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LIFE ON THE EDGE:

THE ROLE OF HABITAT SELECTION ON VOLE DENSITY NEAR

FOREST BOUNDARIES

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ABSTRACT

Theories of density-dependent habitat selection predict pronounced gradients of population density near habitat edges. Population density in high-quality habitats should decline toward edges with lower-quality habitats, and population density in low-quality habitats should increase toward boundaries with higher-quality habitats. This pattern should be more obvious near abrupt boundaries than near ecotones where habitats gradually grade one into the other. I tested the predictions using the density of red-backed voles (Clethrionomys gapperi) along eight belt transects crossing edges between natural and anthropogenic boreal forest habitats in northwestern Ontario. Transects were classified as having either a gradual (70 m to 90 m ecotone) or abrupt edge ($\leq$20 m ecotone). Vole density varied consistently between pairs of habitats, but there was no detectable gradient in density at either abrupt or gradual edges. The absence of an edge effect may be related to errors in the assessment of habitat quality by individuals confronted with a matrix of patch types near edges separating similar habitats. Another possibility is that an, as yet, unidentified agent or process alters the quality of red-backed vole habitats near boreal-forest edges.

Key Words: Clethrionomys, conservation, population density, ecotone, edge effect, forest boundaries, habitat selection, landscape, Ontario, spatial scale.

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INTRODUCTION

A founding principle of wildlife ecology and management states that habitat edges are 'beneficial' because individuals have access to more than one habitat or a greater diversity and supply of resources (Leopold 1933). The resulting increase in population density or species richness near edges (the edge effect) has become part of the folklore of conservation and applied ecology (e.g., Harris 1988, Yahner 1988, Odum 1993). Though few ecologists would promulgate Leopold's view, there remains a dogma associated with edge effects as exemplified by terms such as 'negative' edge effects (Mills 1995) for situations where small mammal density declines near habitat boundaries (e.g., Walters 1991, Hansson 1994, Mills 1995). Similar negative effects are implied by observations that avian nest parasitism and predation increase near habitat edges (review by Paton 1994).

The polar interpretations of edge effects may originate because studies of habitat edges have seldom addressed, explicitly, the ecological processes that create spatial patterns in density. I find it curious that such an important feature of landscape composition influencing the spatial distribution and abundance of species lacks a formal theoretical framework. I begin to build the framework by applying and expanding theories of patch use and density-dependent habitat selection (Fretwell and Lucas 1970, Rosenzweig 1974, 1979, 1981, 1991, Charnov 1976, Morris 1988, 1992, Pulliam and Danielson 1991) to spatial gradients crossing habitat edges. I phrase the predictions in the context of abrupt versus gradual edges and simultaneously develop

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field and analytical protocols necessary to test the predictions. I provide examples of the protocols, and of the tests, with data on red-backed voles (Clethrionomys gapperi) occupying areas near ecotones between undisturbed conifer forest and adjacent habitats either dominated by deciduous trees or recovering from clearcut harvesting. Red-backed voles occupy virtually all terrestrial boreal-forest habitats and are suitable subjects for tests of edge effects that may otherwise be biased if a species with more restrictive habitat tolerances is used (e.g., a forest interior species may exploit only one side of the edge).

Habitat selection across abrupt and gradual boundaries

Theories of density-dependent habitat selection assume that per capita fitness declines with increased population density (Fretwell and Lucas 1970; Fretwell 1972; Rosenzweig 1974, 1979, 1981, 1991) and that individuals preferentially occupy habitats in a way that maximizes their evolutionary fitness. Consider the situation where a high-quality habitat (A) shares an abrupt boundary with a low-quality habitat (B) and individuals adopt an evolutionarily stable strategy (ESS) that maximizes mean fitness (i.e., an ideal free distribution). Habitat B will not be selected until a threshold density (t) in habitat A reduces the fitness of individuals to the maximum obtainable in habitat B (Figure 1). For population densities greater than the threshold, the density in each habitat will be adjusted such that the fitness is the same in both habitats (Fretwell and Lucas 1970, Rosenzweig 1974, 1981). It should be possible to use the ESS of habitat selection to predict the pattern of density across abrupt and gradual boundaries.

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Figure 1: Fitness-density graph showing the threshold density (t) in the high-quality habitat (A) where per capita fitness has been decreased to the maximum fitness obtainabie in the low-quality habitat (B).

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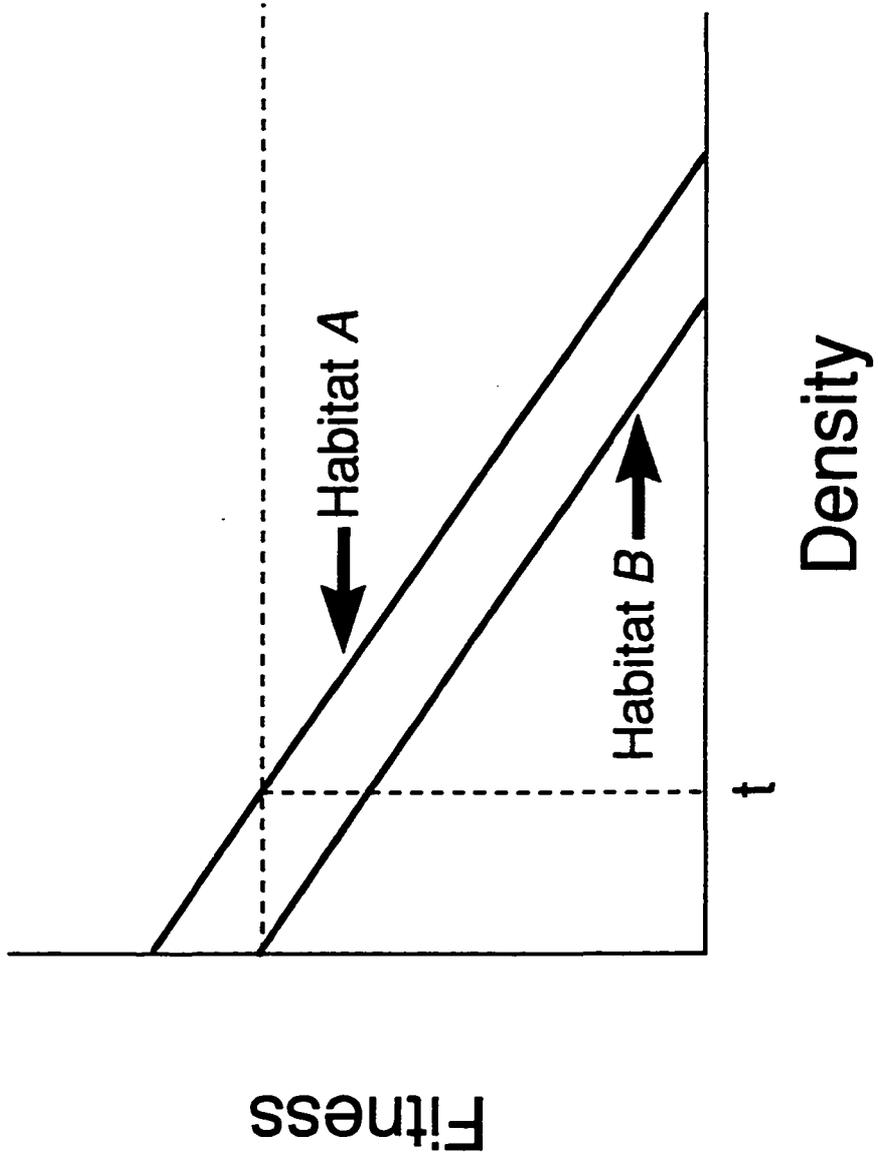
Imagine that each habitat (*A* and *B*) is composed of homogeneous patches (*a* and *b* respectively). The *a* patches are more valuable to foraging individuals (e.g., higher resource renewal rates, higher-quality resources, lower risks of predation) than *b* patches. If individuals forage in a way that maximizes their net energy gain and if energy obtained from foraging is strongly associated with fitness, the ratio of *a* to *b* patches in an area will effect spatial variation in population density. To see this, note that an individual should forage in both *a* and *b* only when

$$\ln W_a \leq \ln W_b (1 + t_m/t_a) \tag{1}$$

where $\ln W_i$ is the net fitness while foraging in patch *i*, t_m is the time spent searching for foraging patches, and t_a is the time spent harvesting resources in patches of *a* (Rosenzweig 1974, 1981, 1985). The relative abundance of the patches will influence t_a and whether both should be foraged in. The proportions of *a* to *b* will depend on the nature of the habitat boundary and on the location of an individual's foraging range (Figure 2). If patch quality within habitats and population density between habitats are constant, average fitness will be higher for individuals whose foraging ranges are located in areas with a large proportion of *a* patches (e.g., on the habitat *A* side of the boundary) than for individuals foraging in areas with a lower proportion of *a* patches (habitat *B*). Some individuals will be less likely to use both patches than will others. But if net fitness declines with increasing density and habitat selection is an ESS, the occupation of both patches depends not only on their quality, but also on the

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Figure 2: Diagrammatic representation of variation in high-quality (shaded outlines) and low-quality (unshaded outlines) patches near abrupt (top) and gradual (bottom) habitat boundaries. Circles represent equal sample areas. Foraging ranges centred on the habitat A/ecotone interface will have a larger proportion of high-quality patches than ranges centred on the abrupt habitat boundary. Foraging ranges centred on the habitat B/ecotone interface will have a smaller proportion of high-quality patches. The schematics assume that the density, size distribution, and quality of patches do not vary near edges or between gradual and abrupt boundaries.

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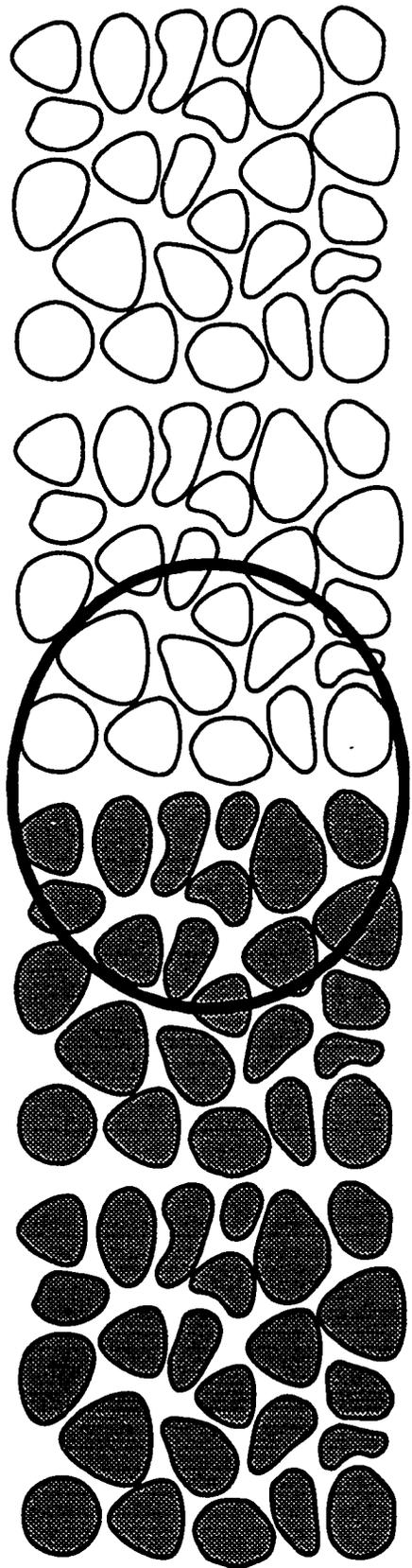
Habitat *B*

