: If individuals are density-dependent habitat selectors, but assess and choose habitat at the microhabitat scale, then the isodar will be significant, but microhabitat alone will predict site use (equations 7 and 3).

H₂: If individuals are density-dependent habitat selectors and assess and choose habitat at the larger habitat scale, then the isodar will be significant and the habitat identifier will predict site use (equations 7 and 9, including only *I*).

H₃: If individuals assess and choose habitat at the microhabitat scale independent of density, then the isodar will not be significant, but microhabitat will predict site use (equation 3 only).

H₀: If individuals do not choose some sites or habitats over others, then the isodar will not be significant and neither microhabitat nor density-dependent habitat selection will predict site use.

Methods

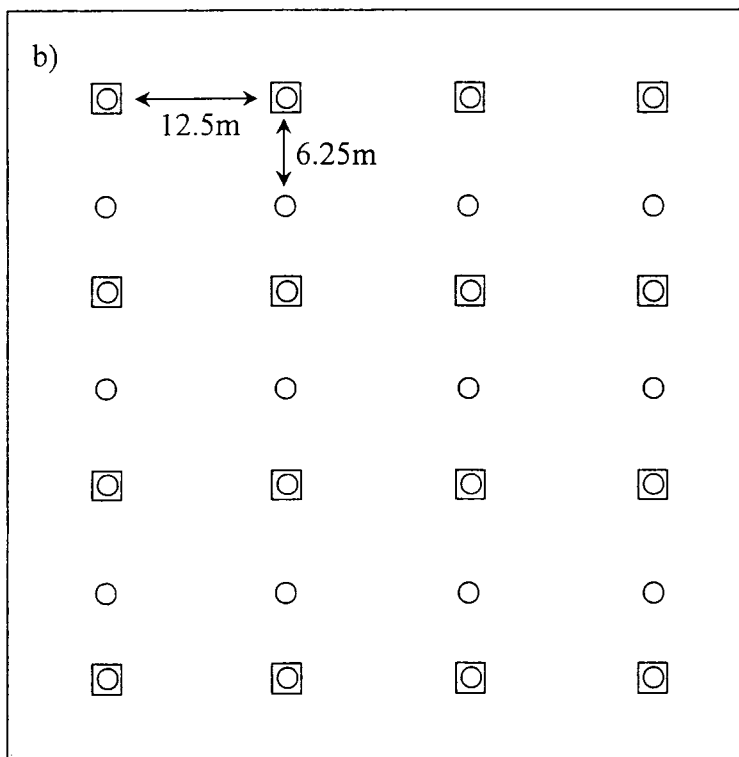
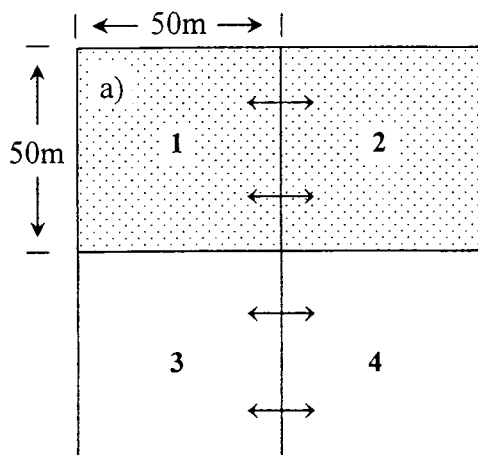
Study species

I used the meadow vole (*Microtus pennsylvanicus*), as a model to test the theory. *M. pennsylvanicus* is a widespread, herbivorous rodent that lives in a variety of open habitats (Getz, 1985). Meadow voles occupy relatively small home ranges (average size = 0.04-0.40 ha; Reich, 1981), but also explore areas outside the home range (Madison, 1985). Meadow-vole habitat selection is determined by availability of food and amount of cover (Jones, 1990; Fortier & Tamarin, 1998; Lin & Batzli, 2001; Pusenius & Schmidt, 2002; Lin & Batzli, 2004), fragmentation of the landscape (Bowers *et al.*, 1996; Collins & Barrett, 1997; Basquill & Bondrup-Nielson, 1999), and population density (Verner & Getz, 1985; Fortier & Tamarin, 1998; Pugh & Ostfeld, 1998; Lin & Batzli, 2001). Meadow voles are ideal-free habitat selectors (Pusenius & Schmidt, 2002; Lin & Batzli, 2004), except in very high-quality habitats where habitat selection may be related to dominance (ideal-despotic distribution; Pusenius & Schmidt, 2002). *M. pennsylvanicus* is thus an appropriate species to test whether the use of sites by density-dependent habitat selectors is determined by fine-scale microhabitat variation or by larger-scale density dependence.

Study site

I monitored the distribution of meadow voles and their use of trapping stations in two pairs of 50 x 50m galvanized metal enclosures (Figure 2a) at the Lakehead University Habitron (Morris, 2003) located near Thunder Bay, Ontario, Canada (Appendix Ia), from May 2005 to September 2005. The enclosures were situated in old-field habitat planted with red-pine (*Pinus resinosa*) saplings.

FIGURE 2. (a) An illustration of the two pairs of 50 x 50m enclosures used to test theories of habitat selection in northern Ontario, Canada. Animals were added first to enclosures 1 and 2 (stippled) and then moved systematically to enclosures 3 and 4. Two gates (arrows) located at ground level were opened to allow movement between paired enclosures. (b) Each enclosure contained 16 trap stations (squares) and 28 feeding tubes (circles; supplemental-food treatment only).



Each enclosure had 16 trapping stations spaced 6.25m from the fences and 12.5m from each other (Figure 2b). Animals were incapable of moving between enclosures except when 9.25cm diameter gates located at ground level were open. Fences were buried 0.50m below ground to inhibit burrowing between enclosures and extended 0.75m above ground (Appendix Ib). Dominant plant species in the four enclosures included red clover (*Trifolium pratense*), common strawberry (*Fragaria virginiana*), dandelion (*Taraxacum spp.*), common yarrow (*Achillea millefolium*), as well as red-pine saplings (~1-2m tall) that had been planted at approximately 5m spacing.

Experimental design

I tested the scale at which meadow voles used capture sites in both unmanipulated (control) and nutritionally-supplemented treatments (one enclosure in each pair received extra food). The supplemental-food treatment was designed to test for potential changes in habitat selection when enclosures differed in resource abundance. Prior to each treatment, I live-trapped each enclosure for a minimum of three consecutive days and nights and removed all captured animals from the enclosures. I placed these captured voles, plus those trapped from other enclosures in the habitron, in two smaller (25 x 25m) old-field holding enclosures where food (Living World Extrusion Rabbit Chow) and water were provided *ad libitum*. Animals were housed in these enclosures until needed for the experiments.

I manipulated meadow-vole density in paired enclosures and tested for density-dependent habitat selection. I followed the same density protocol in both control and supplemental-food treatments.

