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## HOW MANY HABITATS DO LANDSCAPES CONTAIN?<sup>1</sup>

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**Abstract.** The successful integration of theories of habitat selection into landscape ecology depends upon the proper identification of habitat. Habitats must be distinguished at appropriate spatial scales, and evidence must be provided that individuals recognize and respond to the habitat classification. We use evolutionary theories to document how density-dependent habitat selection and habitat variation can be applied to identify habitats in landscapes. We apply our protocol to small-mammal (*Clethrionomys gapperi*) populations across a series of repeated landscapes in the Hudson Bay Lowland of Ontario, Canada. We postulated initially that the landscapes were composed of two easily distinguishable habitats, but our protocol demonstrated three habitat types influencing density-dependent habitat selection by *C. gapperi*. The third habitat has profound implications for population regulation in the lowland and highlights the importance of proper habitat identification.

**Key words:** *Clethrionomys*; density-dependent habitat selection; evolutionary theories of habitat selection; habitat classification across landscapes; habitat identification within landscapes; Hudson Bay, Ontario; isodar analysis; landscapes; northern wetlands; population regulation; small mammals.

### INTRODUCTION

Numerous protocols have been proposed to detect relevant spatial scales of habitat variability in ecological landscapes (e.g., Allen and Hoekstra 1991, O'Neill et al. 1991, Johnson et al. 1992). Few explicitly recognize that a landscape is a matrix of habitats (sensu Dunning et al. 1992) whose identity, scale, and spatial organization are determined by the individuals that exploit it. The ecological and evolutionary significance of habitats to individuals must, therefore, be included among the criteria that ecologists use to identify habitat.

We demonstrate how to use density-dependent habitat selection and microhabitat variation to differentiate objectively among habitats. We apply our approach to small mammals occupying repeated northern landscapes. The results illustrate that our interpretations of landscapes, patterns of abundance, and even spatial population regulation, depend critically upon the correct classification of habitat.

### HABITAT SELECTION IN LANDSCAPES

Imagine a series of simple landscapes with a repeated pattern of two alternating and structurally distinct habitats. Assume that each patch of habitat is larger than an individual's home range (e.g., a coarse-grained environment, Levins 1968). Individuals moving from one patch to another would necessarily relocate their home range. We interpret density-dependent habitat selection

to imply that the distribution of individuals among habitats changes with density. This definition is consistent with the view that average individual fitness in each habitat declines with increased density and that individuals assess the trade-off between potential reproductive success and density to select habitat in a way that maximizes individual fitness (Fretwell and Lucas 1970, Rosenzweig 1981, Morris 1987). The density in each habitat can thus be used to estimate its relative suitability.

Consider two adjacent habitats, 1 and 2, where Habitat 2 yields a lower maximum fitness than does Habitat 1 (Fig. 1). At low population densities ideal individuals will always select Habitat 1 because it conveys greater individual fitness. This is true until the population density in Habitat 1 reaches a threshold ( $t$ ) at which individuals expect to achieve equal fitness regardless of which habitat they choose. From this density upwards individuals will distribute themselves between habitats in such a way that their expected fitness is equal across all occupied patches.

The ideal free distribution (Fretwell and Lucas 1970) in Fig. 1 can be redrawn as an isodar, a plot of the joint densities in the two habitats, such that the expected fitness of an individual is identical in each (Morris 1988, 1990, 1992). The isodar can be estimated by

$$N_{A1} = C + bN_{A2} \quad (1)$$

where  $N_{A1}$  and  $N_{A2}$  are the densities of species *A* in Habitats 1 and 2 respectively,  $C$  represents the intercept, and  $b$  is the isodar slope (Morris 1987, 1988, 1989).

Isodars with non-zero intercepts (fitness at low density is unequal between habitats), isodars with slopes different from unity (the relationships between fitness and density in the habitats diverge or converge; e.g.,

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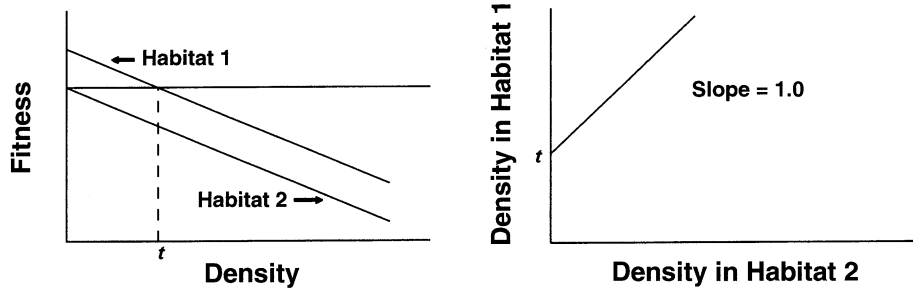


FIG. 1. Hypothetical fitness–density graph (left) and corresponding isodar for ideal free habitat selectors (right). Individuals should always choose Habitat 1 at low population densities until the threshold ( $t$ ), beyond which equivalent fitness can be attained in Habitat 2. Isodars can be constructed for other forms of ideal habitat selection (Morris 1994, 1995).

