Voles looking for an edge: habitat selection across forest ecotones

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Abstract: We searched for the presence of "edge effects" in the occupation of adjacent boreal-forest habitats by red-backed voles (*Clethrionomys gapperi*). First, we reviewed four models that differ in their predictions of abundance at habitat boundaries. Three of the models predicted an edge effect, while the so-called matrix or habitat model served as a null expectation. We then developed a protocol to detect, objectively, the ecotone between two habitats that is necessary to differentiate among the four models. The protocol revealed both abrupt and gradual ecotones along transects crossing conifer to cutover and conifer to deciduous habitats. Though vole density was almost always higher on one side of the ecotone than on the other, we were unable to detect an edge effect of any kind. Vole density within ecotones was intermediate to that on each side (refuting the existence of an ecotone effect). There were also no differences in the pattern of density between abrupt and gradual ecotones (refuting the existence of a permeability effect), and no consistent pattern of vole density away from either type of ecotone (refuting the existence of a habitat-selection effect). Simulations that manipulated vole densities along the transects suggested, however, that the habitats may have been too similar to allow a habitat-selection effect to be detected. We suspect that our result will be common to moderately generalised species, and we recommend that controlled experiments be carried out to evaluate the conditions under which habitat-selecting species may exhibit edge effects.

Résumé : Nous avons tenté de déterminer si des effets de bordure affectaient l'occupation d'habitats boréaux-forestiers adjacents chez des Campagnols-à-dos-roux de Gapper (*Clethrionomys gapperi*). Nous avons d'abord réexaminé quatre modèles qui donnent des prévisions différentes de l'abondance en bordure des habitats. Trois des modèles prévoient un effet de bordure et le quatrième, appelé modèle de la matrice ou modèle de l'habitat, a servi d'hypothèse nulle. Par la suite, nous avons mis au point un protocole dans le but de déterminer objectivement quel écotone entre deux habitats permettra de différencier les quatre modèles. Ce protocole a mis en lumière des écotones progressifs et des écotones abrupts le long de transects allant des conifères aux zones de coupe à blanc et des conifères aux forêts de décidus. La densité des campagnols était toujours plus élevée d'un côté de l'écotone que de l'autre, mais nous n'avons pas pu déceler d'effet de bordure de quelque type que ce soit. La densité des campagnols dans les écotones était intermédiaire entre les densités enregistrées de chaque côté (réfutant l'existence d'un effet d'écotone). Il n'y avait pas non plus de différence dans les tendances de la densité entre l'écotone graduel et l'écotone abrupt (réfutant l'existence d'un effet de perméabilité), et il n'y avait pas non plus de tendance définie de la densité loin de l'un ou l'autre type d'écotone (réfutant l'existence d'un effet du choix d'habitat). Des simulations au cours desquelles les densités des campagnols ont été manipulées le long des transects ont indiqué, cependant, que les habitats peuvent avoir été trop semblables pour que l'effet du choix d'habitat soit détecté. Nous soupçonnons que nos résultats s'appliqueront à des espèces modérément généralistes et nous recommandons des expériences en conditions contrôlées pour évaluer les conditions dans lesquelles les espèces qui choisissent leur habitat manifesteront des effets de bordure.

[Traduit par la Rédaction]

Introduction

An understanding of species abundance along the boundary between abutting habitats is essential to ecologists and conservation/wildlife managers (Harris 1988; Yahner 1988; Lidicker 1999). The abundance of generalist species may, for example, be enhanced along habitat edges that provide access to new habitats and resources (Leopold 1933 and many others). An appropriate response for managing such species might be to increase the amount of edge in the landscape. The abundance of other species may, however, decline near edges (e.g., Walters 1991; Hansson 1994; Mills 1995; Morris 1997; Manson et al. 1999), where predation and avian nest parasitism reduce survival and recruitment (e.g., Paton 1994), though such effects appear to be linked to fragmented landscapes (Andrén 1995; Donovan et al. 1997; Heske et al. 1999). Appropriate conservation efforts directed at these species would include attempts to reduce the amount of edge. Yet other patterns of density may emerge for habitat-selecting species (Morris 1997) and for those that respond differentially to the "permeability" of the edge itself (Stamps et al. 1987a, 1987b; Duelli et al. 1990).