Density Treatments

I added 22 randomly-selected voles (ten males, twelve females) marked with ear tags from the holding enclosures to one randomly chosen enclosure in each treatment (enclosure 1 in the control treatment, enclosure 2 in the supplemental-food treatment). I kept the gates closed for two nights while the animals familiarized themselves with the enclosure and each other. I opened the gates between enclosures 1 and 2 for two consecutive days and nights on day three. I closed the gates in the late evening on day five, placed one trap at each of the 32 trapping stations, and checked traps three times the following day (06:30, 12:00 and 16:00). I chose one of the two unoccupied enclosures (enclosures 3 and 4; Figure 2a) at random to receive voles. Then, prior to releasing animals caught in the first trapping session (06:30), I randomly selected two closed traps from enclosures 1 and 2 and moved the animals inside to the predetermined unoccupied enclosure. I removed the traps and re-opened the gates following the third trapping session (16:00). I left the gates open for two more days and nights before closing the gates and live-trapping. I repeated the three-day cycle eleven times. Thus, the design reduced density in enclosures 1 and 2 from 22 to 2 animals, while increasing density in enclosures 3 and 4 from 2 to 22 animals (Appendix II). I defined any unmarked animal caught during an experiment a residual animal not encountered during the initial removal period. I removed these animals (8). I assumed that the live-capture data represents an unbiased assessment of habitat quality by the voles.

Altering food availability

Following the control experiment, I added rabbit chow to one randomly chosen enclosure in each pair in an attempt to create differences in resource abundance (July 21 to August 29, 2005). I placed twenty-eight ABS tubes (~ 30cm in length and 3cm in diameter) in each enclosure at 6.25m spacing along the four trapping lines (Figure 2b). I added 250mL of rabbit chow (Lin & Batzli, 2001) to each tube in the supplemented enclosures only (enclosures 2 and 4). I measured and removed leftover food every three days when I set live traps and replenished tubes the next day when I removed the traps.

Live-trapping protocol

I trapped animals with Sherman and Tomahawk small-mammal live traps protected from the sun and rain by aluminum trap-covers. I supplied traps with a potato wedge and cotton mattress stuffing and baited traps with oats and peanut butter. I identified each trapped animal by ear tag, confirmed its sex and sexual condition (females – perforate or imperforate vagina, lactating, pregnant; males – testes scrotal or abdominal), weighed (supplemental-food treatment only) and subsequently moved or released the animal at the point of capture. I replaced all soiled traps with fresh ones that had been washed, sanitized, rinsed, and dried.

Habitat Structure

I recorded site characteristics used to detect small-mammal habitat selection (e.g., Morris, 1979; Appendix III) at each trapping station when I judged the vegetation cover to be maximum (July 29 to August 7, 2005). I measured mat depth (vertical height of litter)

in each corner of a 25 x 50cm quadrat placed to the east and west within 1 metre of the N-S trap lines. I estimated the percent ground cover of sedges, grasses, and herbaceous plants in each 25 x 50cm quadrat. I pooled estimates of sedge and grass species because they have similar structure. I quantified the vertical structure of the vegetation by estimating the cover of 10 x 20cm checkered boards located 0.125, 0.25, 0.50, 0.75, 1.00, 1.25, 1.50, and 1.75m above ground level (Morris, 1979; Kingston & Morris, 2000) at a distance of 1m on a five-point scale (1: 0-20% to 5: 80-100% of the board covered by vegetation). I also estimated the percent ground cover of shrubs and trees in four 2 x 2m quadrats centered at each trap station.

Statistical design

Vegetation analysis

I used principal components analysis (PCA, Varimax rotation, SPSS, version 13) to summarize microhabitat across all of the Habitron's 240 trapping stations (3.75ha). I reasoned that this large sample would yield the most complete description of local habitat variation. I eliminated all microhabitat variables occurring in less than five percent of the samples, as well as any lacking variance (Morris, 1984). I then calculated the mean values of the remaining variables at each trap station. I used arcsine square root and square root transformations to improve the fit of the variables to a normal distribution before analysis with PCA. I further screened variables and deleted those with correlation coefficients less than 0.25 (Appendix III), as well as those with a highly skewed frequency distribution. I then reanalyzed the remaining variables (PCA; Appendix IV). I retained PC's based on the

scree plot (Cattell & Vogelmann, 1977), and then confirmed their retention using the broken-stick method (Jackson, 1993).

I used forward stepwise discriminant functions analysis (DFA, SPSS, version 13) to verify that microhabitat variables (scores from the first three PCs) could differentiate the four experimental enclosures. I reasoned that if the estimates of microhabitat reveal differences among enclosures, then the habitat identifier variable (I) will be included in the site-use model only if the animals choose habitat at a larger scale. If the estimates of microhabitat do not reveal differences among enclosures, then a significant identifier variable could simply be caused by structural differences among enclosures that were not summarized by my measures of microhabitat.

Habitat selection

I used isodar analysis (Morris, 1987b, 1988) to test for density-dependent habitat selection (geometric-mean regressions of the number of animals caught in one enclosure versus the number of animals caught in its paired enclosure at each density treatment). I then used forward stepwise multiple linear regressions (SPSS, version 13) to determine which of the four hypotheses best reveal the use of sites by meadow voles. I used the number of captures at trapping stations to represent the dependent variable (SU_{ij}). I summarized microhabitat (Z_{ij}) with scores from the first three principal components and, included a binary identifier variable (I), scored 0 for enclosures 1 and 3 and scored 1 for their corresponding treatment pair (enclosures 2 and 4). I analyzed the data with four separate site-use multiple regressions (one for each pair of enclosures and each treatment). I reasoned that if two or more variables were statistically significant, each variable alone, and in combination, represented potentially competing site-use models. Although it would

seem appropriate to use model selection (e.g. Akaike's Information Criterion; Burnham & Anderson, 2002)) to compare competing site-use models, such comparisons cannot be made amongst the different data sets represented by my four experiments. Furthermore, all final regressions included but one variable, so there were no competing models to select. I differentiated four *a priori* predictions:

- (1) If meadow voles are density-dependent habitat selectors (significant isodar), but use fine-scale variation in microhabitat to choose sites, then the site-use regression will include only microhabitat (one or more of the principal components, accept H_1).
- (2) If meadow voles are density-dependent habitat selectors (significant isodar) and choose habitat at a larger scale corresponding to the enclosures, then the site-use regression will include only the binary identifier variable (I , accept H_2).
- (3) If meadow voles choose sites based on microhabitat independent of density (non-significant isodar), then the site-use regression will include only microhabitat (one or more of the principal components, accept H_3).
- (4) If meadow voles do not choose some sites or habitats over others, then neither the isodar nor the site-use regression will be significant (accept H_0).

Results

Habitat variation was summarized by three principal components

I used the first three principal components (PCs), accounting for 56% of the total variation in the 17 habitat variables, to summarize site characteristics. Additional PCs accounted for substantially less variation (Appendix V). Principal component 1, accounting for 32% of habitat variation, described a succession gradient ranging from stations dominated by pine saplings and clover to stations with much taller vegetation (at or above 0.50m; Appendix IV). Principal component 2, (15% of the habitat variation), defined a cline from sites covered with alder and goldenrod to those with dense short forbs with deep litter (Appendix IV). Principal component 3, (9% of the habitat variation), also reflected a succession gradient from overgrown alder thickets to abandoned hayfield (Appendix IV).

Three of four enclosures were similar in habitat structure

Enclosures differed in their successional status (PC1 was significant in the DFA; Table I). Enclosure 4 was different from all the others (Table II). Enclosure 4 had more clover and pine saplings, and shorter vegetation (lower mean score on PC1; Appendix VI). No other pairwise comparison was significantly different in habitat structure (Table II).

TABLE I. Summary of the stepwise discriminant functions analysis (DFA) assessing differences in microhabitat (first three PCs) among experimental enclosures.

Source	<i>df</i>	<i>F</i>	<i>P</i>
PC1	3, 60	3.77	0.015
PC2	3, 60	0.84	0.476
PC3	3, 60	1.31	0.281

TABLE II. Pairwise comparisons of differences in habitat structure between four small-mammal enclosures near Thunder Bay, Ontario, Canada (stepwise DFA).