Habitat *A*
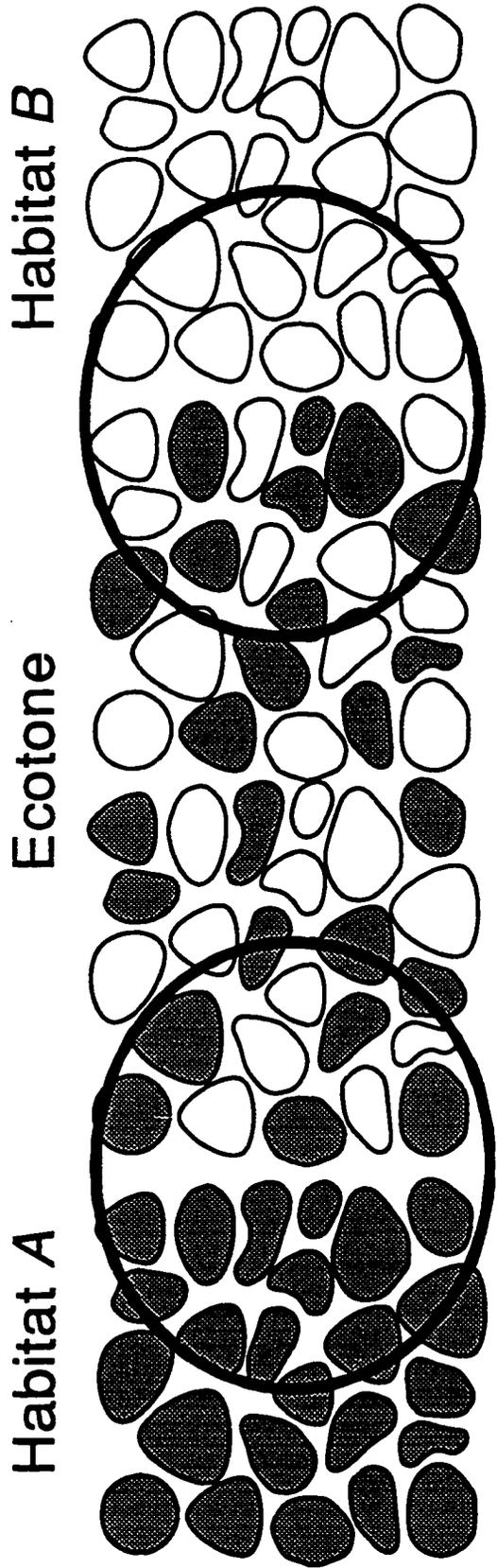
Habitat *B*

Ecotone

Habitat *A*

relationship between quality and population density. Individuals living in areas with a high proportion of *a* patches will exist at higher density than those in areas with a smaller proportion of the same high-quality patches (Morris 1992). The fitness that individuals can expect to gain from each patch will be the same and they should use patches of each type. Population density will vary gradually across the habitat boundary.

Now imagine that habitats *A* and *B* are separated by a wide ecotone consisting of a mixture of the two patch types. Foraging ranges centred on the interface between habitat *A* and the ecotone will contain a higher proportion of *a* patches than ranges centred on the abrupt boundary (Figure 2). Average population density will be greater near the gradual habitat 'boundary' than near the abrupt one. Note that the highest density will be in areas where foraging ranges consist of *a* patches only (pure habitat *A*).

Similarly, foraging ranges centred on the interface between habitat *B* and the wide ecotone will contain a smaller proportion of *a* patches than ranges centred on an abrupt boundary (Figure 2). The corresponding population density will be lower than near an abrupt boundary. The lowest density will occur in areas where foraging ranges consist of *b* patches only (pure habitat *B*).

Note that the habitat selection theory predictions of population density may be different if the density, size distribution, or quality of foraging patches changes near the boundary between habitats. In addition, the predictions assume that vole density responds to the mix of patches an individual encounters rather than the quality of

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individual patches.

A design to test for edge effects

Does the density of red-backed voles change near habitat edges? Recall that habitat selection theory predicts reduced vole density within the high-quality habitat and inflated vole density within the low-quality habitat near edges. The density pattern will also be more pronounced near abrupt compared to gradual boundaries. In an analysis of variance (ANOVA) design, the habitat selection predictions lead to a three-way interaction of habitat (high or low quality), distance (distance from the ecotone), and boundary type (abrupt or gradual). I provide a rigorous test of the predictions by: 1) estimating the ecotone location and width between adjacent boreal-forest habitats, 2) determining the high and low-quality habitat , 3) testing the assumption that vole density responds to the mix of patches an individual encounters, and 4) testing for distance related interactions of red-backed vole density along transects bisecting the abutting forest habitats.

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METHODS

Field sites and data collection

I established eight belt transects across habitat edges in boreal forest habitats near Raith, Ontario (48°55'N, 89°55'W) during the summers of 1994 and 1995. Four transects crossed edges between conifer forest and contiguous cutover habitats (approximately 15-years old). Conifer habitats consisted of mature jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), black spruce (*P. mariana*), a relatively open understory, and a ground cover dominated by mosses (e.g., *Pleurozium shreberi, Ptilium crista-castrensis, Hylacomnium splendens*). Cutover habitats ranged from dense to sparse jack pine with a grassy ground cover (especially *Calamagrostis canadensis*). The remaining four transects crossed boundaries between conifer and deciduous forest. Deciduous forests were composed primarily of trembling aspen (*Populus tremuloides*), balsam poplar (*P. balsamifera*), white birch (*Betula papyrifera*), and a dense shrub understory dominated by alder (*Alnus viridis*), mountain maple (*Acer spicatum*), and beaked hazel (*Corylus cornuta*). Deciduous and conifer forests shared a common history; both originated following a fire that burned the entire study area in 1911.

I set two parallel live-trapping lines 10 m apart perpendicular to, and centred on, apparent habitat edges for each transect. Each trapping line consisted of forty stations set at 10 m intervals (Figure 3).

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Figure 3: Schematic of a belt transect used to assess rodent densities and habitat variation with respect to ecotones separating high-quality (*A*) and low-quality (*B*) boreal forest habitats in northwestern Ontario. Dashed lines represent ecotone boundaries and 'X's correspond to live-trap and habitat sampling stations.

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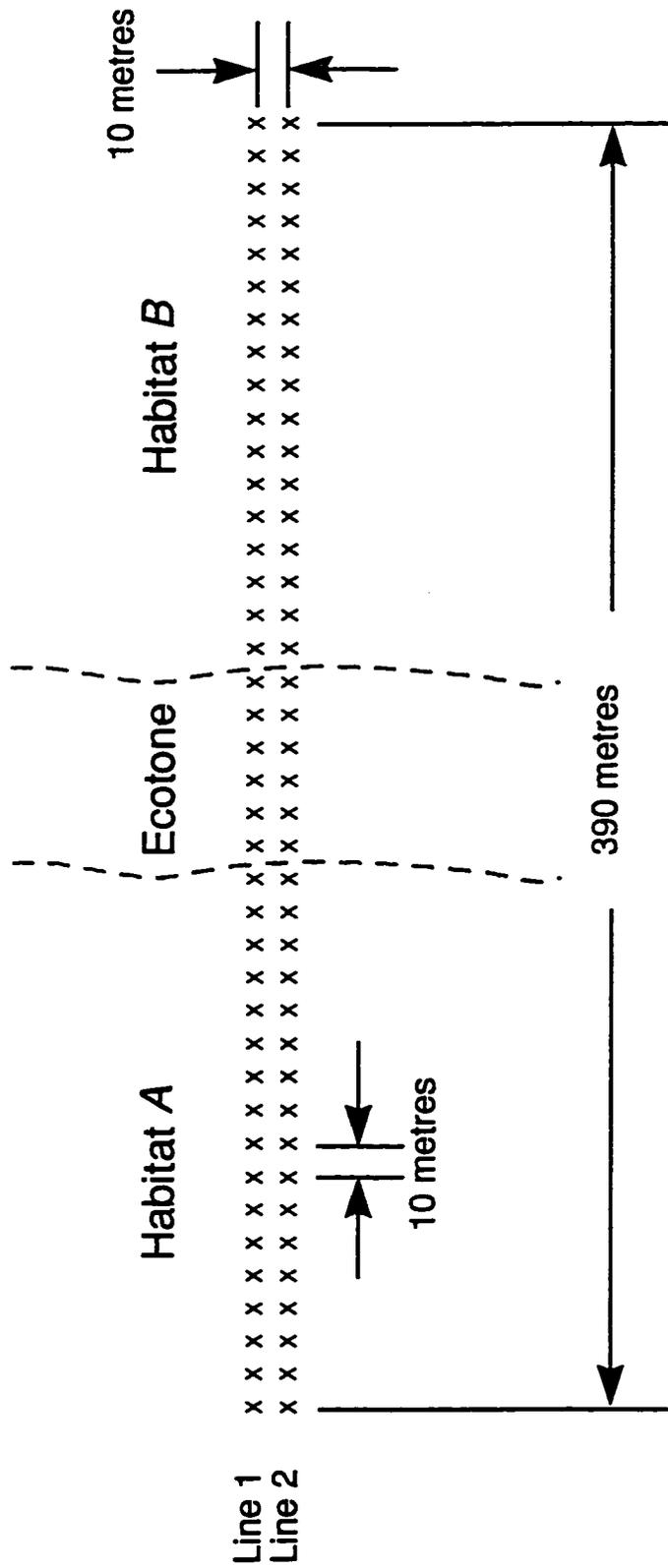
I trapped each transect at two week intervals for at least four weeks between June 8 and August 12 in 1994 or between May 29 and September 8 in 1995. I set a single Sherman live-trap baited with oats, a slice of potato, and cotton nesting at each station and checked each trap for two consecutive morning and evening trap runs. All captured rodents were individually marked, measured (body length, mass), sexed, and released.

I quantified structural components of vegetation known to be important predictors of small-mammal density (Rosenzweig and Winakur 1969, M'Closkey and Fieldwick 1975, M'Closkey and Lajoie 1975, Morris 1979, 1984, 1987, 1989, Adler 1985, 1987, Wywialowski and Smith 1988) at each station (Table 1). I measured horizontal foliage profiles (Q_1-Q_5) by estimating the percentage cover by vegetation of a 10 cm by 20 cm 'board' located 3 m from the station at heights of 0.125, 0.25, 0.5, 1.0, and 1.75 m above ground level (technique adapted from Rosenzweig and Winakur (1969) and Morris (1979)). Measurements were taken at the four cardinal directions relative to an initial random heading and the mean calculated to yield a single value for each station. I measured the depth of litter (structurally intact dead vegetation) at the four corners of a 4 m by 4 m randomly oriented plot, centred at the station. I estimated habitat composition by the percentage cover by shrubs, forbs, grass, wood, moss, litter, rock and soil, and ferns and club mosses at each station within the 16 m^2 plot. Finally, I recorded the number of stumps and fallen logs, and the diameter at breast height (dbh > 4 cm, converted to basal areas) for all tree species within a radius of 3 m from each station.

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Table 1: Variables used to quantify habitat structure and composition at 640 live-trap stations in boreal-forest habitats in northwestern Ontario.