Though implicit in early views of habitat edges, the width and character of the ecotone between habitats have often been ignored in studies exploring "edge effects." Most mod-
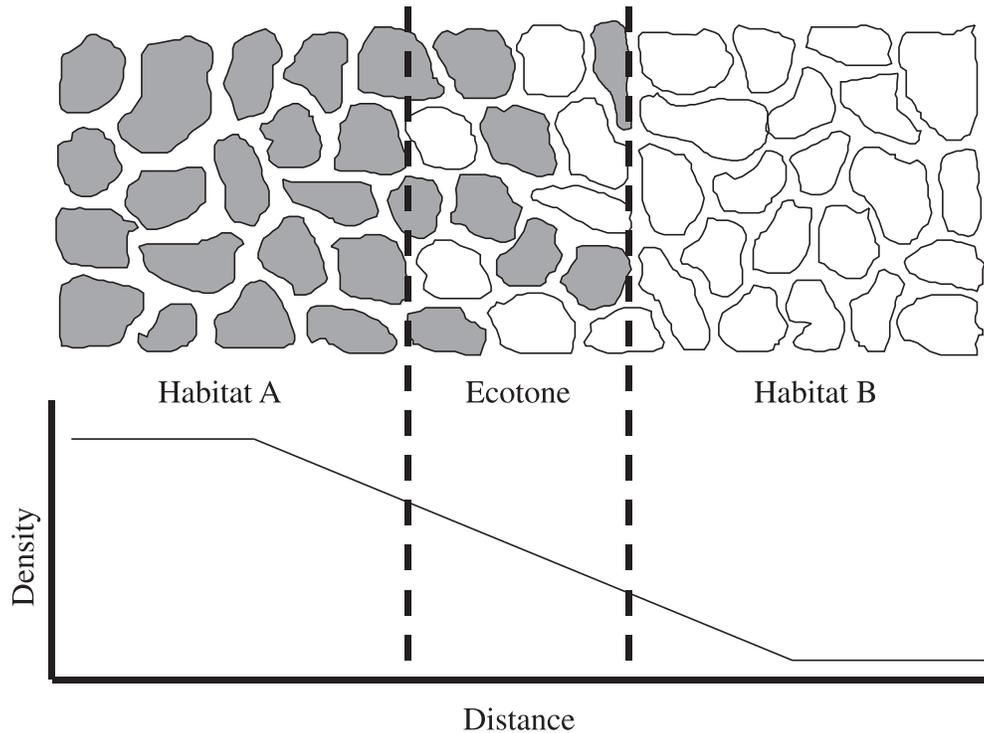
Fig. 1. At the top is an idealised representation of the distribution of high-quality patches (shaded) and low-quality patches (open) between two habitats (A and B) and within their ecotone. At the bottom is a hypothetical graph of the expected pattern of density caused by density-dependent habitat selection.

els, or at least schematics of those models (e.g., Lidicker 1999), assume that the researcher knows exactly where the edge between habitats occurs. We suspect that edges are seldom discrete and that their continuous nature may easily bias our attempts to differentiate among patterns and explanations of abundance along the margins of adjoining habitats. We suspect, as well, that the nature of the ecotone, and the difference in quality between habitats, will also play major roles in the optimum management strategy.

We begin, therefore, with a brief review of alternative models that yield unique predictions of abundance near habitat edges. We develop a strict but simple protocol for locating the boundaries between habitats and measuring the width of the ecotone. We test the protocol in boreal-forest habitats that should possess both gradual and abrupt boundaries. We then evaluate which of the "edge" models best applies to red-backed voles (*Clethrionomys gapperi*), which are suitable subjects because they appear not to compete with other common small mammals of the boreal forest (Getz 1969; Grant 1970; Morris 1983, 1996; Wolff and Dueser 1986; Stewart 1991; but see Crowell and Pimm 1976) and they occupy virtually all terrestrial boreal-forest habitats.

Patterns of abundance at ecotones

Imagine two homogeneous habitats, each composed of unique patches representing high- and low-quality microhabitats (Fig. 1). Quality can include such factors as predation risk and resource abundance. Imagine further that the ecotone between those habitats is composed of a mixture of the two patch types. Depending on which processes control density, three classes of abundance pattern have been described (Lidicker 1999; Lidicker and Peterson 1999).

The first and simplest is the null model that the abundance of individuals reflects the relative qualities of the two habitats and their ecotonal mix (1; the so-called matrix effect (Lidicker 1999; Lidicker and Peterson 1999); we prefer to call this the habitat effect). We interpret this null habitat model to mean that local density reflects local variation in population growth rate and, thereby, habitat quality. We differentiate it from models assuming density-dependent movements among habitats. Density-dependent movements imply that the boundary itself has an "emergent" effect on the pattern of density beyond that which can be explained by the separate influences of each habitat.

Though the emergent property is referred to commonly as an edge effect (Lidicker 1999), it carries additional significance because it suggests that the character of the landscape has an influence on distribution and abundance exceeding that of the sum of its component parts. The abundance of individuals in the ecotone may, for example, be higher or lower than that in either pure habitat (2; positive and negative "ecotonal effects," respectively; Lidicker 1999; Lidicker and Peterson 1999), or may be asymmetrically biased toward one habitat or another.

The abundance of individuals may drop off sharply from rich to poor habitat, or may even increase near the ecotone, if the edge represents a hard boundary that individuals cannot cross (3; the "edge-permeability effect"; Stamps et al. 1987a, 1987b; Duelli et al. 1990). Soft boundaries allow individuals to cross into, and through, the ecotone and may therefore be associated with either habitat or ecotone effects. For a given difference in "quality" between two adjoining habitats, one might expect that the "hardness" of an ecotone would vary inversely with its width.