Enclosure		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

Voles did not consume supplemental food

My attempt to alter resource abundance between pairs of enclosures by adding rabbit chow was unsuccessful. Though I added 7L of food each three-day cycle to both enclosures 2 and 4, the voles ate on average less than 0.2L. This result is rather surprising because meadow voles, at high densities, typically alter habitat selection in response to increased food (Fortier & Tamarin, 1998; Lin & Batzli, 2001; Pusenius & Schmidt, 2002). The enclosures were, however, rich in natural food sources and voles may not respond to supplemental food when their densities are low and food is available in unlimited supply. So rather than testing for differences caused by improved habitat quality, I used this treatment as a temporal replicate to test for the scale of meadow-vole habitat selection.

Meadow vole captures were similar in both treatments

I recorded 287 and 331 captures in the control and supplemental-food treatments, respectively. All animals caught during the control experiment were *M. pennsylvanicus*. Two deer mice (*Peromyscus maniculatus*) and one red-backed vole (*Clethrionomys gapperi*) that escaped from adjacent enclosures were caught in the supplemental-food treatment. Many females gave birth during the experiments. I captured, and subsequently removed, 28 juveniles from the control experiment and 19 from the supplemental-food treatment.

One experimental animal died of heat exhaustion in an exposed trap during the control treatment, and three experimental animals died similarly during the supplemental-food treatment. Four meadow voles were not captured at the end of the control experiment,

but all voles were accounted for in the supplemental-food experiment. I was nevertheless able to manipulate vole densities across a suitable range of densities to assess the theory.

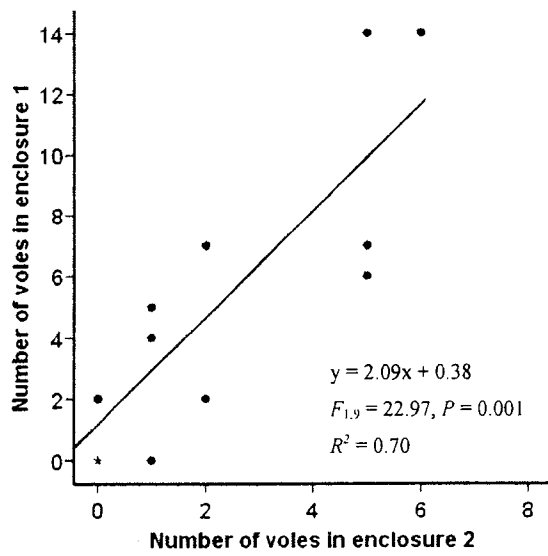
Trap success was low on very hot, sunny days, and when nights were clear. I was concerned that variation in trap success could bias the isodar analysis. So I calculated trap success (by dividing the number of animals caught during a trapping period by the minimum number known alive; Appendix II). Mean trap success for both pairs of enclosures was 77% and 74% in the control and supplemental-food treatments, respectively. Nevertheless, the residual variation in the isodars was not related to trap success. Data points corresponding to low trap success (less than one standard deviation below the mean) did not bias the regression (Figure 3).

Meadow voles were vague density-dependent habitat selectors

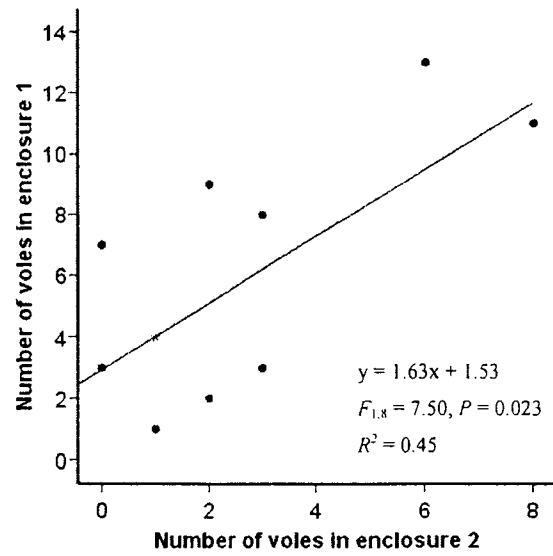
Meadow voles based their habitat selection on enclosure densities in three of the four comparisons (isodar analysis; Figure 3). Meadow-vole preference for enclosure 1 over enclosure 2 increased with increasing density (slope > 1 ; 95% CI = 1.28 to 2.91, intercept not different from zero; 95% CI = -2.22 to 2.97; Figure 3a) in the control experiment, but voles showed no preference for either enclosure in the supplemental-food treatment (slope not different from one; 95% CI = 0.72 to 2.53, intercept not different from zero; 95% CI = -1.66 to 4.72; Figure 3b).

FIGURE 3. Isodars for both pairs of enclosures (control and supplemental-food treatments). Panels (a) and (b) correspond to control versus supplemental-food treatments for enclosures 1 and 2, (c) and (d) correspond to those for enclosures 3 and 4. Asterisks indicate data points generated from periods with low trap success.

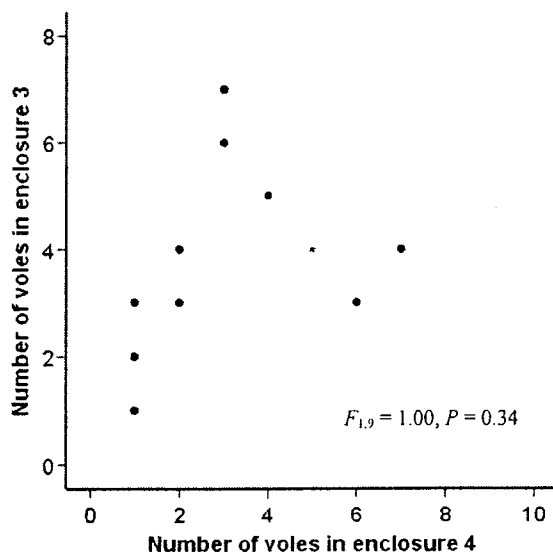
a) CONTROL



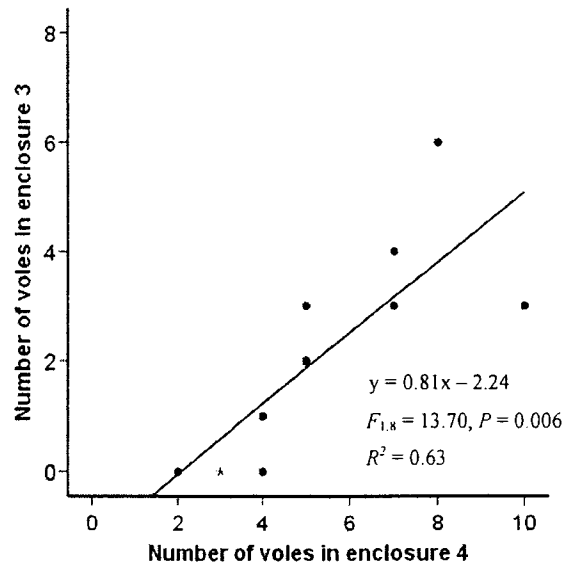
b) REPLICATE



c) CONTROL



d) REPLICATE



Meadow voles also exhibited no preference for either enclosure in the supplemental-food treatment (slope not different from one; 95% CI = 0.41 to 1.21, intercept not different from zero; 95% CI = -4.64 to 0.15; Figure 3d). Density had no influence on vole habitat selection in the control experiment of enclosures 3 and 4 (the isodar was not significant; Figure 3c).