Variable	Description
Q_1	mean quantity of vegetation at 0.125 m above ground level
Q_2	mean quantity of vegetation at 0.25 m above ground level
Q_3	mean quantity of vegetation at 0.5 m above ground level
Q_4	mean quantity of vegetation at 1.0 m above ground level
Q_5	mean quantity of vegetation at 1.75 m above ground level
FHD	foliage height diversity, $(1/\Sigma P_i^2$; where $P_i=Q_i/\Sigma Q_i)$
Mat	mean depth of litter (mm of dead but structurally intact vegetative matter)
Numcon	number of conifer trees within 3.0 m radius
Numdec	number of deciduous trees within 3.0 m radius
Areacon	summed basal area of all conifer trees within 3.0 m radius
Areadec	summed basal area of all deciduous trees within 3.0 m radius
Stumps	number of stumps within 3.0 m radius
Fallen	number of fallen trees within 3.0 m radius
ShrubC	percentage cover by shrubs within 16 m^2
ForbC	percentage cover by forbs within 16 m^2
GrassC	percentage cover by grasses within 16 m^2
WoodC	percentage cover by wood within 16 m^2
MossC	percentage cover by mosses within 16 m^2
LitterC	percentage cover by litter within 16 m^2
BarrenC	percentage cover by rock and soil within 16 m^2
FernC	percentage cover by ferns and club mosses within 16 m^2

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Analysis

I began my analyses of edge effects by developing a rigorous and objective assessment of the location and width of the ecotone between adjacent habitats (Table 2). My protocol summarized habitat composition along each transect by principal components analysis (PCA). I excluded variables from each PCA with the lowest measure of sampling adequacy until the overall Kaiser-Meyer-Olkin measure of sampling adequacy was greater than 0.75 (Norušis 1994a: Procedure FACTOR). I retained principal components (PCs) with eigenvalues greater than 1.6, which corresponded, in each case, to a substantial change in the variance explained by successive PCs.

I tested for edge effects using relative densities of <u>Clethrionomys</u> estimated by the minimum number of individuals known alive (MNA, Hilborn et al. 1976) during the final two weeks of trapping on each transect. The final two weeks provided adequate sampling to acquire suitable density estimates for analysis and reduced complications caused by individuals moving their foraging ranges from one sample period to another. I would have preferred to analyze temporal measures of density in a repeated measures analysis, but low vole density on some transects would have produced an unbalanced design (a balanced design is necessary for repeated measures ANOVA). The MNA can produce biased density estimates (Efford 1992), but for several samples of boreal-forest rodents it is highly correlated ($r > 0.9$) with mark-recapture estimates of population density (Morris 1996). The densities of other species were too low for a reliable assessment of patterns in population density. I excluded

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Table 2: A protocol to determine the location and width of habitat ecotones.

Step	Action
1	Locate transects perpendicular to an apparent edge between adjacent and homogeneous habitats and quantify habitat at each sampling station.
2	Ordinate the habitat data array for each transect to derive simplified and independent habitat variables (I used principal components analysis with varimax rotations (Norušis 1994a: Procedure FACTOR)).
3	Divide the transect in two at the apparent habitat edge and select stations in the homogeneous central portion of each segment (stations 5-12 and stations 29-36 in my study) to represent each habitat.
4	Use MANOVA (I chose discriminant function analysis (Norušis 1994a: Procedure DISCRIMINANT)) on the unrotated ordination scores of the selected stations to differentiate between the two habitats.
5	Choose one of the two habitats and, using the results of step 4, calculate the probability that each station belongs to that habitat (I used the discriminant function scores).
6	If using belt transects, calculate the mean classification probabilities of stations on adjacent lines (this step forces the ecotone to 'cut' the transect at right angles; alternatively, merge the ordination scores before MANOVA).

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Table 2 continued

Step	Action
7	Define ecotone boundaries to occur where the classification probabilities of consecutive stations fall below a level corresponding to a discontinuity in the data (I chose 0.67 and 0.33 to divide the probability into three equal groups (one for each habitat and one for the ecotone, $P \geq 0.67$, $P \leq 0.33$, $0.67 > P > .33$ respectively)).
8	Define ecotone width as the distance between ecotone boundaries.

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stations at the ends of each transect (stations 1 and 40 of both parallel trapping lines) to reduce biases associated with unequal rodent sampling by terminal traps (van Horne 1982). I created subplots consisting of two by two live-trap grids (10 m X 10 m) along each transect to calculate density.

I assumed that density, or the pattern of density, is a reliable indicator of average habitat quality at the scale of my habitat classifications (caused by density-dependent habitat selection). I identified a high and low-quality habitat for each transect using a t-test on densities estimated for stations paired across adjacent trap lines. I could not use my larger sub-plots for this analysis because sample sizes within transects would be too small to detect differences. I confirmed, nevertheless, that mean densities at the 10 m X 10 m subplot scale were consistent with the results of each t-test. I excluded stations ≤ 60 m from calculated ecotone boundaries to minimize sampling the zone where densities should respond to the mix of patches at edges. Sixty metres represents the approximate diameter of a circular red-backed vole home-range (0.28 hectares, Blair 1941, Morris 1955, Beer 1961, Tallmon and Mills 1994).

The predictions I test here assume that variation in population density at edges occurs primarily because the mix of patches varies rather than the quality of individual patches. If this assumption is valid, population density in different habitats is unlikely to be significantly correlated with small-scale variation in habitat. If the assumption is violated, patch quality and population density should covary and I would need to refine my predictions to compensate for differences in patch quality near habitat edges. I tested the assumption using a stepwise multiple regression (Morris 1987, 1989,

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Norušis 1994a: Procedure REGRESSION). I used the 10 m X 10 m subplot estimates of density and calculated the arithmetic means for each of the 21 habitat variables in each subplot to represent patch quality. The analysis implicitly assumes that my measurements correspond primarily to values for individual foraging patches rather than a mix of patch types. I pooled data from all transects, repeated the PCA to summarize small-scale variation in habitat, and analyzed for an association between patch quality and density using the linear model

$$N = a_0 + b_1 PC_1 + b_2 PC_2 + ... + b_n PC_n + b_{n+1} D_1 + b_{n+2} D_2 + ... + b_{n+m} D_m + e \qquad (2)$$

where N is the predicted red-backed vole density, PCs are principal component scores summarizing the habitat variables, Ds are indicator variables coded 0 or 1 representing the three habitats (conifer forest, deciduous forest, cutover), and e is normally distributed error variation (Morris 1989). I omitted ecotone stations from this analysis because it is impossible to classify the habitat to which they belong. Prior to the regression, I verified that my measurements of habitat (principal component scores) were different among the three habitats using discriminant functions analysis (Norušis 1994a: Procedure DISCRIMINANT). Otherwise, I would have no valid test of the assumption of homogeneous patches.

I tested for edge effects with a two by two by six repeated-measures analysis of variance on the minimum number of rodents known alive in each 10 m X 10 m subplot (Norušis 1994b: Procedure REPEATED MEASURES). Repeated-measures

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designs are most frequently used for the analysis of temporal data (e.g., von Ende 1993), but are also suited to the analysis of spatial effects (Morris In Press). My design treated transects as subjects, boundary type (abrupt or gradual) as a between-transects factor, and habitat (high or low density) and distance from the ecotone (six classes) as within-transects factors. Positive or negative edge effects would be revealed by a significant distance effect on density (density is different away from the ecotone than it is near the habitat-ecotone interface). Differences in edge effects between abrupt and gradual boundaries would produce a significant interaction between boundary type and distance. Patterns in density consistent with density-dependent habitat selection would yield a significant habitat by distance interaction (if boundary type is not important) or a three-way habitat by boundary by distance interaction.

I was concerned that my emphasis on patterns of density near ecotone boundaries might reduce my chances of detecting edge effects. Population densities near gradual boundaries should be more similar to those in pure habitat than population densities near the abrupt boundaries. I repeated the ANOVA with distance classes calculated from the boundary between habitats. I estimated the habitat boundary as the midpoint between the first and last station where the classification probability was less than and greater than 0.5 respectively (the rule worked for even numbers of stations; when there was an odd number of stations in the ecotone the central one was grouped with the habitat corresponding to its classification probability). This protocol worked well for all transects except D4 and C4 where

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some stations were located near small openings in the interior of the conifer forests

(Appendix 1). I ignored such 'peculiar' stations when estimating the habitat boundary

for transects D4 and C4.

RESULTS

Ecotone location and width

Two to four principal components accounted for between 50 and 67 per cent of the habitat variation along each transect (Table 3). The first component generally revealed a gradient ranging from areas with a diverse foliage cover of tall shrubs to areas with a relatively open understory and low horizontal diversity. Additional components tended to describe clines between dense forests with a deep litter layer to open forests with a shallow litter layer (Appendix 2).

Two-group discriminant function analyses (DFA) demonstrated the ability of the extracted PCs to distinguish between habitats for every transect (Table 3). All DFAs were highly significant. Each DFA correctly classified the vast majority of paired stations (91 to 100% classification success, Table 3).

Calculated widths of ecotones represented two classes corresponding to abrupt ($\leq$20 m) and gradual edges (70 m to 90 m, Table 3, Appendix 1). Three of the four cutover/conifer contrasts had the narrowest ecotone width that I could detect with my protocol (the minimum sampling distance of 10 m). Contrary to my original field design, one cutover/conifer boundary was far more gradual than intended (transect C4, 70 m). Similarly, one conifer/deciduous boundary had a surprisingly abrupt boundary (transect D4, 20 m). The results from the two 'unusual' transects emphasize the importance of using objective criteria to identify the location of boundaries and the widths of ecotones.

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Table 3: Principal component (PC) and discriminant function summaries and ecotone width for transects crossing deciduous-conifer (D) and cutover-conifer (C) boundaries in northwestern Ontario.

Transect	Number of PCs extracted[a]	Habitat variance 'explained' (%)	Classification success (%)[b]	Estimated ecotone width (m)
D1	3	57.6	100	70
D2	2	50.6	100	70
D3	4	63.9	100	90
D4	4	66.9	93.75	20
C1	3	63.4	100	<10
C2	3	60.9	100	<10
C3	3	61.5	93.75	<10
C4	3	60.0	90.63	70

[a] - eigenvalues greater than 1.6; [b] based on discriminant scores, $P<.0001$ for all discriminant function analyses

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Patterns of density near habitat boundaries

Red-backed voles dominated the small-mammal community (Table 4) and their density was significantly higher in one habitat than in the other for seven of the eight transects (Table 5). Other species, including deer mice, were not abundant enough to test for edge effects. It is unlikely that any of these species seriously modify the density or habitat selection of red-backed voles (Appendix 3). Mean vole density was higher in deciduous habitat than in adjacent conifer forest (three of four comparisons). Habitat preference between conifer and adjacent cutover habitats (as indicated by density) was unpredictable (higher mean density in conifer on two transects, higher in cutover on two transects).

Differences in vole density between the two years of the study could affect my ability to detect differences between boundary types. I was unable to include annual effects in my repeated measures analysis of edge effects (to do so would create an unbalanced design), so I used a t-test to search for annual differences in voles captured in each type of habitat. Mean density in cutover habitat was significantly higher in 1994 than in 1995 (t_{31}=7.77, P<0.001). Only one cutover transect (C3, high vole density) was trapped in 1994 and may represent especially suitable vole habitat (Table 5). There was no significant annual change in population density for either deciduous (t_{30}=1.36, P=0.19) or conifer habitats (t_{66}=0.69, P=0.49). The fire-origin deciduous and conifer forests are more comparable than cutovers which have slightly different ages and somewhat different harvest and silvicultural histories that could create apparent annual differences in density that actually represent differences in habitat. I find no

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Table 4: Small-mammal captures (number of individuals in parentheses) during the final two census periods on transects crossing deciduous-conifer (D) and cutover-conifer (C) habitat boundaries near Raith, Ontario, 1994-1995. Cg = _Clethrionomys gapperi_, Pm = _Peromyscus maniculatus_, Ts = _Tamias striatus_, Tm = _Tamias minimus_, Ni = _Napaeozapus insignis_, Zh = _Zapus hudsonius_, Mp = _Microtus pennsylvanicus_, Mc = _Microtus chrotorrhinus_. There were negligible captures of six additional species (_Synaptomys cooperi_ 16(14), _Lepus americanus_ 6([a]), _Tamiasciurus hudsonicus_ 5([a]), _Sorex cinereus_ 6([a]), _Mustela erminea_ 5([a]), and _Glaucomys sabrinus_ 1(1)).