A fourth effect is likely for density-dependent habitat selectors. If individuals select habitat in a way that maximises their fitness, and if they are free to occupy the habitat that they choose, their population density should reflect local variation in habitat quality as well as the quality of other nearby patches (Fretwell and Lucas 1970; Pulliam and Caraco 1984; Fagen 1987, 1988; Milinski and Parker 1991; Morris 1994, 1995). When individual home ranges at the boundary include elements of both habitats, for example, preferential exploitation of rich patches comes at the cost of moving through poorer ones (Rosenzweig 1981). Rich habitats subsidise the exploitation of their poorer neighbours. The "habitat-selection effect" will inflate density in poor habitat near the boundary. But just as rich habitats subsidise poor ones, exploitation of poor habitats tends to devalue adjacent rich ones. Density-dependent habitat selectors will experience deflated density in a rich habitat near the boundary with a poor one (Morris 1992). The habitat-selection effect should therefore be considered an emergent property of the landscape because the pattern of density in each habitat is altered by the presence of the ecotone.

If ecotones were all of the same width, one could easily test for the various edge effects by observing the change in density along a cline from one habitat into another. However, ecotones are unlikely to be of constant width, so the ability to detect an edge effect presupposes that we can first measure the ecotone between habitats. A subsequent comparison of mean densities on either side of, and within, the ecotone would then reveal whether density changes abruptly, or is inflated or deflated in the ecotone. A comparison of patterns of density on either side of variably wide ecotones would reveal asymmetries as well as the effect of habitat selection.

The first step in the search for edge effects must therefore include a measure of the ecotone itself. Though several algorithms exist in the literature for both one-dimensional data (e.g., moving split-windows; Ludwig and Cornelius 1987) and two-dimensional data (Fortin 1994), they are often designed for data sets that "cross" many habitat boundaries. A much simpler protocol can be used where sample transects cross the ecotone between two well-defined habitats.

A protocol for measuring ecotones between two habitats

Imagine a transition between two pure habitats composed of unique patches of high and low quality (Fig. 1). The objective is to determine which points along a transect perpendicular to the common border correspond to the ecotone. An effective protocol will include measures of habitat along the transect plus an objective statistical analysis that can detect where one habitat grades into the other. We outline such a protocol, and the specific techniques we used, in Table 1.

Our protocol assumes that transects extend into each habitat for a distance exceeding the ecotone. An implicit assumption, therefore, is that the habitats are different enough, and the investigator has sufficient acumen in natural history, that transects can be located more or less symmetrically across the habitat boundary. We do not perceive this as a crucial limitation because similar assumptions apply to any field study in ecology.

Table 1. An objective protocol to determine the location and width of ecotones between two habitats.

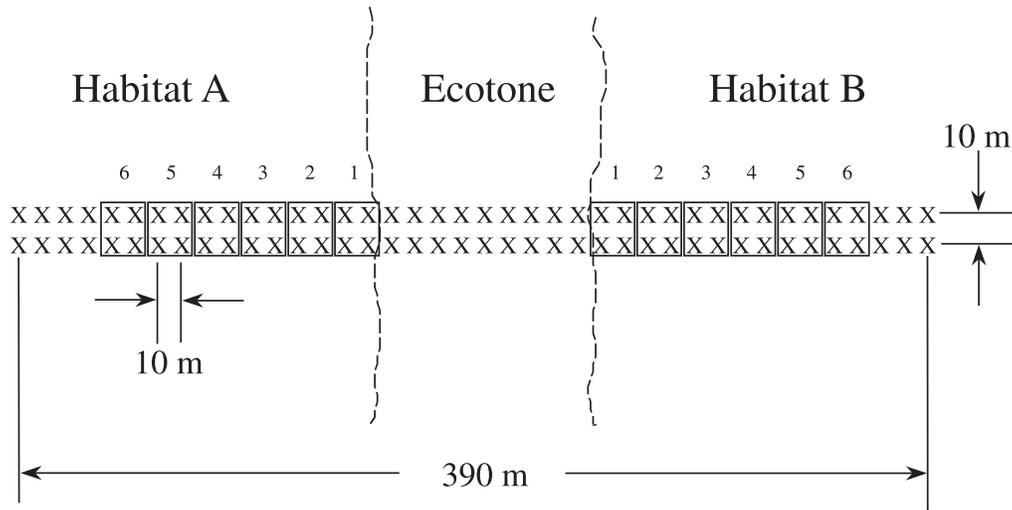| Step	Description
1	Locate transects perpendicular to an apparent edge between adjacent homogeneous habitats and quantify characters of habitat relevant to the species of interest at each of many systematically located sampling stations
2	Ordinate the habitat data array for each transect to derive simplified and independent habitat variables (we used PC analysis (Norušis 1994a; FACTOR procedure))
3	Select a subset of homogeneous stations near each end of the transect to represent the standard of comparison for each habitat (we used stations 5–12 and 29–36 in our 40-station transects)
4	Use multivariate ANOVA (we chose DFA (Norušis 1994a; DISCRIMINANT procedure)) on the ordination scores of the selected stations to differentiate between the two habitats
5	Choose one of the two habitats and calculate the probability that each station belongs to that habitat (we calculated the probabilities from the frequency distribution of DFA scores; Norušis 1994a)
6	Define ecotone boundaries to occur where the classification probabilities of consecutive stations correspond to a discontinuity in the data (we chose 0.67 and 0.33 to divide the probability of habitat membership into three equal groups (one for each of the two habitats plus the ecotone, $P \geq 0.67$, $P \leq 0.33$, and $0.67 > P > 0.33$, respectively))
7	Define the ecotone as the distance between ecotone boundaries