I was concerned that the non-significant isodar (Figure 3c) may have been caused by a bias in sex or weight classes among enclosures. So I tested for each effect.

I tested for a sex bias by comparing the expected starting ratio of ten males to twelve females with the actual ratio of sexes caught in both experiments using Chi-square analysis. Sex ratios were not biased in the control experiment ($\chi^2 = 1.41, P = 0.23$), but I caught more males and fewer females than expected in the supplemental-food treatment ($\chi^2 = 21.51, P < 0.001$). Because the sex bias occurred only in the supplemental-food treatment, it was not responsible for the absence of density-dependent habitat selection revealed in Figure 3c. I also tested whether I caught more females or males in one enclosure versus its pair for both experiments separately. I did not (all analyses yielded $P > 0.15$).

I tested for a possible weight bias by comparing the mean initial weights of the animals caught in one enclosure versus its pair for both enclosure pairs and experiments separately. Animals caught in enclosure 1 (mean = 30.8g) weighed on average 2 grams more than those caught in enclosure 2 (mean = 28.8g) in the control experiment ($F_{1, 65} = 4.39, P = 0.04$). Vole body weight thus correlated with habitat preference in this case (Figure 3a). There was no weight bias in the other three comparisons.

Meadow-vole site use was best predicted by density-dependent habitat selection

Site-use models for enclosures 1 and 2 (both experiments) included the binary habitat identifier only (Table III). Recall that any station in enclosure 1 was given a value of zero, while those in enclosure 2 were coded equal to one. Therefore, there were more vole captures in enclosure 1 than in enclosure 2 in both experiments (Table III). This important result was caused by higher density in enclosure 1 (Figure 3a, b).

The use of capture sites by meadow voles in enclosures 3 and 4 differed between control and supplemental-food treatments. Meadow-vole site use depended on density only in the supplemental-food treatment (Table III). Stations in enclosure 3 received a value of zero, while those in enclosure 4 were given a value of one. There were more vole captures in enclosure 4 than in enclosure 3 (Table III). Therefore, again, capture frequency was related to population density (Figure 3d). But site use in the control experiment was independent of density and related only to microhabitat (significant PC_2 ; Table III). Although microhabitat predicted site use, the coefficient of determination (adjusted R^2) was less than half of that in the three density-dependent models (Table III).

TABLE III. Summary of the multiple linear site-use regression assessing four models of habitat selection by meadow voles in northern Ontario, Canada. The indicator for density-dependent habitat selection (I) was the best predictor of site use (SU_{ij}). The number of trap stations ($N = 32$) was constant for all analyses (the total numbers of captures in paired habitat enclosures are in parentheses).

Experiment	Comparison	Model	N	*Adj. R^2	F	P
Control	Enclosures 1 & 2	$SU_{ij} = 6.13 - 3.31 I$	32 (143)	0.27	12.41	0.001
Control	Enclosures 3 & 4	$SU_{ij} = 4.04 + 0.98 PC_2$	32 (117)	0.11	4.66	0.039
Replicate	Enclosures 1 & 2	$SU_{ij} = 4.94 - 2.56 I$	32 (121)	0.26	12.06	0.002
Replicate	Enclosures 3 & 4	$SU_{ij} = 2.25 + 3.75 I$	32 (132)	0.23	10.45	0.003

* Adjusted to exclude variance accounted for by chance alone (degrees of freedom reduced; Motulsky & Christopoulos, 2004).

Some readers may be concerned that because I eliminated a subset of uncorrelated and poorly distributed habitat variables, the PCA did not capture site characteristics as detected by meadow voles. Cover is an important component of meadow-vole habitat selection (Lin & Batzli, 2001; Pusenius & Schmidt, 2002; Lin & Batzli, 2004), so I summed cover separately for all herbaceous and woody plants and repeated the principal component and discriminant function analyses. The second PCA was significant with two PC's 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 (Figure 3), the habitat identifier was the only significant variable in the site-use regression. When habitat selection did not depend on density (Figure 3c) however, no variable was associated with site use.

Discussion

Meadow-vole site use was determined at the habitat scale in each instance where selection depended on density (accept H_2). Whenever isodars were significant, the density-dependent indicator variable was the best single predictor of vole captures. And when density did not determine habitat selection, meadow voles appeared to rely on microhabitat cues to make their site-use choices (accept H_3).

Capture-frequencies of meadow voles generally depended on density (ideal habitat selection). But in one case, they did not. What sense can we make of the exception? If animals are capable of assessing and responding to habitat quality at a fine-scale, then measures of microhabitat should predict their use of sites (equation 3). And they did. But in most cases, the voles appear to make even better habitat assessments at a larger scale not captured by my measures of microhabitat.

Although microhabitat predicted site use by meadow voles when their habitat selection was independent of density, much of the variance in capture frequencies was unexplained. And there was also considerable variance in capture frequencies when habitat selection depended on density. So we must explain why the voles were vague density-dependent habitat selectors and why microhabitat was an insufficient predictor of meadow-vole captures.

One possibility is that individual voles are incapable of assessing habitat quality. Patches will then be used in proportion to their frequency and there will be no relationship between site use and my estimate of microhabitat. Individuals will be distributed randomly within habitats and the resulting isodar may be non-significant (Morris, 1988). We can discard this scenario because the significant isodars imply that voles can both assess habitat

quality and respond to differences in habitat by dispersing from one to the other (Figure 3; also see Lin & Batzli, 2001; Pusenius & Schmidt, 2002).

Another possibility is that individuals are capable of assessing habitat quality, but are habitat generalists, and all sites are equally profitable. Under this scenario, there will be no relationship between site use and microhabitat, but the isodar will be significant as individuals distribute themselves through space to maximize their fitness (Morris, 1988). Both habitats are perceived equal, so the isodar should pass through the origin with a slope of one. This possibility too seems unlikely because enclosures differed in habitat structure, and the voles showed a clear habitat preference in at least one isodar.

Voles might also be habitat specialists, but assess and respond to habitat at a scale such that their use of sites is related to each habitat's mean site quality. The relationship between microhabitat and site use will again be non-significant even if the isodar is significant (Morris, 1988). This interpretation appears to be the best fit with meadow-vole habitat selection. The voles chose some microhabitats over others, but usually they based site use on mean habitat quality rather than on local variation.

One of the most intriguing results of this experiment is that meadow-vole capture frequencies were better predicted by large-scale indicators than by fine-scale differences in microhabitat. So why should voles express a clear pattern of habitat selection at one scale and not at a smaller one? Theory tells us that if individuals are free to choose among sites and have perfect knowledge of their surrounding environment (ideal free distribution; Fretwell & Lucas, 1969), they will be distributed so that density matches resource distributions (Morris, 1994). Animals may, however, undermatch resources (use high quality patches less frequently than expected) when they have limited knowledge of site

quality (Abrahams, 1986; Ranta *et al.*, 1999) and when there is strong interference that forces subordinate individuals to use otherwise suboptimal sites (ideal despotic distribution; Fretwell & Lucas, 1969; Sutherland, 1983).