		Small-mammal species							
Transect	Year	Cg	Pm	Ts	Tm	Ni	Zh	Mp	Mc
D1	1994	141(38)	20(12)	17(8)	0(0)	2(2)	1(1)	2(2)	2(2)
D2	1994	115(29)	34(16)	17(10)	2(2)	0(0)	1(1)	4(4)	0(0)
D3	1995	143(42)	24(13)	23(9)	0(0)	9(8)	5(4)	0(0)	34(16)
D4	1995	82(31)	16(10)	70([a])	2(2)	2(2)	0(0)	0(0)	0(0)
C1	1995	76(28)	20(9)	16([a])	2(2)	0(0)	1(1)	6(5)	3(2)
C2	1995	52(18)	24(13)	5([a])	9(5)	0(0)	3(2)	9(4)	3(1)
C3	1994	148(35)	20(9)	7(4)	8(5)	1(1)	6(5)	11(2)	0(0)
C4	1995	38(12)	21(11)	18(6)	17(12)	0(0)	4(2)	0(0)	0(0)

[a] - number of individuals unknown because some rarely captured or large species were unmarked

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Table 5: Density of <u>Clethrionomys</u> <u>gapperi</u> between habitats for transects crossing deciduous-conifer (D) and cutover-conifer (C) habitat boundaries in northwestern Ontario.

Transect	Habitat	mean N^a	Habitat	mean N	t	*P*
D1	deciduous	4.13	conifer	1.73	2.98	.008
D2	deciduous	2.00	conifer	0.88	2.43	.026
D3	deciduous	4.22	conifer	1.75	3.00	.009
D4	deciduous	1.88	conifer	1.64	0.39	.703
C1	cutover	0.08	conifer	2.29	6.05	<.001
C2	cutover	0.62	conifer	1.62	2.35	.031
C3	cutover	2.83	conifer	1.38	2.23	.036
C4	cutover	1.50	conifer	0.31	2.64	.017

[a] - minimum number of individuals known alive at pairs of capture stations in two adjacent trap lines

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compelling evidence of interannual differences in population density that would bias my conifer-dominated analyses.

The PCA summarizing habitat variability within subplots (data pooled from all transects) extracted four PCs that accounted for 68% of the common variation in habitat structure and composition (Appendix 4). The first component described a cline from subplots with thick and diverse shrub cover to those with a deep mat of mosses. The second component characterised a gradient from deciduous to conifer forest. The third represented a cline from dense grass in cutovers to an open understory in mature forests. The fourth component described subplots ranging from those in mature conifer forests with fallen trees to those in standing cutover and deciduous forests.

The three habitats (conifer forest, deciduous forest, cutover) were distinctly different (DFA, χ^2=396.28, df=8, P<0.0001). All cutover subplots were correctly classified as belonging to the cutover habitat. Only two forest subplots were misclassified as cutover (one of 32 deciduous subplots and one of 68 conifer subplots). The distinct differences in habitat reinforce my selection of sample sites for each transect. At some point, there must be boundaries between one habitat and the other.

The stepwise multiple regression evaluating variation in patch quality was also highly significant. Habitat type was the only statistically significant predictor of vole density (higher density in deciduous forest than elsewhere, Table 6). No other indicator variable or PC came close to statistically explaining residual vole density after the deciduous habitat indicator variable was entered into the model (P>0.13 in all cases). This result is consistent with my assumption that vole density responds to the

Table 6: Stepwise multiple regression assessing the assumption that population density responds primarily to the mix of patches rather than small-scale variation in habitat. The dummy variable representing deciduous forest was the only variable included by the analysis. None of the small-scale habitat variables represented by principal component scores was significantly related to the substantial residual variation in vole density.

Regression Summary			
Step	Variable	b	r
1	Density in deciduous forest	2.09	.42

Analysis of variance			
Source	df	Mean Square	P
Regression	1	106.31	<.0001
Residual	131	3.87	

mix of patches in a habitat rather than to the quality of individual patches.

Vole density varied significantly between habitats (repeated measures ANOVA, $F_{1,6}=18.87$, $P=0.005$). No other main effect or interaction was close to statistical significance (Table 7). The significant habitat effect was inevitable given that I defined habitats on the basis of density. I was concerned that the analysis could be biased by the two 'unusual' transects (i.e., the abrupt boundary between coniferous and deciduous forest; the gradual boundary between conifer forest and cutover, Appendix 1). I deleted both transects and repeated the analysis. The results were unchanged. Habitat was the only significant effect ($F_{1,4}=18.67$, $P=0.012$). There was a slight although nonsignificant trend for transects with gradual boundaries to have a higher mean density than transects with abrupt boundaries ($P=0.13$), but none of the main effects or interactions which tested for an edge effect was close to statistical significance ($P>0.40$). The results were also unchanged when I calculated distance from the habitat boundary (seven distance classes) rather than distance from the ecotone. No main effect other than habitat ($F_{1,6}=11.85$, $P=0.014$) and no interaction was close to statistical significance ($P\geq0.43$). The absence of significant interactions occurred because population densities showed more or less consistent declines toward low-density habitat across some ecotones but mimicked the high within-habitat variability in density across others (Appendix 1). There was no edge effect.

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Table 7: Repeated measures ANOVA rejecting edge effects in red-backed vole density relative to distance from ecotone, type of habitat (high or low density), and type of habitat boundary (abrupt or gradual).

Source	Between-transects			
	SS	df	F	P
Boundary (B)	14.26	1	0.81	.402
Error	105.15	6		

Source	Within-transects			
	SS	df	F	P
Habitat (H)	68.34	1	18.87	.005
Distance (D)	11.68	5	0.83	.541
Habitat x Distance	10.59	5	0.64	.670
Boundary x Habitat	0.84	1	0.23	.646
Boundary x Distance	4.18	5	0.30	.911
B x H x D	10.84	5	0.66	.659

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DISCUSSION

Despite significant differences in density between clearly-defined habitats on my transects, I was unable to detect an edge effect of any kind for red-backed voles. The absence of an edge effect rejects Leopold's maxim that edges tend to increase population density and provides, in the case of red-backed voles, no support for hypotheses of complementary resources or increased resource density near edges. The lack of an edge effect also rejects the emerging alternative view that density often declines near edges.

My results are unsettling, however, because I failed to detect clines in density predicted by theories of patch use and habitat selection, and because such clines are readily apparent in other ecosystems (Morris 1992, In Press). Similar clines are implied by the frequent observation of differences in small mammal density near habitat borders (e.g., Walters 1991, Hansson 1994, Mills 1995, Sekgororoane and Dilworth 1995). Could my inability to detect clines in density be caused by insufficient sampling with low statistical power? There were, after all, only eight transects, and two of these yielded unexpectedly narrow or wide ecotones. Recall, however, that I had little difficulty documenting significant differences in density between habitats on either side of the edge. I should have also been able to detect consistent spatial trends in density if they existed. It appears that I need to look elsewhere to explain the absence of edge effects.

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One possibility is that high- and low-density habitats have discrete red-backed vole populations whose members simply do not cross habitat boundaries (e.g., Kirkland et al. 1985). I tested the 'discrete population' hypothesis by examining the habitat use of voles adjacent (≤ 20 m) to ecotone boundaries. Twelve of the 28 (43%) recaptured individuals were captured on both sides of the boundary. The nature of the boundary also had no effect on the proportion of animals crossing ecotones (three of seven individuals crossed abrupt boundaries, nine of twenty-one individuals crossed gradual boundaries).

Another possibility is that individual red-backed voles are incapable of recognizing and responding to habitat quality. The hypothesis is inconsistent with numerous studies noting clear habitat preferences, at least in terms of density, by red-backed voles (e.g. Kirkland and Griffin 1974, Vickery 1981, Morris 1984, 1987, 1989, Wywialowski and Smith 1988, Knight and Morris 1996). The hypothesis is also incompatible with my observation of consistently higher vole density in deciduous than in conifer forest. But I observed, nevertheless, major inconsistencies in comparisons between conifer and cutover habitats. Voles were most abundant in cutovers on two transects, they were most abundant in conifer forest on the other two. The differences in relative vole density in cutovers, as well as the interannual differences in density observed only for cutovers, suggest that cutovers vary in composition and in their ability to support red-backed voles. I tested the hypothesis by discriminant function analysis between the two sets of cutover habitats. The two sets were dramatically different ($\chi^2=38.53$, df=4, $P<0.0001$) confirming my earlier suspicion that the high

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1994 density in cutover was caused by differences in habitat. The DFA result is also consistent with a similar study by Knight and Morris (1996) that documented the ability of red-backed voles to recognize a finer distinction of habitats than those typically used by field ecologists. Different densities in different habitats can arise in many ways and do not, in and of themselves, constitute reliable evidence of density-dependent habitat selection. The balance of data, however, is heavily tilted toward the ability of voles to recognize and respond in a density dependent manner to differences in habitat quality, at least at relatively large spatial scales.

A related possibility is that individual voles exposed to a mixture of different habitats near edges have difficultly assessing the average quality of their home ranges. An animal occupying a home range composed mainly of deciduous forest may, for example, value its home range the same as an individual whose entire home range occurs within deciduous forest. An animal whose home range is composed partly of conifers and mainly of cutover habitat may value its home range similar to one living exclusively in cutover habitat. Inaccurate assessments of home-range quality would alter density-dependent decisions of habitat selection (e.g., individuals on the high-density side of the boundary may continue to occupy a sub-optimal habitat because they perceive that their expected fitness is higher than it actually is, few individuals may move toward the low-density side because they perceive it to be of even lower quality than it actually is).

Alternatively, assessment errors may create a high variance in density across ecotones that destroys the consistent cline predicted by theory. Assessment errors at

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this scale should be related to the degree of difference between habitats. Large differences with conspicuous boundaries provide a sharper contrast than small differences and should improve the ability of animals to assess patch or home-range quality (Schmidt and Brown 1996). Fox squirrels, for example, are more capable of optimizing their foraging among patches with large differences in resource density and with distinct boundaries, than when the differences are small or when the boundaries are vague (Schmidt and Brown 1996). In general, foragers appear more capable of correctly assessing patch quality, at a variety of scales, when there are distinct boundaries or landmarks that they can use to determine the edges of patches (reviewed in Schmidt and Brown 1996). Should the same not also be true of the much larger scales of habitat variation that I address here? Assessment errors at any scale will influence spatial variation in fitness and the equilibrium densities produced by evolutionarily stable strategies of density-dependent habitat selection.

All habitats exploited by voles in my study represent forests (albeit of different types and different ages) and may be so similar that voles at the boundary between them are incapable of accurately assessing habitat quality. By way of comparison, obvious clines in deer mouse density across prairie-badland boundaries (Morris 1992, In Press) are associated with sharp discontinuities in topography, micro-climate, substrate, plant density, and plant community composition.

Did my design violate the assumptions of constant quality, density, and size distribution of foraging patches? Variation in the quality of patches at edges seems unlikely because I was unable to detect any correspondence between vole density and

local variation in my measures of habitat, even though vole density was consistently higher on one side of the edge than on the other. Similarly, I can tentatively reject variation in the density of patches of similar quality because such variation should normally produce either inflated or depressed population density near the edge. I observed neither.