Methods

Field sites and data collection

We applied the ecotone-detection protocol along eight belt transects crossing habitat edges in a 25-km^2 study area located within the boreal forest of northwestern Ontario (48°55′N, 89°55′W) during the summers of 1994 and 1995. Four transects crossed apparently sharp edges between contiguous conifer and cutover (approximately 15 years old) habitats. Coniferous forest consisted of mature jack pine (*Pinus banksiana*), white spruce (*Picea glauca*), and black spruce (*Picea mariana*), with a relatively open understorey 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 grass ground cover (especially *Calamagrostis canadensis*). The remaining four transects crossed what we expected to be more gradual boundaries between coniferous and deciduous forest composed primarily of trembling aspen (*Populus tremuloides*), balsam poplar (*Populus balsamifera*), and white birch (*Betula papyrifera*), with a dense shrub understorey dominated by alder (*Alnus viridis*), mountain maple (*Acer spicatum*), and beaked hazel (*Corylus cornuta*). Deciduous and coniferous forests originated following a fire that burned the entire study area in 1911.

We located two parallel livetrapping lines 10 m apart perpendicular to, and centred on, apparent habitat edges. Trapping lines comprised 40 stations at 10-m intervals (Fig. 2). We set a single Sherman live trap baited with oats, a slice of potato, and cotton nesting material at each station and checked every trap during the morning and evening of each 48-h trapping session. We habituated

Fig. 2. Schematic of a belt transect used to assess edge effects for red-backed voles inhabiting two boreal-forest habitats (A and B) in northwestern Ontario. The broken lines represent ecotone boundaries, the "X"s correspond to live-trap and habitat-sampling stations, and the 12 boxes enclose stations used to estimate red-backed vole density at six distance classes.

Table 2. Variables used to quantify the structure and composition of habitats used by red-backed voles occupying boreal-forest habitats in northwestern Ontario.

Variable	Description
Q_1	Mean quantity of vegetation 0.125 m above the ground
Q_2	Mean quantity of vegetation 0.25 m above the ground
Q_3	Mean quantity of vegetation 0.5 m above the ground
Q_4	Mean quantity of vegetation 1.0 m above the ground
Q_5	Mean quantity of vegetation 1.75 m above the ground
FHD	Foliage height diversity ($1/\Sigma P_i^2$, where $P_i = Q_i/\Sigma Q_i$)
Mat	Mean depth of litter (dead but structurally intact vegetative matter; mm)
Numcon	Number of conifer trees within a 3.0-m radius
Numdec	Number of deciduous trees within a 3.0-m radius
Areacon	Summed basal area of conifer trees within a 3.0-m radius
Areadec	Summed basal area of deciduous trees within a 3.0-m radius
Stumps	Number of stumps within a 3.0-m radius
Fallen	Number of fallen trees within a 3.0-m radius
ShrubC	Percent ground cover of shrubs within 16-m^2 plot
ForbC	Percent ground cover of forbs within 16-m^2 plot
GrassC	Percent ground cover of grasses within 16-m^2 plot
WoodC	Percent ground cover of woody material within 16-m^2 plot
MossC	Percent ground cover of mosses within 16-m^2 plot
LitterC	Percent ground cover of litter within 16-m^2 plot
BarrenC	Percent ground cover of rock and soil within 16-m^2 plot
FernC	Percent ground cover of ferns and club mosses within 16-m^2 plot

animals to capture by livetrapping each transect at least twice at 2-week intervals. All analyses were conducted on data from the final 2 weeks of each census, corresponding to the time period when we measured vegetation and habitat structure. Captured animals were individually marked and measured (body length, body mass), their sex was recorded, and they were released.

We quantified structural components of vegetation known to be important predictors of small-mammal density (e.g., 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 2). We measured horizontal foliage profiles (Q_1–Q_5) by estimating the percent vegetation cover using a 10×20 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 in the four cardinal directions relative to an initial random heading. We measured the depth of litter (dead but structurally intact vegetation) at the four corners of a 4×4 m randomly oriented plot centred at the station. We estimated percent cover of shrubs, forbs, grass, woody material, mosses, litter, rock and soil, and ferns/club mosses at each station within the 16-m^2 plot. Finally, we recorded the number of stumps and fallen logs and the diameter at breast height (> 4 cm) for all tree species within a radius of 3 m from each station.