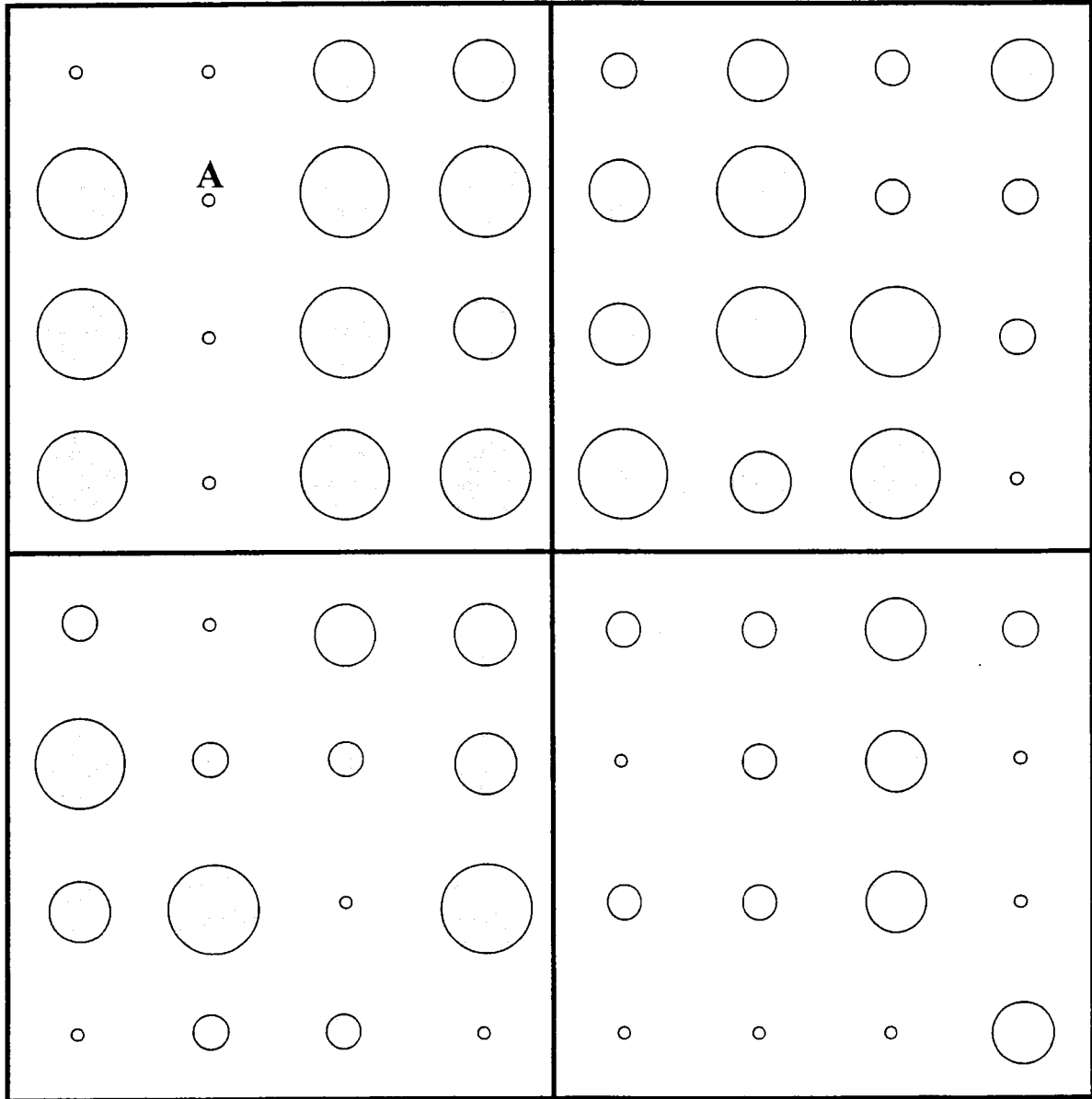
But it is also possible that meadow voles underused high-quality sites because the grain size of the Habitron environment is large. When the environment is fine-grained (neighbouring patches vary greatly), but has high spatial correlation, foragers tend to match patch quality no matter how limited their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

I illustrate this effect for the Habitron enclosures in Figure 4. Circles represent quartile PC1 scores at capture stations (PC1 was the only significant microhabitat variable that differentiated enclosures), where scores increase with increasing circle diameter. Imagine an individual at site 'A'. Any movement in a northward or southward direction places the animal in the same microhabitat (positive correlation), however, easterly or westerly movements place the animal in an extremely different microhabitat (negative correlation). In such a predictable fine-grained-environment, foragers should match site use with resource distributions (Ranta *et al.*, 2000). The spatial distribution of microhabitat in the Habitron, however, varies from enclosure to enclosure and unless animals have clearly directed movements that also vary by enclosure, their knowledge of the spatial variation in microhabitat will be relatively low (low spatial correlation). Site use will undermatch site quality (Ranta *et al.*, 2000).

FIGURE 4. The distribution of principal component 1 scores (as quartiles) illustrating low spatial correlation in experimental enclosures used to assess meadow-vole habitat selection in northern Ontario, Canada. Scores increase with increasing circle diameter.

Enclosure 1

Enclosure 2



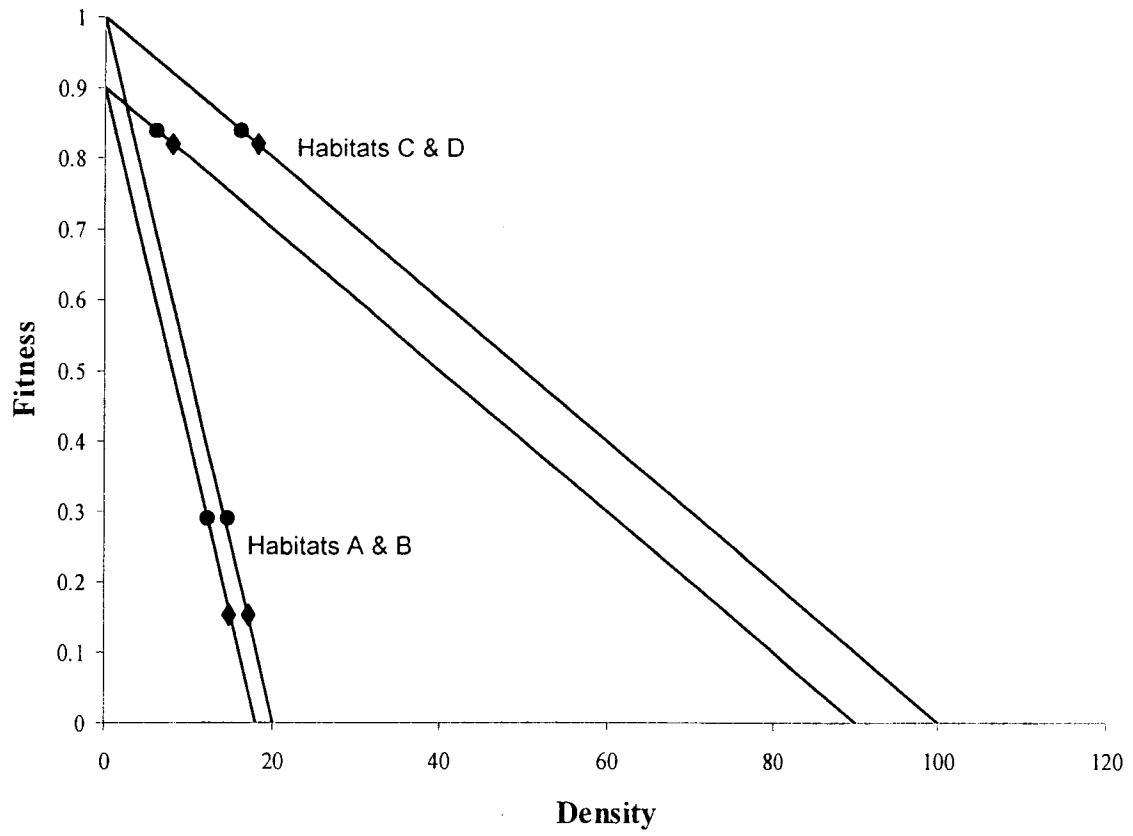
Enclosure 3

Enclosure 4

It is important to note, even when I re-analyzed the site characteristics at a different resolution by lumping cover variables, that the key result was the same. The frequency of site use by meadow voles was best revealed at the habitat scale. It is interesting however, 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. I interpret these results as evidence that enclosures actually did differ in site characteristics (Table II) that were obscured at a more coarse “resolution” of microhabitat. I echo Jorgensen (2004) in urging ecologists to be cautious of how they define and measure microhabitat.