I can not exclude differences in the size distribution of patches or the possibility of complementary changes in habitat quality on opposite sides of the boundary that would destroy clines in density. Any consistent trend in size distribution should, nevertheless, consistently change the relative occupation of each type of patch, modify fitness, and thereby create predictable and detectable spatial patterns in density at habitat edges. I detected none. Complementary changes in quality are more difficult to dispel. Complementary changes could occur, for example, if edge-specializing predators (e.g., long-tailed weasels, coyotes, red foxes (Heske 1995)) reduce the quality of patches in cutovers while the absence of 'interior' predators near edges (e.g., goshawks (Widén 1989)) inflate the quality of patches in forests. It is difficult to imagine, however, that such an effect applies to my gradual transitions between conifer and deciduous forests of the same age. If complementary differences in quality obscure clines in density, I suspect that they do so in conjunction with assessment errors between similar habitats.

Regardless, four points are worth re-emphasizing. First, inflated population densities at habitat boundaries should not occur unless the quality, size distribution, or density of patches also increases at edges. Second, the patterns predicted by density-

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dependent habitat selection may be obscured by complementary changes in the quality and density of patches or by errors in habitat assessment. Third, despite the absence of an edge effect or clinal variation in density, my protocol for identifying ecotones and habitat boundaries worked exceptionally well. Fourth, studies of so-called edge effects are likely to be far more profitable if they concentrate on processes that effect changes in population density across edges rather than if they simply observe patterns in density at edges.

ACKNOWLEDGMENTS

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APPENDIX 1

Habitat classification probability and population density of red-backed voles along eight transects sampled in northwestern Ontario

APPENDIX 1 PAGE 1

Figure A1.1: The probability of paired stations belonging to deciduous habitat (solid triangles) and red-backed vole density in subplots (solid squares) along transect D1. Lines between symbols are included to enhance interpretation. Distance is calculated from the centre of the ecotone. Stations with low habitat classification probabilities belong to conifer habitat.

Transect D1
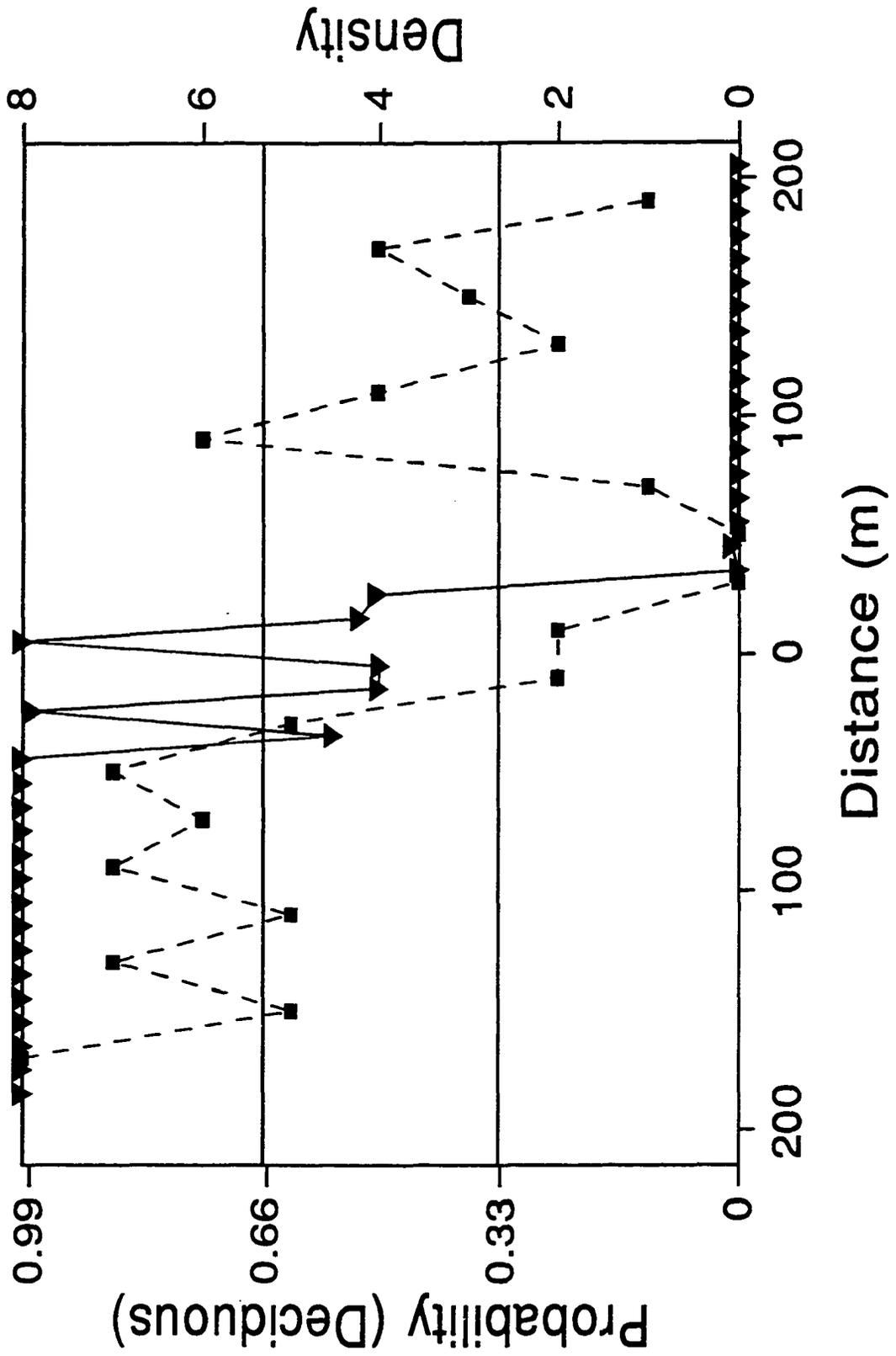
Figure A1.2: The probability of paired stations belonging to deciduous habitat (solid triangles) and red-backed vole density in subplots (solid squares) along transect D2. Lines between symbols are included to enhance interpretation. Distance is calculated from the centre of the ecotone. Stations with low habitat classification probabilities belong to conifer habitat.

APPENDIX 1 PAGE 3
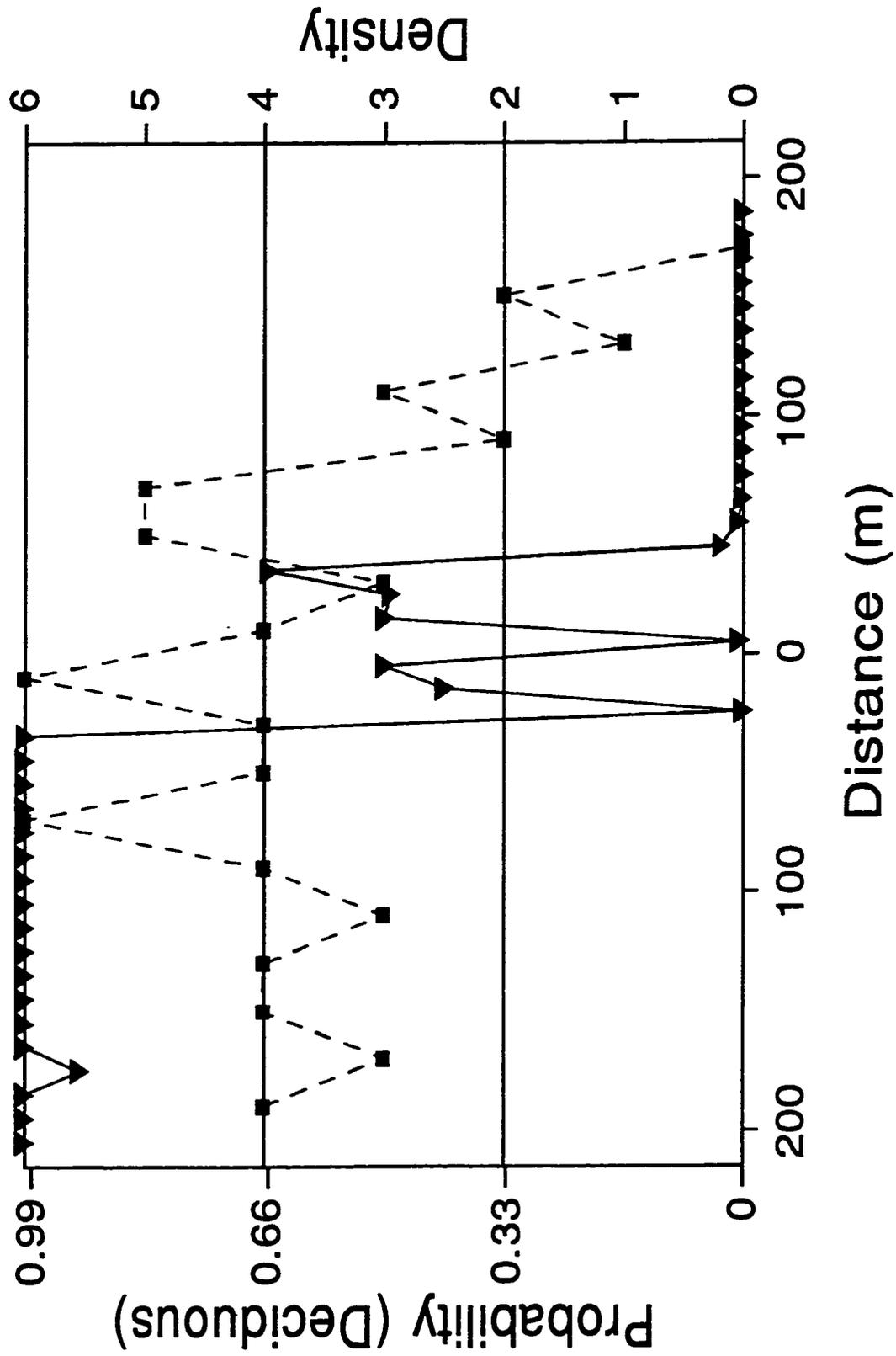
Transect D2

Figure A1.3: The probability of paired stations belonging to deciduous habitat (solid triangles) and red-backed vole density in subplots (solid squares) along transect D3. Lines between symbols are included to enhance interpretation. Distance is calculated from the centre of the ecotone. Stations with low habitat classification probabilities belong to conifer habitat.