Analysis

We began our analyses by applying the ecotone protocol (Table 1). At step 2 we excluded variables from the principal components (PC) analysis with minimum measures of sampling adequacy (Norušis 1994a; FACTOR procedure) until the overall Kaiser–Meyer–Olkin measure was greater than 0.75. We retained PCs that corresponded, in each case, to a substantial increment in the variance "explained" by successive PCs (eigenvalues > 1.6). We selected eight stations in the centre of each uniform habitat (stations 5–12 and 29–36) to represent homogeneous units for habitat classification, then completed steps 3–7 of the protocol.

We searched for the four edge effects using relative densities of *Clethrionomys gapperi* estimated from the minimum number of individuals known alive (MNA; Hilborn et al. 1976) in six 2×2 live-trap grids (10×10 m) oriented adjacent to the ecotone along each transect (Fig. 2). Stations at the ends of a transect (stations 1 and 40 of both parallel trapping lines) were never included because unequal rodent sampling by means of terminal traps might bias estimates of density (van Horne 1982). The MNA can itself produce biased density estimates (Efford 1992), but for boreal-forest rodents it is highly correlated ($r > 0.9$) with mark–recapture estimates of population density (Morris 1996). The densities of species other than *Clethrionomys* were too low for a reliable assessment of patterns of population density.

Table 3. PC summary, DFA classification success, and ecotone width for transects crossing deciduous–conifer (D) and cutover–conifer (C) habitat boundaries in northwestern Ontario.

Transect	No. 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 > 1.6.
[b]Based on discriminant scores, $P < 0.0001$ for all DFAs.

Our estimates of local density are spatially interdependent. An individual vole could, in principle, contribute to our MNA estimates on four different "grids" (four trapping rotations in 48 h). Areas with many voles would nevertheless yield higher estimates of local density than areas with few voles. The lack of spatial independence can thus act as a form of "smoothing" along our transects that reduces spatial variance in density, and maximises our ability to detect spatial clines in density. Our habitat data are also spatially correlated. Spatial correlation does not represent a problem for the ecotone protocol, however, because habitats are classified on the basis of homogeneous subsets of stations well away from the ecotone.

We tested for ecotone and permeability effects by contrasting densities in the ecotone with those on either side. Positive or negative ecotonal effects would be revealed if densities were respectively higher or lower in the ecotone than in either habitat. A permeability effect (hardness) would occur if voles tended to avoid the ecotone altogether.

We tested for habitat-selection effects with two $2 \times 2 \times 6$ repeated-measures analyses of variance (ANOVAs) of the MNA for red-backed voles in each 10×10 m subplot (Norušis 1994b; REPEATED MEASURES procedure). Repeated-measures designs are most frequently used for analysing temporal data (e.g., von Ende 1993), but are also suited to the analysis of spatial effects (Morris 1997). One analysis (design 1) was used to test for an edge effect, based on our a priori classification of conifer versus non-conifer habitats. We were concerned that voles might classify habitats differently. We repeated the analysis (design 2) by contrasting habitats with high and low densities of red-backed voles, irrespective of our original classification. Transects were treated as subjects, with boundary type (abrupt or gradual) as a between-transects factor and distance from the ecotone (six classes) and habitat as within-transects factors.

We identified the habitats with high and low vole density in each transect by means of a t test on densities estimated for stations paired across adjacent trap lines. We excluded terminal stations as well as those ≤60 m from calculated ecotone boundaries to minimise sampling in the zone where densities may respond to the presence of the edge. Sixty metres represents the approximate diameter of the circular home range of a red-backed vole (0.28 ha; Blair 1941; Morris 1955; Beer 1961; Tallmon and Mills 1994).

We analysed each repeated-measures design with and without covariates of PC scores calculated for each sample plot. Our purpose in doing so was to partial out any variation in vole density that could be attributed to microhabitat. All analyses had similar outcomes. A significant habitat-selection effect would be revealed if vole densities are different in the two habitats, and if density is intermediate near the habitat–ecotone interface (a significant distance × habitat interaction). Note that the design can also assess permeability differences between abrupt (hard) and gradual (soft) boundaries (revealed by a significant interaction between type of boundary and distance).

Results

The location and width of ecotones

Two to four PCs accounted for 50–67% of the habitat variation along each transect (Table 3). The first PC revealed a gradient from areas with a diverse foliage profile of tall shrubs to areas with a relatively open understorey and low horizontal diversity. Additional PCs tended to describe clines between dense forests with a deep litter layer to open forests with shallow litter (Kingston 1997).