Some readers may still be concerned that the variance in the isodars reveals relatively vague density-dependent habitat selection by voles that cannot be accounted for by undermatching. What else could cause vague density dependence? Imagine two pairs of habitats that have the same maximum fitness values, but different carrying capacities (Figure 5). When carrying capacity is small (habitats A and B), the change in fitness with population growth or decline is great. When carrying capacity is large (habitats C and D), the change in fitness for an equivalent growth or decline in population density is small. So, several individuals could change habitats and yet have relatively little effect on mean fitness. The resulting isodar would have substantially more variance than one generated in similar habitats with lower carrying capacities.

FIGURE 5. Hypothetical fitness functions for two pairs of habitats (A & B and C & D) that have the same maximum fitness, but differ in carrying capacities. For the same increase in population density (circles to diamonds), the reduction in fitness is much smaller when carrying capacities are large than when they are small.



I manipulated meadow-vole densities in paired enclosures from 2 to 22 animals (1 to 11 animals/ha). Meadow vole populations in other old-field enclosures in Illinois have been observed as high as 300 voles/ha (Lin & Batzli, 2001) and even higher in upper New York State (100-800 voles/ha; Pusenius & Schmidt, 2002). The fitness gains and penalties at the low densities in my experiments were likely negligible. It is hardly surprising, therefore, to find rather substantial variation in meadow-vole habitat selection. Even so, the significant isodars imply that voles can detect relatively small differences in fitness potential.

It is also possible that temporal changes in habitat can produce substantial variation around isodars. If two habitats are similar at the beginning of the growing season, but later diverge, animals may switch their habitat choices to account for the changes in fitness potential. This sort of temporal change should yield isodars with gradual changes in slope, a result that is inconsistent with my experiments on meadow-vole habitat selection.

Alternatively, vague density dependence may occur if animals simply “diffuse” down a density gradient. Habitat selection via diffusion (Levin, 1974; Flather & Bevers, 2002) implies density equalization that is independent of habitat quality and should yield only isodars with slopes not different from one and intercepts not different from zero. But the hypothesis fails because one of the isodars had a slope greater than one (Figure 3a). Meadow voles actively select habitat.

Individuals' habitat choice effects the abundance and distribution of species (Fretwell & Lucas, 1969; Rosenzweig, 1974, 1981; Morris, 1988), intra- and inter-specific species' interactions (Rosenzweig 1974, 1981; Morris 1988; Danielson, 1992; Abramsky *et al.*, 1997), resource distributions (Morris & Knight, 1996) and species' persistence through

space and time (Guissan & Zimmerman, 2000; Fahrig, 2001; Jonzén *et al.*, 2005). Habitat selection by meadow voles creates patterns of species abundance that are strong and undeniable, but the links to process can be nebulous. Ecologists must determine both the scale and mechanism driving habitat choices to successfully understand the intricate dynamics of animal populations and communities.

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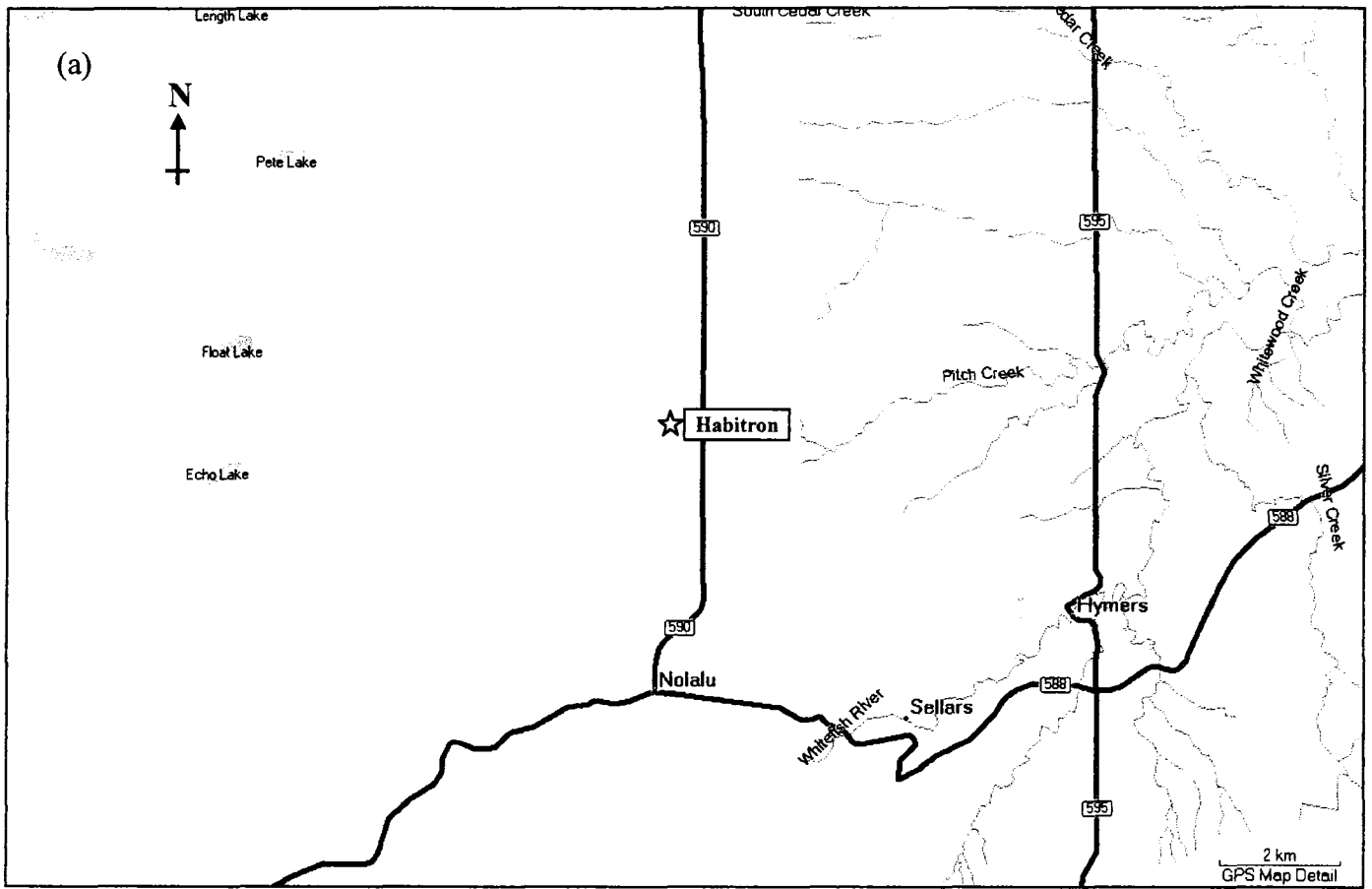
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APPENDIX I. (a) Location of the Lakehead University Habitron, outside Thunder Bay, Ontario. (b) The enclosures were situated in old-field habitat. Galvanized fences eliminated uncontrolled movement by meadow voles.