Morris 1994), or curvilinear/nonlinear isodars (the underlying fitness–density curves deviate from linearity), reflect changes in the distribution of individuals among habitats with changes in density (Morris 1994). Such statistically significant regressions of population density in a pair of habitats are consistent with density-dependent habitat selection but are also consistent with alternatives such as habitat-specific differences in growth rate (Morris 1988). These alternatives may be a concern if the research aims to evaluate density-dependent habitat selection and its mechanisms. They should not be a concern if the objective is, as here, to document the number of different habitats that influence population density.

Imagine that we have obtained replicated estimates of relative population density in pairs of habitat patches representing each of the two habitats. To create an isodar empirically we plot the density from one habitat against the other for each pair, and solve by model II regression (independent variation in both the X and Y variables [Sokal and Rohlf 1981]) (Morris 1987). A significant regression is consistent with density-dependent habitat selection. If, on the other hand, the isodar is nonsignificant we may speculate that habitat selection, if it occurred at all between that pair of habitats, is independent of density.

Now imagine that the relative qualities of the two

habitats vary across landscapes. Although the habitats appear superficially similar to the investigator they may differ dramatically in the relative fitness conveyed to individuals of the habitat-selecting species. We consider two alternatives. (1) One or both habitats vary randomly within and among landscapes (Fig. 2). This will increase the scatter about the common isodar. (2) The habitats may be exploited as three or more functionally different types, each with its own relationship between fitness and density (Fig. 3). Residual scatter about the isodar will reflect the third (or more) habitat(s). This would mean that the individuals had recognized two or more habitats that had been improperly lumped together by the investigator (Morris 1995).

We imbed these characteristics of habitat selection in a simple field protocol (Table 1: steps 1–3) and apply it to patterns of red-backed vole (*Clethrionomys gapperi*) population abundance in vast northern wetlands. The wetlands are simple landscapes composed of two easily distinguishable habitat types.

We begin by using regression analysis to identify whether habitat selection occurs between habitats. We then examine residuals of the regression for patterns suggesting that red-backed voles recognize further subdivisions in habitat. We use detailed measures of microhabitat and cluster analyses to objectively divide one of the habitats in two and repeat the regression.

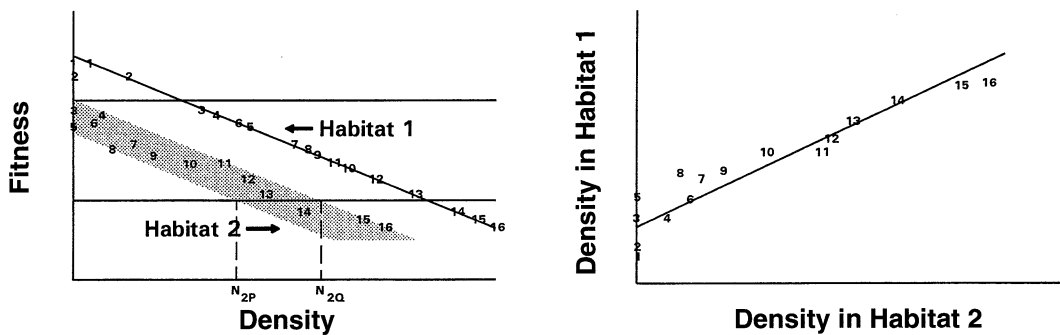


FIG. 2. Habitat quality may vary within a habitat. Variation results in a band of possible fitness–density combinations (left) and consequently an increased scatter about the isodar (right). Corresponding numbers identify paired habitats. In this example,  $N_{2P}$  and  $N_{2Q}$  identify the range of population densities possible at a given level of fitness in Habitat 2.