All two-group discriminant function analyses (DFA) distinguishing between habitats were highly significant. Each DFA correctly classified the vast majority of paired stations (91–100% classification success; Table 3). Two classes of ecotones corresponded to abrupt (≤20 m) and gradual edges (70–90 m; Table 3) that might reasonably be associated with conifer–cutover and conifer–deciduous habitat boundaries. Indeed, three of the four ecotones between conifer and cutover habitats were narrower than we could detect with our protocol (minimum sampling distance 10 m). Contrary to our original field design, one conifer–cutover habitat boundary was more gradual than expected (transect C4, 70 m). Similarly, one conifer–deciduous habitat boundary was abrupt (transect D4, 20 m). The results from the two "unusual" transects emphasise the importance of using objective criteria to determine the location and width of ecotones.

Patterns of density near habitat boundaries

Red-backed voles dominated the small-mammal community (Table 4). Vole density was significantly higher in one habitat than in the other for seven of the eight transects (Table 5). Mean vole density was higher in deciduous habitat than in adjacent coniferous forest (three of four comparisons). Habitat preference between conifer and adjacent cutover habitats (as indicated by population density) was unpredictable (mean density was higher in conifer habitat on two transects and higher in cutover habitat on two transects).

There was no obvious ecotonal effect. The density of voles in the ecotone was intermediate to that in the two habitats in two of five comparisons where ecotones were wide enough to allow vole density to be calculated (Table 5). Vole density was lower in the ecotone than in either adjacent habitat in

Table 4. Small-mammal captures during the final census period on transects crossing deciduous–conifer (D) and cutover–conifer (C) habitat boundaries in northwestern Ontario.

Transect	Year	Species							
		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 (—)	2 (2)	2 (2)	0 (0)	0 (0)	0 (0)
C1	1995	76 (28)	20 (9)	16 (—)	2 (2)	0 (0)	1 (1)	6 (5)	3 (2)
C2	1995	52 (18)	24 (13)	5 (—)	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)

Note: 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), *Lepus americanus* (6), *Tamiasciurus hudsonicus* (5), *Sorex cinereus* (6), *Mustela erminea* (5), and *Glaucomys sabrinus* (1). Numbers in parentheses show the number of individuals; a dash indicates that the number is not known because some individuals were unmarked.

Table 5. Density of red-backed voles along transects crossing deciduous–conifer (D) and cutover–conifer (C) habitat boundaries in northwestern Ontario.

Transect	Habitat	Mean N	Ecotone N	Habitat	Mean N	t	P
D1	Deciduous	4.13	1.57	Conifer	1.73	2.98	0.008
D2	Deciduous	2.00	2.71	Conifer	0.88	2.43	0.026
D3	Deciduous	4.22	2.44	Conifer	1.75	3.00	0.009
D4	Deciduous	1.88	0.00	Conifer	1.64	0.39	0.703
C1	Cutover	0.08	—	Conifer	2.29	6.05	<0.001
C2	Cutover	0.62	—	Conifer	1.62	2.35	0.031
C3	Cutover	2.83	—	Conifer	1.38	2.23	0.036
C4	Cutover	1.50	0.57	Conifer	0.31	2.64	0.017

Note: N is the minimum number of individuals known to be alive (MNA) at pairs of capture stations on two adjacent trap lines; abrupt ecotones in transects C1, C2, and C3 did not contain capture stations.

two other transects and higher in one. Voles had no consistent preference for, or aversion to, ecotones; there was no permeability effect.

Differences in vole density between the 2 years of our study could have affected our ability to detect permeability differences between abrupt and gradual boundaries because three gradual boundaries were enumerated in 1994 compared with three abrupt ones in 1995 (Tables 4 and 5). We were unable to include annual effects in our repeated-measures analyses (to do so would have created an unbalanced design), so we used t tests to search for annual differences in voles captured in cutover, deciduous, and conifer habitats. There was no significant annual change in population density in either deciduous ($t_{30} = 1.36$, $P > 0.18$) or conifer habitats ($t_{66} = 0.69$, $P > 0.49$). Mean density in cutover habitats was significantly higher in 1994 than in 1995 ($t_{31} = 7.77$, $P < 0.001$). Only one cutover transect (C3) was trapped in 1994, however, and it may represent especially suitable vole habitat because voles were more abundant there than in the adjacent coniferous forest (Table 5). The fire-origin deciduous and coniferous forest replicates are more similar to one another than are the cutover replicates of slightly different ages and with somewhat different harvest and silvicultural histories. We find no compelling evidence of interannual differences in population density that would bias our conifer-dominated analyses.

No main effect or interaction was close to statistical significance for either of the repeated-measures ANOVA designs. All significance values were greater than 0.20 for the conifer – non-conifer analysis (design 1) and greater than 0.23 for the high–low vole density analysis (design 2). We were concerned that the analysis could be biased by the two "unusual" transects (i.e., D4, the abrupt boundary between coniferous and deciduous forest, and C4, the gradual boundary between coniferous forest and cutover). We deleted both transects and repeated the analysis. The results were unchanged. No main effect or interaction was close to statistical significance for either design 1 (all $P > 0.28$) or design 2 (all $P > 0.16$). There was no habitat-selection or permeability effect.