Transect D3
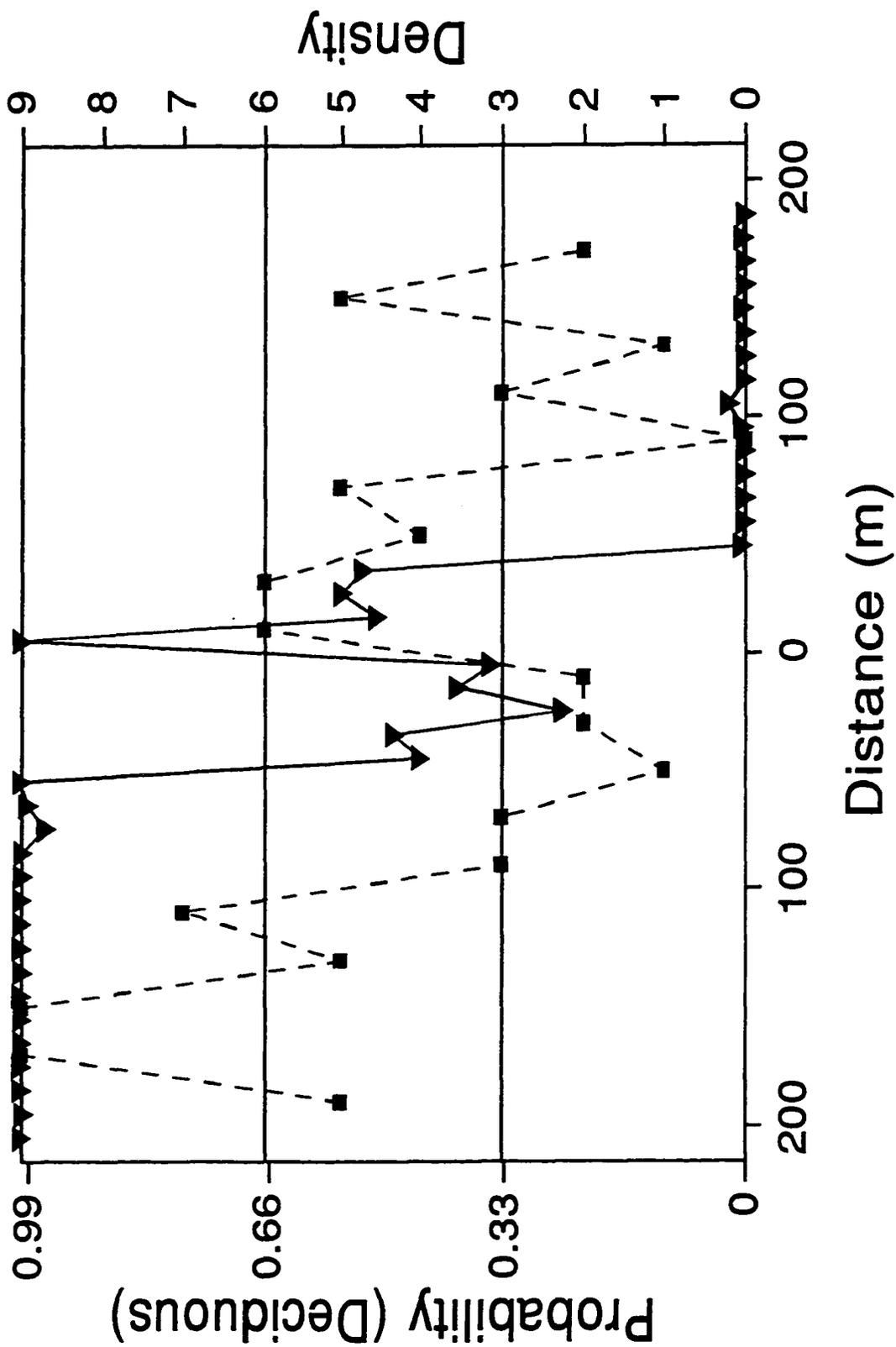
Figure A1.4: The probability of paired stations belonging to deciduous habitat (solid triangles) and red-backed vole density in subplots (solid squares) along transect D4. Lines between symbols are included to enhance interpretation. Distance is calculated from the centre of the ecotone. Stations with low habitat classification probabilities belong to conifer habitat.

APPENDIX 1 PAGE 5
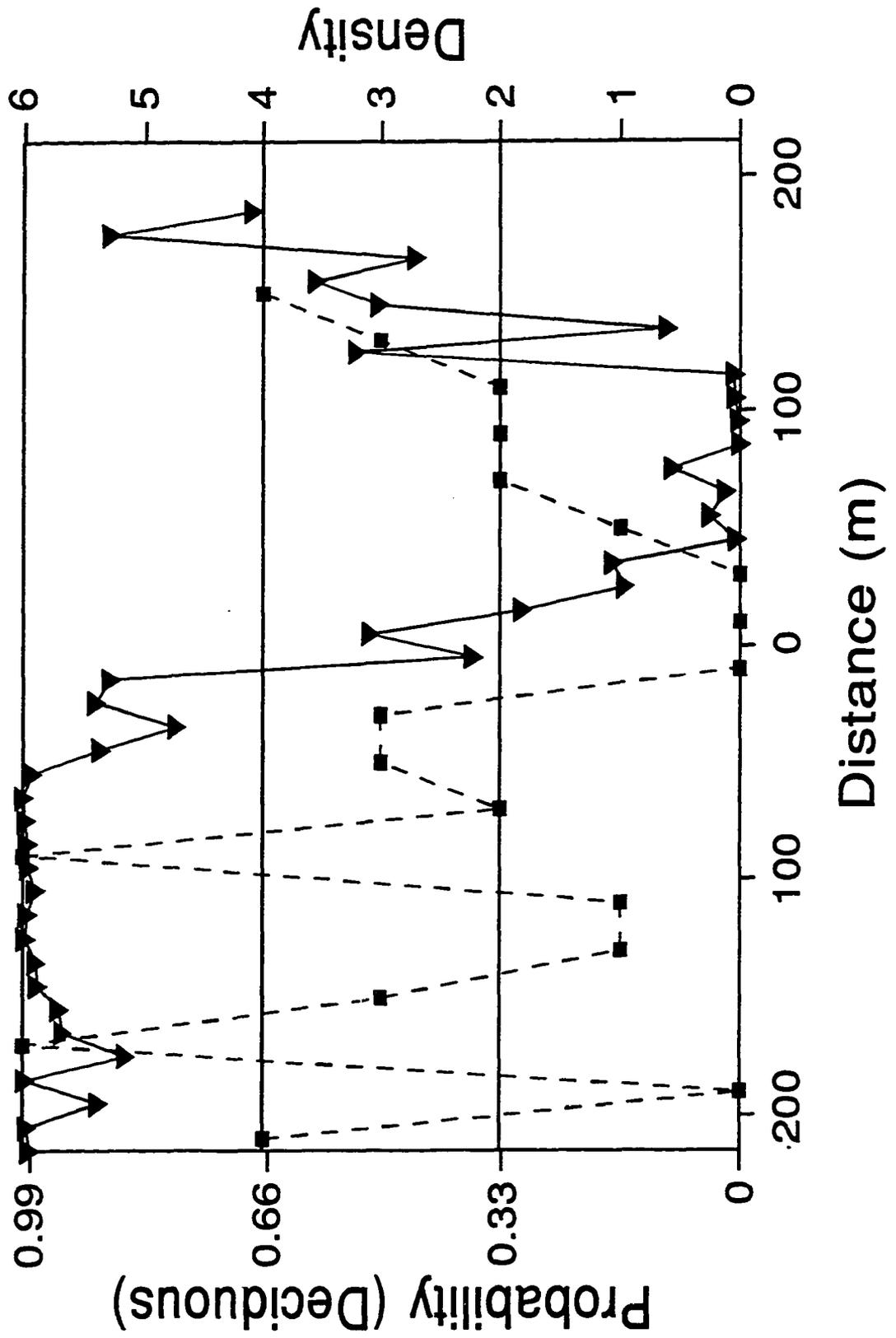
Transect D4

Figure A1.5: The probability of paired stations belonging to cutover habitat (solid triangles) and red-backed vole density in subplots (solid squares) along transect C1. Lines between symbols are included to enhance interpretation. Distance is calculated from the centre of the ecotone. Stations with low habitat classification probabilities belong to conifer habitat.

Transect C1
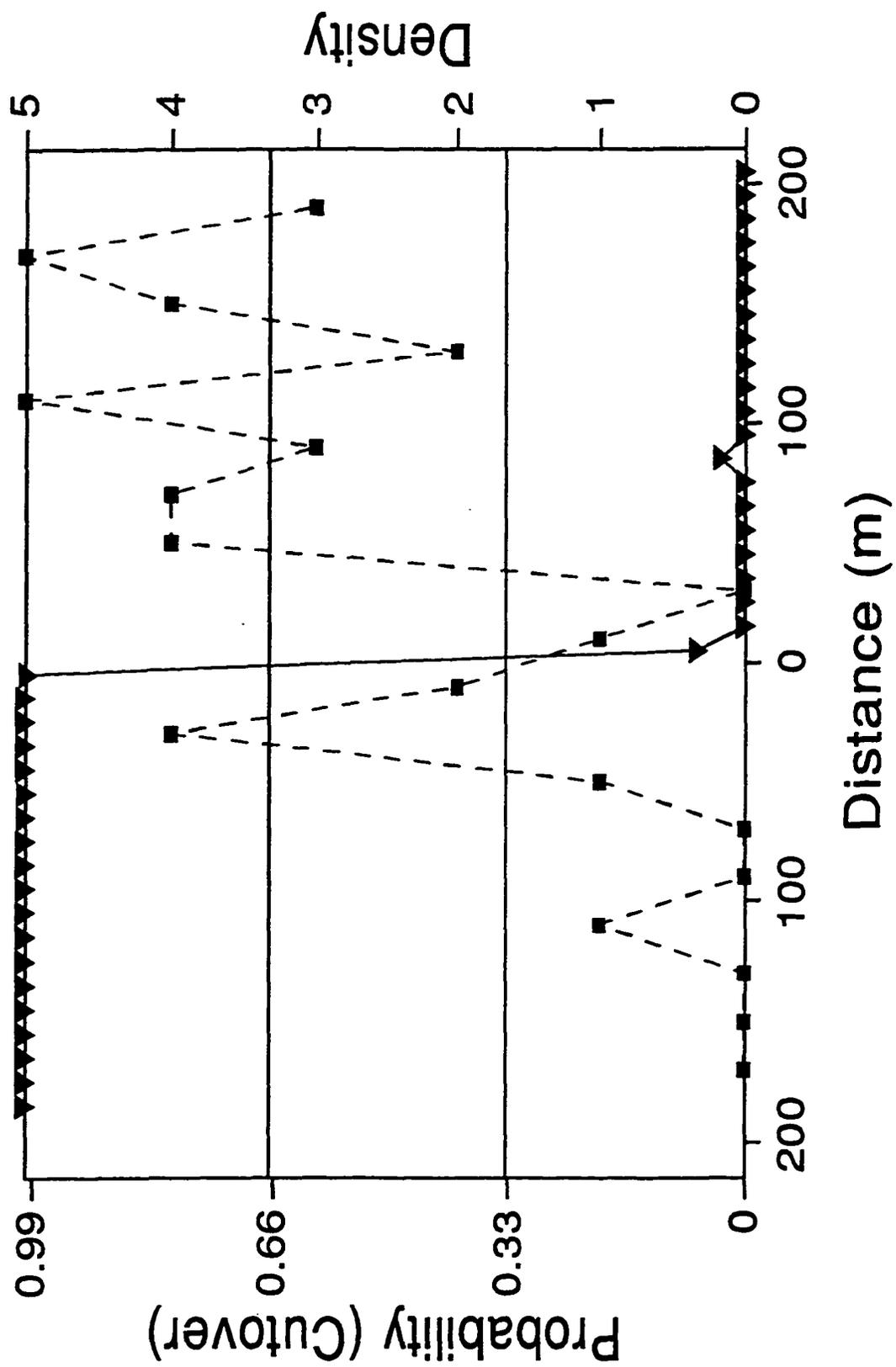
Figure A1.6: The probability of paired stations belonging to cutover habitat (solid triangles) and red-backed vole density in subplots (solid squares) along transect C2. Lines between symbols are included to enhance interpretation. Distance is calculated from the centre of the ecotone. Stations with low habitat classification probabilities belong to conifer habitat.