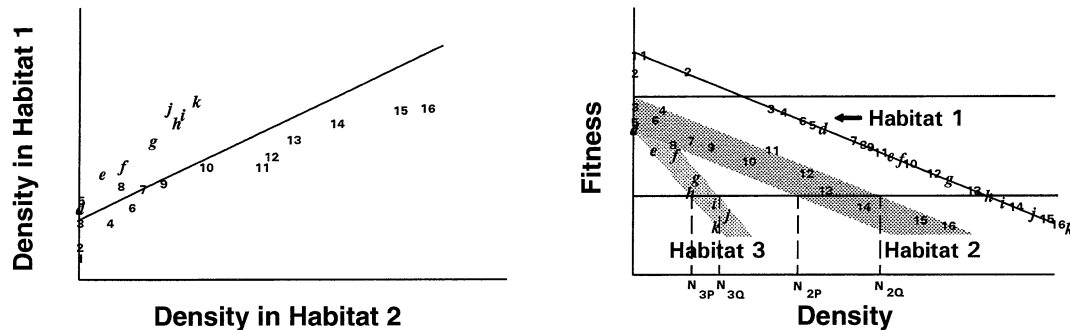


FIG. 3. An isodar with patterned residuals (left) may indicate multiple habitats (right). Habitats perceived as different by the organism have been lumped into one habitat classification. Corresponding numbers (Habitats 1 and 2) and letters (Habitats 1 and 3) identify paired habitats. In this example,  $N_{2P}$ ,  $N_{2Q}$  and  $N_{3P}$ ,  $N_{3Q}$  identify the ranges of population densities possible at a given fitness in Habitats 2 and 3, respectively.

This process is iterated until all habitats are identified. Each successive iteration enhances the resolution of habitat classification.

#### STUDY AREA AND METHODS

We tested the protocol (Table 1) over a large geographic scale, encompassing 700 km along the coasts of both Hudson and James bays in the Hudson Bay Lowland of Ontario, Canada (HBL). Isostatic uplift has created a series of landscapes composed of two simple and repeated landforms: raised beach ridges interspersed with low-lying wetlands. These landforms provide two basic habitats occupied by ubiquitous red-backed voles.

Three sites isolated over  $4^\circ$  latitude and  $6^\circ$  longitude were sampled intensively, two during 1990, and one during 1991. Shagamu (1990;  $55^\circ 49' N$ ,  $86^\circ 37' W$ ), a site on the Hudson Bay coast, has a climate that is heavily influenced by the cooling effects of the bay. Ridges are characterized by open subarctic tundra with sparse tree distribution. Wetlands range from open fen to shrub-covered fen. Ekwan (1990;  $53^\circ 27' N$ ,  $82^\circ 10'$

W) and Longridge (1991;  $51^\circ 49' N$ ,  $80^\circ 41' W$ ), sites on the James Bay coast, have more "temperate" climates characterized by boreal forest vegetation. Ridges are generally covered with mature spruce-lichen forest. Wetlands are more variable than those on the Hudson Bay coast, ranging from open sedge fen to sparse black spruce and tamarack forest with deep sphagnum and moss cover (Knight 1993).

#### Sampling across landscapes—Steps 1 to 3

**Paired sampling plots—Step 1.**—Red-backed voles, as well as other small mammals, were censused and habitat was quantified from May to September during each of the 2 yr. Two live-trap transects separated by  $\approx 1$  km were set roughly perpendicular to the orientation of the ridge-wetland landscape at each of the three sites (Fig. 4). Four pairs of  $60 \times 60$  m plots were trapped ( $4 \times 4$  array, 20-m spacing) along each transect. A pair consisted of one plot in ridge habitat and one in wetland habitat separated by 100 m (Fig. 4). The same ridge or wetland was sampled once only.

**Small mammal trapping—Step 2.**—Three sampling

TABLE 1. A protocol to identify habitats.

|                                 |  |
|---------------------------------|--|
| Field portion, steps 1–3        |  |
| 1)                              | Select two or more primary habitat types within or across landscapes.  |
| 2)                              | Estimate population density in sampling plots (or transects, Morris [1992]) located in paired patches of each habitat. Attempt to design a sampling regime that maximizes the number of paired samples.  |
| 3)                              | Measure microhabitat (e.g., Morris 1987) in each of the sampling plots.  |
| Statistical analysis, steps 4–8 |  |
| 4)                              | Summarize the microhabitat measures with multivariate analysis (we use principal components analysis).   |
| 5)                              | Use the resulting summary (e.g., principal component scores) to confirm the initial habitat divisions (we use discriminant function analysis).   |
| 6)                              | Create an isodar for each pair of habitats with model II regression (we use geometric mean regression) of population density in one habitat against density in another for all paired estimates.   |
| 7)                              | Examine the residuals from the statistically significant isodars.  |
| 8a)                             | If patterns suggesting an additional habitat exist in the isodar residuals then: <ol style="list-style-type: none"> <li>i) Identify potential subdivisions in habitat by cluster analysis on the microhabitat summary (principal components) for all sampling plots within each of the initial habitat divisions,</li> <li>ii) Use the largest microhabitat discontinuity to divide one of the habitat types in two;</li> <li>iii) Create new isodars based on the new habitat divisions;</li> <li>iv) Repeat step 7;</li> </ol> |
| 8b)                             | Otherwise stop.  |