Discussion

Despite significant differences in population density between clearly defined habitats on our transects, we were unable to detect anything other than a matrix (habitat) effect for red-backed voles. The absence of an edge effect is consistent with the results of a recent study by Bayne and Hobson (1998), who failed to detect an edge effect for this species (though our designs were quite different).

Differences in vole density between habitats agree with the results of earlier studies that implicated density-dependent

Fig. 3. Mean densities of red-backed voles along eight transects crossing ecotones between boreal-forest habitats in northwestern Ontario. (A) Actual mean densities observed along transects. (B) Simulated mean densities resulting from increasing and decreasing the density in subplots adjacent to the ecotone. (C) Simulated mean densities resulting from increasing and decreasing the density in all subplots (except the most distal one) to alter the "slope" of density toward the ecotone. Distance classes correspond to 10×10 m subplots.
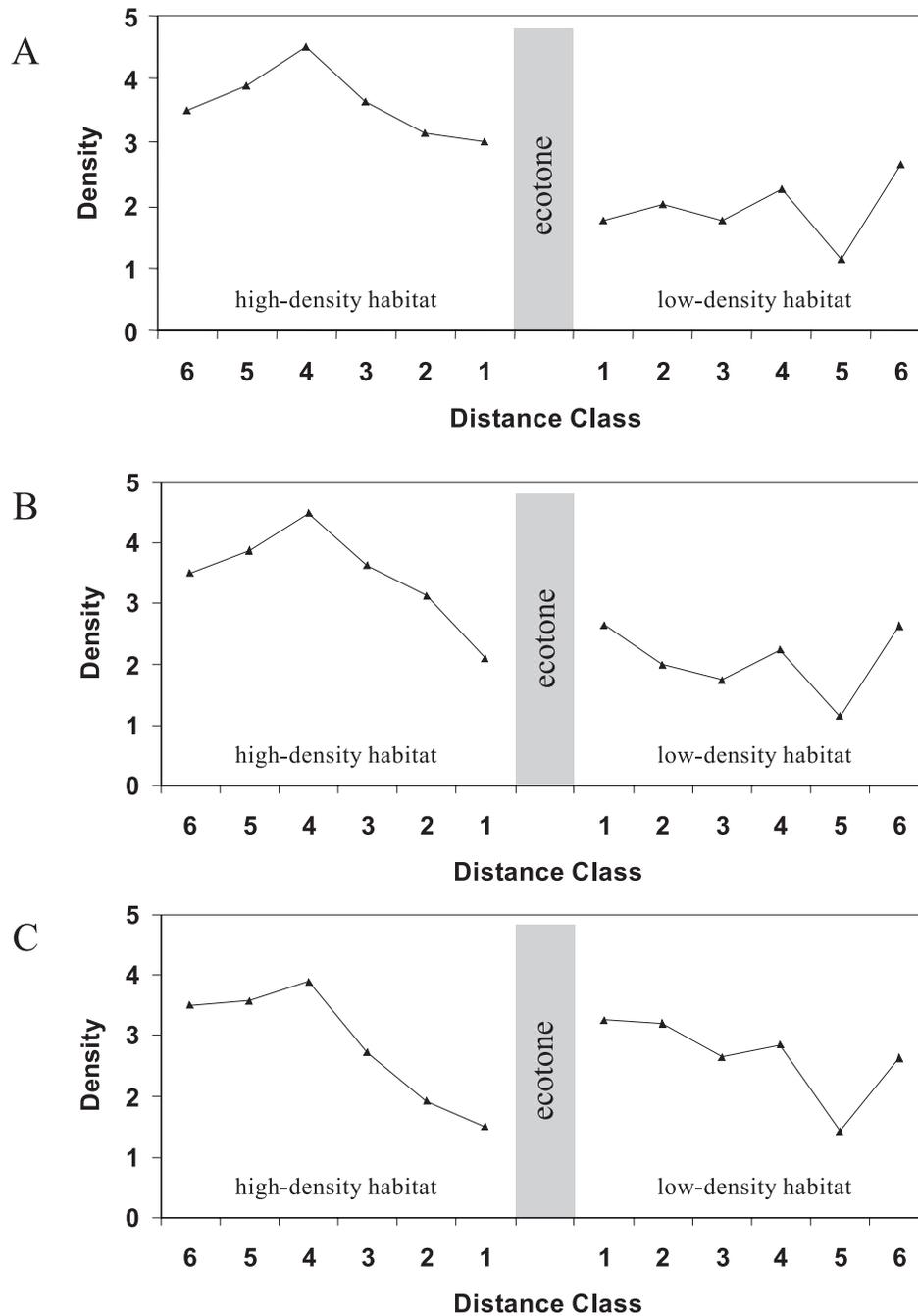
habitat selection by red-backed voles (e.g., Kirkland and Griffin 1974; Vickery 1981; Morris 1984, 1987, 1989, 1996; Wywialowski and Smith 1988; Knight and Morris 1996). There was no consistent pattern of higher vole density in one kind of habitat than in another. The density of red-backed voles in northern Ontario, at the scale of our study, appears to respond more to local differences between habitats than to overall habitat type (density-dependent habitat selection). But the absence of an edge effect in a habitat-