DMTI Spatial Inc., 2003



(b)



APPENDIX II. Intended density manipulations, minimum number of voles known alive, number of captures, and trap success of meadow voles in two pairs of enclosures.

Asterisks indicate days with very low trap success used to assess potential bias in the habitat isodars.

Supplemental Food	Target density (enclosures 1 & 2)	Target density (enclosures 3 & 4)	Minimum number of voles known alive	Number of captures	Trap success (%)
No (June 12 – July 15, 2005)	22	0	22	20	91
	20	2	22	21	95
	18	4	18	16	89
	16	6	18	16	89
	14	8	18	13	72
	12	10	18	12	67
	10	12	17	14	82
	8	14	17	13	76
	6	16	17	12	71
	4	18	17	11	65
	2	20	17	9*	53
0	22	17	12	71	
Yes (July 21 – August 29, 2005)	22	0	22	21	95
	20	2	22	20	91
	18	4	22	14	64
	16	6	22	16	73
	14	8	20	14	64
	12	10	19	14	64
	10	12	19	9*	47
	8	14	19	16	84
	6	16	19	17	89
	4	18	19	13	68
	2	20	19	16	84
0	22	19	13	68	

APPENDIX III. Correlation coefficient matrix (a) and a description (b) of the 28 candidate habitat (site characteristic) variables. Highly skewed variables and those with coefficients less than 0.25 (shaded) were deleted from principal components analysis.

(a)

	Tr Pr	Ta Of	So Sp	Ac Mi	As Ci	Fr Vi	Ch Le	Se Gr	Tr Re	Vi Am	Mat	H1	H2	H3	H4	H5	H6	H7	Pr Vi	Al Vi	Co St	Ro Ac	Pr Pe	Ru Id	Am Sp	Sa Sp	Pi Re	Ab Ba	
Tr Pr	1.00																												
TaSp	0.37	1.00																											
SoSp	-0.23	0.00	1.00																										
AcMi	0.37	0.16	-0.40	1.00																									
AsCi	0.13	0.08	-0.13	0.19	1.00																								
FrVi	0.18	0.08	-0.34	0.30	0.20	1.00																							
ChLe	-0.10	-0.09	-0.05	0.07	-0.01	0.08	1.00																						
SeGr	-0.45	-0.33	-0.07	-0.09	-0.19	-0.08	0.12	1.00																					
TrRe	0.25	0.01	-0.31	0.32	0.09	0.02	-0.08	-0.13	1.00																				
ViAm	-0.03	0.02	-0.13	0.14	0.06	0.24	0.00	-0.04	-0.02	1.00																			
Mat	0.13	0.20	0.01	0.24	-0.23	0.10	-0.02	0.09	0.02	0.15	1.00																		
H1	0.30	0.15	-0.35	0.48	0.17	0.41	0.05	-0.04	0.17	0.19	0.24	1.00																	
H2	0.23	0.29	-0.23	0.29	-0.04	0.24	0.00	-0.02	0.16	0.16	0.31	0.57	1.00																
H3	0.09	0.15	0.30	0.11	-0.08	-0.19	-0.11	-0.10	0.05	-0.10	0.19	0.13	0.40	1.00															
H4	-0.17	0.00	0.41	-0.09	-0.08	-0.26	-0.04	0.05	-0.11	-0.16	0.09	-0.07	0.09	0.66	1.00														
H5	-0.25	-0.07	0.40	-0.20	-0.12	-0.25	-0.14	0.07	-0.18	-0.21	0.06	-0.28	-0.10	0.43	0.74	1.00													
H6	-0.38	-0.13	0.33	-0.25	-0.08	-0.24	-0.04	0.17	-0.31	-0.18	-0.01	-0.34	-0.16	0.25	0.55	0.78	1.00												
H7	-0.38	-0.13	0.31	-0.28	-0.06	-0.18	-0.12	0.07	-0.32	-0.18	-0.12	-0.36	-0.23	0.15	0.41	0.65	0.82	1.00											
PrVi	-0.23	0.00	0.10	-0.28	0.02	-0.13	-0.07	0.05	-0.17	-0.14	-0.21	-0.40	-0.29	-0.13	0.10	0.24	0.28	0.31	1.00										
AlVi	-0.51	-0.21	0.46	-0.45	-0.11	-0.28	-0.07	0.24	-0.37	-0.26	-0.22	-0.55	-0.33	0.04	0.38	0.55	0.64	0.72	0.38	1.00									
CoSt	-0.20	-0.06	-0.12	-0.08	0.01	0.08	0.05	0.11	-0.10	0.17	-0.14	0.04	-0.03	-0.01	0.05	0.12	0.15	0.10	0.01	0.00	1.00								
RoAc	-0.16	-0.13	-0.01	-0.05	-0.02	-0.01	0.08	0.16	-0.43	-0.03	-0.08	0.00	0.03	-0.03	0.04	0.02	0.05	0.09	-0.09	0.01	0.01	1.00							
PrPe	0.01	0.00	-0.02	0.02	0.02	-0.07	0.12	-0.04	-0.06	-0.05	0.02	0.04	-0.11	0.01	0.05	-0.02	0.04	0.04	-0.03	-0.07	0.02	-0.02	1.00						
RuId	-0.21	-0.02	0.23	-0.17	-0.13	-0.17	-0.03	0.08	-0.13	-0.10	0.11	-0.17	0.06	0.26	0.30	0.29	0.22	0.19	0.16	0.23	-0.05	-0.02	-0.05	1.00					
AmSp	0.03	-0.03	-0.11	0.04	0.10	0.01	-0.05	0.00	0.05	0.00	0.01	0.07	-0.09	-0.08	-0.12	-0.06	-0.08	-0.01	0.16	-0.04	0.05	-0.06	0.15	-0.05	1.00				
SaSp	-0.26	-0.02	0.21	-0.33	0.06	-0.25	-0.05	-0.03	-0.23	-0.11	-0.19	-0.15	-0.12	0.08	0.16	0.18	0.15	0.25	0.25	0.17	0.17	0.11	-0.08	0.11	0.07	1.00			
PiRe	0.43	0.28	-0.38	0.27	0.11	0.28	0.01	-0.23	0.17	0.11	-0.09	0.27	0.17	-0.15	-0.29	-0.32	-0.31	-0.29	-0.21	-0.42	-0.08	-0.07	0.01	-0.20	0.00	-0.28	1.00		
AbBa	0.00	-0.03	0.02	0.00	0.02	-0.03	0.17	0.01	-0.08	-0.06	-0.02	-0.06	0.03	0.07	0.06	-0.06	-0.05	-0.04	-0.02	0.01	-0.06	0.20	0.10	-0.03	-0.01	-0.03	-0.07	1.00	

(b)