Transect C2
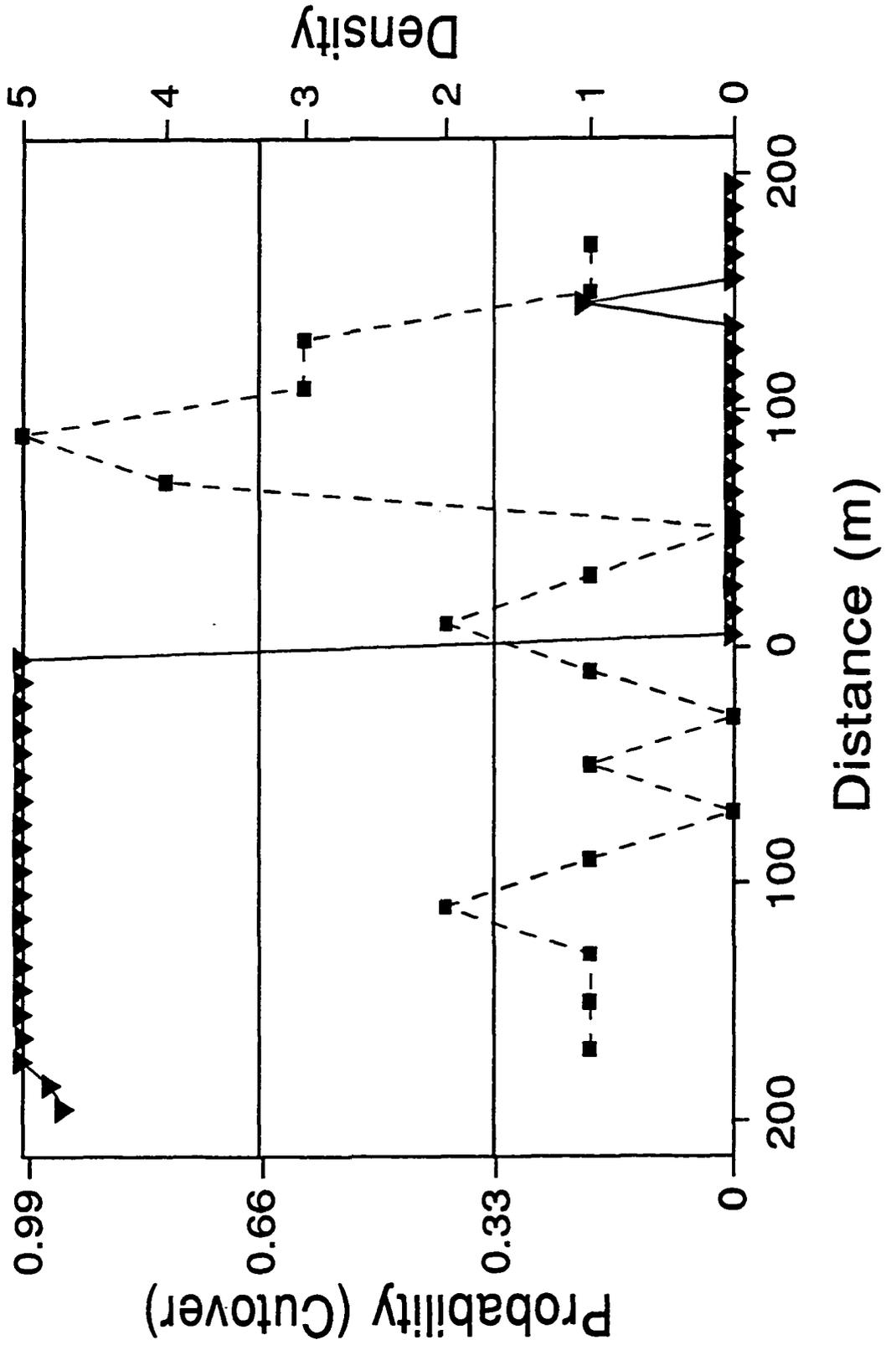
Figure A1.7: The probability of paired stations belonging to cutover habitat (solid triangles) and red-backed vole density in subplots (solid squares) along transect C3. Lines between symbols are included to enhance interpretation. Distance is calculated from the centre of the ecotone. Stations with low habitat classification probabilities belong to conifer habitat.

Transect C3
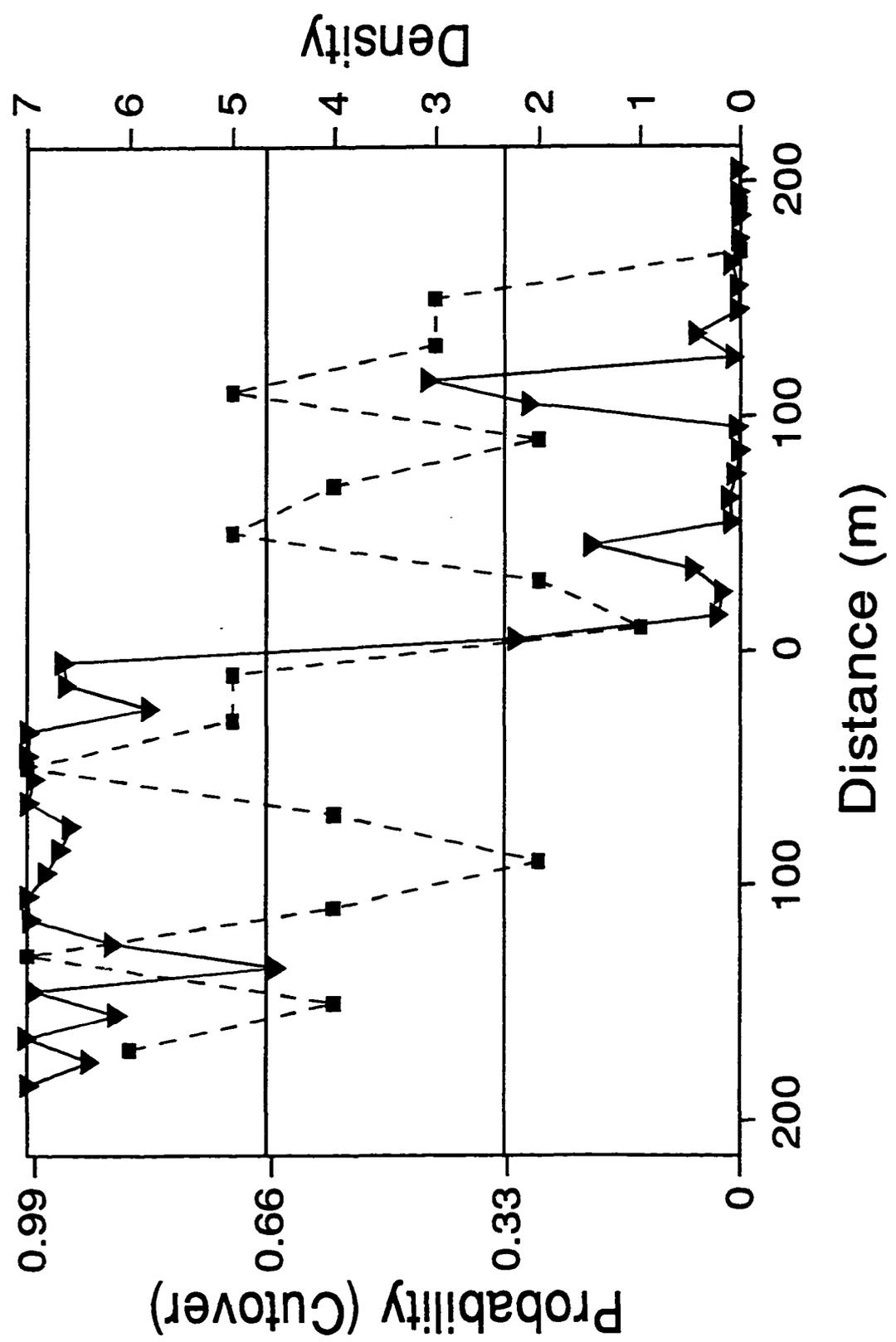
Figure A1.8: The probability of paired stations belonging to cutover habitat (solid triangles) and red-backed vole density in subplots (solid squares) along transect C4. Lines between symbols are included to enhance interpretation. Distance is calculated from the centre of the ecotone. Stations with low habitat classification probabilities belong to conifer habitat.

Transect C4
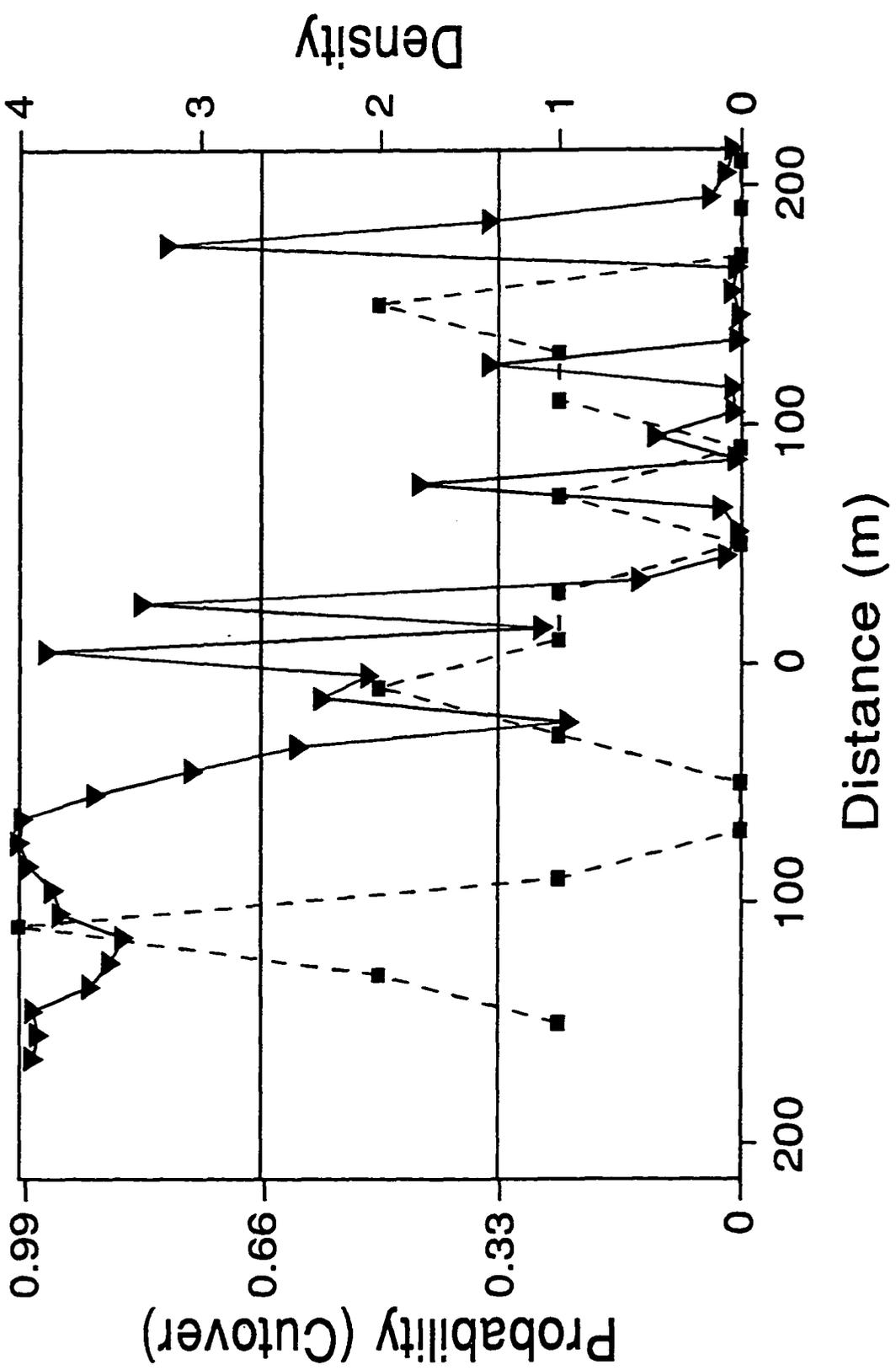
APPENDIX 2

Principal component loadings of eight transects crossing boreal forest habitat

boundaries in northwestern Ontario

APPENDIX 2 PAGE 1

Table A2.1: Varimax-rotated principal component (PC) loadings (standardized regression coefficients) of habitat variables (Table 1) for transect D1.