selecting species is difficult to reconcile with the results of studies on deer mice (*Peromyscus maniculatus*) crossing badland to prairie habitats, which revealed an unambiguous signal caused by habitat selection (Morris 1992, 1997), and studies on other small-mammal species that reported edge-related effects on density (Walters 1991; Hansson 1994; Mills 1995; Sekgororoane and Dilworth 1995; Manson et al. 1999). Three non-independent interpretations seem reasonable. (1) The abundance of red-backed voles varies with lo-

cal differences in quality among the three habitats, but the pattern is inconsistent and may contribute to an apparent inability to recognise boundaries between them. (2) The habitats where we searched for edge effects are not different enough to create a detectable signal in the abundance of habitat-selecting voles. (3) Our sampling regime was not sufficient to detect subtle differences in abundance near ecotones that are caused by habitat selection.

We attempted to differentiate between these three possibilities by means of simulations that investigated, given our sample sizes and measured variance in vole density, the size of gradient in density that would be required to allow us to detect a habitat-selection effect in our analysis. First, we sequentially increased the number of voles captured in the "low-density" 10×10 m subplot adjacent to the ecotone while simultaneously subtracting an equal number on the opposite side of the ecotone in the first adjacent "high-density" subplot. The "treatment" attempts to convert the known differences in density between habitats into a cline of high to low densities adjacent to the ecotone (Fig. 3). The simulation was stopped at that first density where we forced a significant habitat $\times$ distance interaction ($P < 0.05$) in the repeated-measures ANOVA. The analysis became significant ($P = 0.049$) only when the adjusted mean vole density on subplots adjacent to the ecotones was greater in the low-quality habitat (2.65) than in the high-quality habitat (2.10; Fig. 3).

We repeated the simulation by successively increasing (low-density habitat) or decreasing (high-density habitat) vole density linearly along each transect. This simulation created a mirror-image cline in vole abundance from the most distal ends of the transect toward the ecotone. Note that the algorithm alters only the "slope" of vole abundance toward the ecotone (habitat-selection effect) and maintains our measured variance in vole density. Again, the simulated repeated-measures ANOVA was significant only when the adjusted mean density in the low-density subplot adjacent to the ecotone (3.25) exceeded that in the high-quality habitat (1.50; Fig. 3).

Our simulations, and convincing evidence of the habitat preferences of red-backed voles from other studies, support our hypotheses (1 and 2) that differences between these boreal-forest habitats may be too inconsistent and insufficient to allow detection of a habitat-selection effect (but perhaps not other kinds of edge effects). Though red-backed voles use a broad array of forest types, they have more restricted habitat preferences than generalist deer mice, for which Morris (1997) detected a habitat-selection effect across abrupt ecotones. Indeed, all habitats exploited by voles in our study represent forests with a substantial tree canopy (albeit of different types and different ages) which may be so similar to one another that the voles cannot detect an "edge" between them, even when the ecotone is abrupt. Voles appear to respond to differences in habitat (i.e., are more abundant in one habitat than in another), but appear incapable of detecting the actual boundary between habitats of different quality.

Both simulations demonstrated that we could have detected a habitat-selection effect for red-backed voles only if they reversed their habitat preference near the ecotone. A larger sample of transects would, of course, have increased our chances of detecting any small difference in density that may be associated with ecotones between similar habitats (hypothesis 3). Given the results of the simulations, and the

clear signal in deer mice across steep prairie–badland ecotones (Morris 1997), we question whether small differences have any ecological significance. It is true that the process of habitat selection should operate across any ecotone between different habitats. But if the difference between habitats is small relative to the variance in rodent density, the small habitat-selection effect would be easily masked by natural "noise" in abundance. We remind sceptics that our purpose was to evaluate, with reasonable replication, whether or not edge effects exist for red-backed voles across habitat boundaries between adjacent boreal-forest habitats. On this point our results are clear. The abundance of voles responded primarily to differences in habitat, and there is no need, at least in our system and at the scale of our interest, to invoke any form of edge effect to account for their abundance across habitat boundaries.

Theories of habitat selection provide a useful paradigm for evaluating edge effects and generating explicit a priori predictions to be tested in future experiments. Manipulations that modify the width of ecotones, and the differences in quality between adjacent habitats, hold special promise. We urge managers and ecologists, when they have the opportunity and mandate, to design habitat boundaries that will facilitate these essential experiments.

Acknowledgments

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