Site Characteristic	Description
TrPr ¹	Percent cover by <i>Trifolium pratense</i>
TaSp ¹	Percent cover by <i>Taraxacum spp.</i>
SoSp ¹	Percent cover by <i>Solidago spp.</i>
AcMi ¹	Percent cover by <i>Achillea millefolium</i>
AsCi ¹	Percent cover by <i>Aster ciliolatus</i>
FrVi ¹	Percent cover by <i>Fragaria virginiana</i>
ChLe ¹	Percent cover by <i>Chrysanthemum leucanthemum</i>
GrSe ¹	Percent cover by grasses/sedges
TrRe ¹	Percent cover by <i>Trifolium repens</i>
ViAm ¹	Percent cover by <i>Vicia americana</i>
Mat ²	Mean depth of litter (cm)
H1 ³	Percent cover at .125m
H2 ³	Percent cover at .25m
H3 ³	Percent cover at .50m
H4 ³	Percent cover at .75m
H5 ³	Percent cover at 1.00m
H6 ³	Percent cover at 1.25m
H7 ³	Percent cover at 1.50m
PrVi ⁴	Percent cover by <i>Prunus virginiana</i>
AlVi ⁴	Percent cover by <i>Alnus viridis</i>
CoSt ⁴	Percent cover by <i>Cornus stolonifera</i>

RoAc ⁴	Percent cover by <i>Rosa acicularis</i>
PrPe ⁴	Percent cover by <i>Prunus pensylvanica</i>
RuId ⁴	Percent cover by <i>Rubus idaeus</i>
AmSp ⁴	Percent cover by <i>Amelanchier spp.</i>
SaSp ⁴	Percent cover by <i>Salix spp.</i>
PiRe ⁴	Percent cover by <i>Pinus resinosa</i>
AbBa ⁴	Percent cover by <i>Abies balsamea</i>

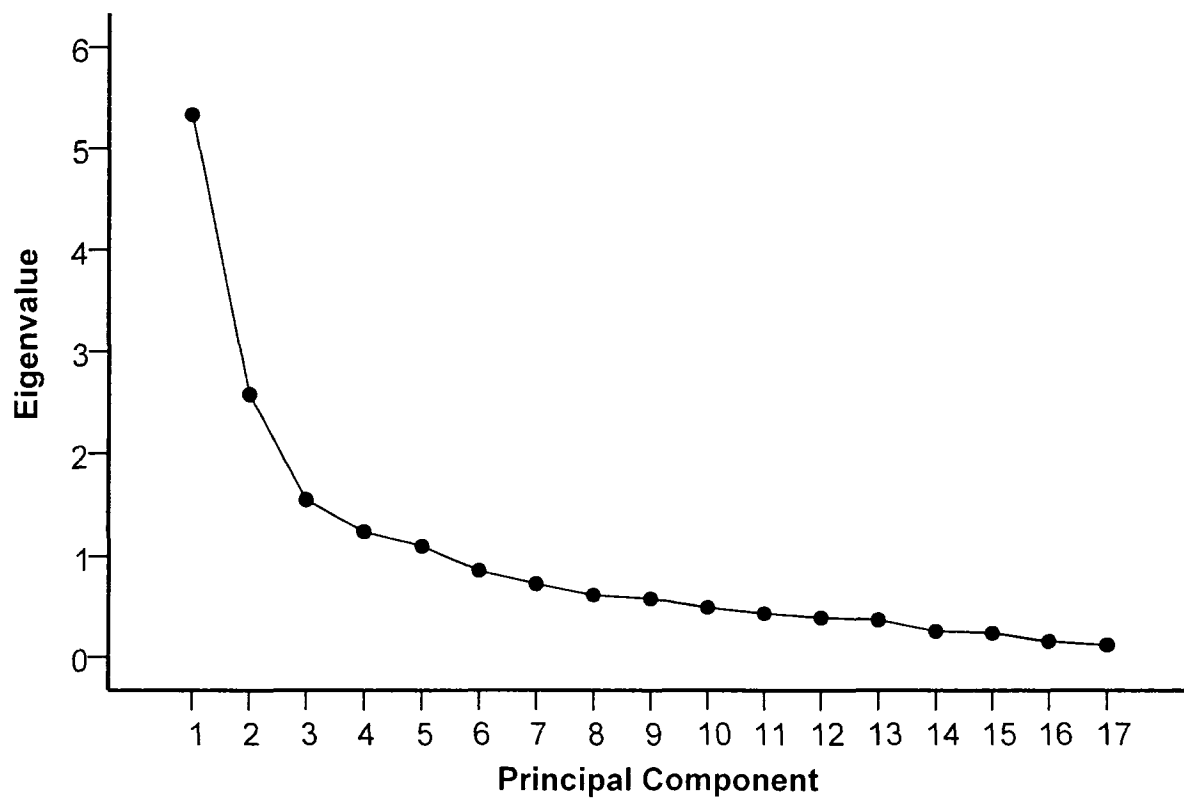
1. Arcsine square root of mean percent cover of sedges, grasses, and herbaceous plants in 25 x 50 cm quadrats placed East and West of the trap lines within 1 m at each station.
2. Square root mean depth of plant litter measured in each corner of the 25 x 50 cm quadrats.
3. Square root of mean percent cover of 10 x 20 cm checkered boards measured on both East and West sides of the 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 & Morris, 2000).
4. Arcsine square root of mean percent cover of shrubs and trees in four 2 x 2 m quadrats centered at each trap station.

APPENDIX IV. List of the habitat variables included in the principal components analysis (PCA), a description of each variable, and the correlation of each variable with the first three principal components. Variables are listed in descending order of their correlation with PC1.

Variable	Description	Correlation		
		PC1	PC2	PC3
H5 ¹	Percent horizontal cover at 1.00m	.867	-.049	-.112
H4 ¹	Percent horizontal cover at .75m	.853	.170	.001
H6 ¹	Percent horizontal cover at 1.25m	.779	-.162	-.287
H7 ¹	Percent horizontal cover at 1.50m	.678	-.290	-.261
H3 ¹	Percent horizontal cover at .50m	.670	.417	.260
AlVi ²	Percent cover by <i>Alnus viridis</i>	.591	-.486	-.386
SoSp ³	Percent cover by <i>Solidago spp.</i>	.588	-.383	.102
Mat ⁴	Litter depth (cm)	.134	.534	.039
TaSp ³	Percent cover by <i>Taraxacum spp.</i>	.066	.172	.650
H2 ¹	Percent horizontal cover at .25m	.051	.769	.147
GrSe ³	Percent cover by grasses/sedges	.013	.149	.803
AcMi ³	Percent cover by <i>Achillea millefolium</i>	-.224	.626	.170
TrPr ³	Percent cover by <i>Trifolium pratense</i>	-.247	.253	.724
H1 ¹	Percent horizontal cover at .125m	-.250	.777	.076
TrRe ³	Percent cover by <i>Trifolium repens</i>	-.263	.271	.211
FrVi ³	Percent cover by <i>Fragaria virginiana</i>	-.364	.389	-.042
PiRe ²	Percent cover by <i>Pinus resinosa</i>	-.399	.205	.418

1. Square root of mean percent cover of 10 x 20 cm checkered boards measured on both East and West sides of the 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 & Morris, 2000).
2. Arcsine square root of mean percent cover of shrubs and trees in four 2 x 2 m quadrats centered at each trap station.
3. Arcsine square root of mean percent cover of sedges, grasses, and herbaceous plants in 25 x 50 cm quadrats placed East and West of the trap lines within 1 m at each station.
4. Square root mean depth of plant litter measured in each corner of the 25 x 50 cm quadrats.

APPENDIX V. Scree plot of the eigenvalues associated with the principal components from the PCA on 17 habitat variables measured at 240 live-trapping stations in the Lakehead University Habitron. The first three principal components, accounting for 56% of the total variation in habitat, were retained.



APPENDIX VI. Boxplot and whiskers illustrating principal component 1 scores for four experimental enclosures used to assess meadow-vole habitat selection in the Lakehead University Habitatron, northern Ontario, Canada.