Variable	PC1	PC2	PC3
FHD	0.88	0.12	-0.03
Q_4	0.85	0.13	0.01
Q_5	0.82	0.23	-0.12
Q_2	-0.57	0.04	0.11
Mat	-0.57	-0.55	0.19
BarrenC	0.52	0.09	0.09
Numcon	-0.15	-0.88	0.08
Areacon	-0.05	-0.85	0.00
ShrubC	0.54	0.68	-0.18
FernC	0.49	0.63	0.24
LitterC	0.53	0.54	-0.39
Stumps	-0.04	-0.40	-0.02
WoodC	0.00	0.19	0.71
Numdec	-0.02	0.37	-0.68
Fallen	-0.26	0.00	0.66
Areadec	0.17	0.36	-0.62
GrassC	0.07	0.28	0.50
ForbC	-0.08	0.40	-0.48

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Table A2.2: Varimax-rotated principal component (PC) loadings (standardized regression coefficients) of habitat variables (Table 1) for transect D2.

Variable	PC1	PC2
FHD	0.87	0.03
ShrubC	0.86	-0.08
Areacon	-0.80	-0.04
Q_4	0.79	0.02
Numcon	-0.78	0.08
Q_5	0.78	-0.01
MossC	-0.64	0.58
Areadec	0.63	-0.46
Q_3	0.63	0.07
Numdec	0.58	-0.40
Stumps	-0.41	0.15
Q_2	0.40	-0.03
WoodC	-0.05	0.75
ForbC	-0.03	-0.73
LitterC	0.61	-0.70
Mat	-0.49	0.55
Fallen	-0.01	0.49
BarrenC	0.14	0.42
GrassC	-0.03	0.30

APPENDIX 2 PAGE 3

Table A2.3: Varimax-rotated principal component (PC) loadings (standardized regression coefficients) of habitat variables (Table 1) for transect D3.

Variable	PC1	PC2	PC3	PC4
LitterC	0.85	0.25	-0.05	-0.01
Numcon	-0.82	-0.25	-0.11	0.20
ShrubC	0.81	0.16	-0.10	0.30
FHD	0.78	-0.10	0.07	0.45
Q_4	0.77	0.09	0.00	0.37
Q_3	0.75	-0.11	0.02	0.20
Q_5	0.73	-0.12	-0.01	0.40
Areacon	-0.71	-0.30	-0.15	0.15
FernC	0.71	0.22	-0.21	0.19
Q_1	0.64	0.13	-0.11	0.20
Q_2	0.53	0.14	0.11	-0.25
Areadec	0.28	0.86	-0.01	0.03
Numdec	0.26	0.85	0.05	0.00
BarrenC	-0.01	-0.42	0.31	-0.20
WoodC	0.18	0.10	0.90	0.00
Fallen	-0.06	-0.09	0.87	0.16
Stumps	-0.36	-0.24	0.48	0.14
Forb	-0.10	-0.03	-0.24	-0.65
Mat	0.11	0.07	0.03	0.64
GrassC	0.14	-0.46	0.15	-0.51

APPENDIX 2 PAGE 4

Table A2.4: Varimax-rotated principal component (PC) loadings (standardized regression coefficients) of habitat variables (Table 1) for transect D4.

Variable	PC1	PC2	PC3	PC4
FHD	0.84	0.33	-0.12	0.14
Q_3	0.75	0.30	0.04	-0.05
Q_2	0.75	-0.01	0.04	-0.20
Q_4	0.70	0.23	-0.27	0.27
Q_5	0.59	0.18	-0.48	0.08
Numcon	-0.27	-0.79	0.25	-0.13
Areacon	-0.24	-0.76	0.06	-0.18
ShrubC	0.32	0.74	-0.42	0.06
ForbC	-0.08	-0.65	-0.11	-0.09
FernC	-0.44	0.50	-0.12	-0.38
Fallen	-0.07	-0.26	0.85	-0.08
WoodC	0.12	-0.02	0.79	-0.20
Stumps	-0.13	0.11	0.66	0.28
LitterC	0.29	0.50	-0.63	0.15
Numdec	0.01	0.06	0.02	0.81
Areadec	-0.09	0.20	-0.04	0.72
Mat	-0.36	-0.06	0.40	-0.57

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Table A2.5: Varimax-rotated principal component (PC) loadings (standardized regression coefficients) of habitat variables (Table 1) for transect C1.

Variable	PC1	PC2	PC3
Q_3	0.89	-0.04	-0.06
Q_4	0.85	-0.06	0.02
FHD	0.84	-0.06	0.03
ShrubC	0.84	-0.31	0.13
Q_2	0.81	-0.15	-0.10
Q_5	0.72	-0.16	-0.10
GrassC	0.72	-0.18	-0.43
MossC	-0.71	0.46	0.33
Areacon	-0.71	0.12	0.02
Q_1	0.64	-0.19	-0.14
Fallen	-0.27	0.83	0.04
WoodC	-0.18	0.81	0.10
BarrenC	0.03	0.65	-0.14
LitterC	0.48	-0.56	-0.24
ForbC	0.05	-0.06	0.73
FernC	-0.03	-0.29	0.71
Mat	-0.46	0.37	0.65
Numcon	-0.27	-0.45	-0.58
Stumps	-0.17	0.10	0.37

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Table A2.6: Varimax-rotated principal component (PC) loadings (standardized regression coefficients) of habitat variables (Table 1) for transect C2.

Variable	PC1	PC2	PC3
Q_2	0.88	0.15	0.12
Q_1	0.82	0.38	-0.10
GrassC	0.82	-0.14	-0.09
ShrubC	0.79	-0.11	0.33
Areacon	-0.66	0.26	-0.14
WoodC	0.31	0.26	0.08
MossC	-0.18	0.82	-0.41
Numcon	0.02	-0.75	0.25
Mat	-0.48	0.69	-0.22
LitterC	-0.09	-0.69	0.37
BarrenC	-0.01	-0.67	-0.02
Stumps	0.09	0.50	0.03
FHD	0.06	-0.26	0.91
Q_4	0.11	-0.13	0.84
Q_5	0.20	0.11	0.74
Q_3	0.48	-0.18	0.68
FernC	0.06	0.09	-0.21

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Table A2.7: Varimax-rotated principal component (PC) loadings (standardized regression coefficients) of habitat variables (Table 1) for transect C3.

Variable	PC1	PC2	PC3
FHD	0.84	0.35	-0.13
ForbC	-0.82	-0.06	-0.02
LitterC	0.80	0.06	-0.08
Numcon	0.80	-0.20	-0.32
Q_5	0.79	0.27	-0.13
Q_4	0.79	0.22	-0.17
Q_1	-0.55	0.50	-0.03
BarrenC	0.51	-0.16	0.16
Q_2	-0.29	0.75	-0.10
ShrubC	0.21	0.74	0.07
Areacon	0.01	-0.72	0.08
Q_3	0.40	0.67	-0.18
MossC	-0.44	-0.47	0.09
WoodC	0.00	-0.08	0.89
Fallen	-0.22	-0.14	0.84
Mat	-0.46	-0.16	0.53
Stumps	0.18	0.34	0.39

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Table A2.8: Varimax-rotated principal component (PC) loadings (standardized regression coefficients) of habitat variables (Table 1) for transect C4.

Variable	PC1	PC2	PC3
MossC	-0.90	-0.07	0.04
LitterC	0.88	-0.12	0.02
FHD	0.83	0.12	0.06
Mat	-0.79	0.04	0.12
Q_4	0.79	0.23	-0.01
Q_5	0.78	0.07	-0.01
ShrubC	0.74	0.42	0.05
Q_3	0.60	0.40	0.15
Areacon	-0.59	-0.27	0.18
Stumps	-0.54	-0.05	0.08
BarrenC	0.42	0.02	-0.20
Q_1	0.03	0.84	0.02
Q_2	0.18	0.81	-0.05
GrassC	0.51	0.59	-0.19
ForbC	-0.09	0.58	-0.17
Numcon	-0.12	-0.54	-0.19
WoodC	-0.20	-0.02	0.90
Fallen	-0.48	0.03	0.75
Numdec	0.24	-0.05	0.69

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APPENDIX 3

Complications associated with using only red-backed voles to detect edge effects

A potential problem associated with several small-mammal species in the study area is that interspecific competition may affect $\underline{C}$. gapperi density or habitat use. Red-backed voles dominated the small-mammal communities, representing approximately 60% of all captures and 49% of all marked individuals (Table 4). The deer mouse (Peromyscus maniculatus) is a potential competitor with red-backed voles and was the second most frequently captured species representing approximately 13% of all captures (20% of all marked individuals). If red-backed voles and deer mice compete and their populations are near equilibrium, then high densities of one species should increase interspecific competition and thereby be associated with low densities of the other species. I tested for competition using a regression analysis predicting red-backed vole density from deer mouse density. The non-significant regression ($F_{1,133}$=2.32, P=0.13) suggests no competition between these two forest species at my study site in northwestern Ontario. Several other studies that searched for competition between deer mice and red-backed voles were unable to document competition in either laboratory experiments (Getz 1969, Grant 1970, Wolff and Dueser 1986) or field tests (Morris 1983, Wolff and Dueser 1986, Stewart 1991, but see Crowell and Pimm 1976). According to Wolff and Dueser (1986), the probability of competition between deer mice and red-backed voles is likely reduced because of two conspicuous differences in resource use. First, deer mice make extensive use of trees for foraging and nesting while red-backed voles remain on the ground. Second, the two species differ substantially in diet, with deer mice foraging mostly on arthropods (berries and

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seeds being seasonally important) and red-backed voles foraging mainly on lichens, green plants, and fungi.

Two chipmunk species (Tamias striatus and T. minimus) and two zapodids (Napaeozapus insignis and Zapus hudsonius) make up a combined 19% of all captures (20% of all marked individuals, Table 4). These species are not expected to compete with red-backed voles because voles have vastly different diets. Chipmunk diets consist mainly of a wide range of seeds, berries, nuts, invertebrates, and even animal material, while green vegetation is rarely eaten (Banfield 1977). Zapodids are mainly granivorous and supplement their diet with fruit and insects (Banfield 1977).

Microtus chrotorrhinus, whose diet may be similar to that of Clethrionomys, was abundant on only one transect (D3), but even here comprised only 14% of captures (24% red-backed vole captures) and 17% of individuals (38% red-backed vole individuals). The remaining small mammals represent less than 6% of all captures (Table 4) and, thus, should have little effect on the densities of red-backed voles or their use of habitat.

APPENDIX 4

Principal component loadings for habitat data pooled across eight transects crossing

boreal forest habitat boundaries in northwestern Ontario

Table A4.1: Varimax-rotated principal component (PC) loadings (standardized regression coefficients) of habitat variables (Table 1) for data pooled across all eight transects.

Variable	PC1	PC2	PC3	PC4
FHD	0.93	-0.06	-0.01	-0.07
Q_4	0.89	-0.10	0.14	-0.11
Q_5	0.87	0.04	0.01	-0.05
MossC	-0.82	-0.29	0.07	0.26
Q_3	0.75	-0.15	0.43	-0.07
ShrubC	0.75	0.51	0.12	-0.14
Areacon	-0.74	-0.30	-0.11	0.03
LitterC	0.65	0.29	0.06	-0.36
Mat	-0.55	0.25	0.33	0.25
Numcon	0.07	-0.79	-0.17	-0.23
ForbC	-0.14	0.73	0.01	-0.02
Areadec	0.33	0.73	-0.21	-0.11
Numdec	0.37	0.62	-0.22	0.05
FernC	0.07	0.51	0.19	0.01
Q_1	0.09	0.22	0.83	0.01
Q_2	0.35	0.01	0.82	-0.06
GrassC	0.26	-0.36	0.71	-0.11
BarrenC	0.28	-0.10	-0.51	0.13
WoodC	-0.03	0.14	0.06	0.87
Fallen	-0.28	0.14	-0.09	0.84
Stumps	-0.14	-0.12	-0.19	0.64

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IMAGE EVALUATION
TEST TARGET (QA–3)

150mm

6"