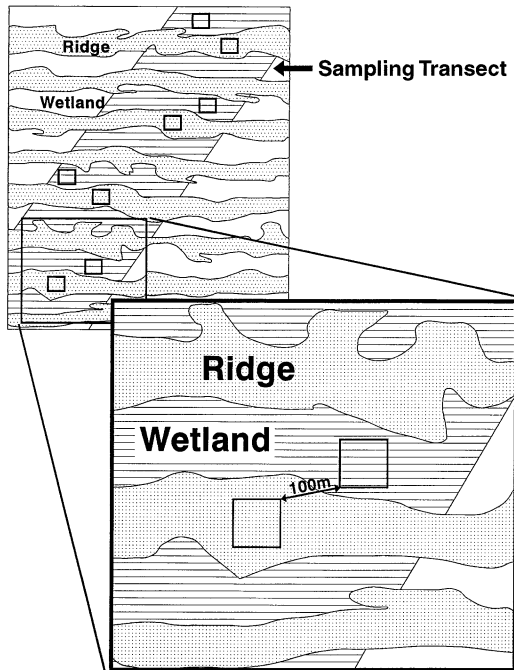


FIG. 4. Illustration of one sampling transect showing paired sampling plots on alternating ridge and wetland habitats in the Hudson Bay Lowland. The inset illustrates one pair of  $60 \times 60$  m plots separated by 100 m.

periods were equally spaced at 6-wk intervals during each field season (15 May–20 June, 21 June–31 July, 1 August–15 September). Single Longworth live-traps (Penlon Ltd., Abingdon, England) were set at all stations on one transect for a period of three consecutive nights and were checked at dawn and dusk each day. Data from the final census only, the period of highest rodent density at all locations, were used in the spatial analyses. Including data from all three seasons would complicate the analyses with autocorrelated density estimates.

All captured mammals were marked individually. Relative density was estimated as the total number of different individuals caught on each grid (minimum number known alive [MNA]; Hilborn et al. 1976). Efford (1992) demonstrated that MNA can yield biased estimates of absolute density; the isodar analyses we report here require only precise relative densities.

**Habitat analysis—Step 3.**—A series of nested quadrats ( $50 \text{ m}^2$ ,  $25 \text{ m}^2$ , and  $0.125 \text{ m}^2$ ) oriented on a randomly selected compass heading were located at the four central stations of each plot to estimate vegetation biomass and physical characteristics of the habitat (Table 2; Knight 1993). Trees, saplings and seedlings were sampled in the largest ( $50\text{-m}^2$ ) quadrat (Hosie 1969); shrubs, wood, rock, soil, and water in the  $25\text{-m}^2$  quadrat (Soper and Heimburger 1982); and grasses, sedges, herbaceous plants (Johnson 1987), lichens and mosses, soil, rock, pebble, and wood in the  $0.125\text{-m}^2$  quadrat.

#### Statistical analysis—Steps 4 to 12

**Summary of microhabitat variables—Step 4.**—Variables describing vegetation and physical measures were summarized by principal components analysis (PCA) (Adler 1985, 1987, Kershaw and Looney 1985, Norušis 1990a: Procedure FACTOR). Only those variables that were represented at  $>5\%$  of plots and that had a unimodal and more-or-less symmetrical distribution after transformation were retained for use in subsequent analyses (Table 3). In all cases, data from the four stations within a sampling plot were pooled to give one estimate of each variable per plot.

**Confirmation of habitat divisions—Step 5.**—We used the principal component scores in two stepwise canonical discriminant function analyses (DFA) (Norušis 1990b: Procedure DSCRIMINANT, Wilks' method) to reconfirm habitat designations. DFA verified that ridges and wetlands were significantly different in terms of microhabitat composition.

**Isodar analysis—Step 6.**—We calculated isodars (Eq. 1) with geometric mean regression (Krebs 1989: 458–464). Low population densities at some plots presented a challenge for the isodar analyses. Eight pairs of plots had no *Clethrionomys gapperi* captures during the three trapping rounds. They were not included. The data were insufficient to determine, with certainty, whether these plots represented very low population densities in both habitats or whether they represented habitats that were incapable of supporting *C. gapperi* populations.

Some unusual density combinations were detected by the first isodar analysis. The isodar residuals suggested that our preliminary habitat divisions (ridge and

TABLE 2. Vegetation and physical sampling regime for each quadrat.

| Quadrat             | Vegetation estimates   | Physical estimates  |
|---------------------|--|---|
| $50 \text{ m}^2$    | Trees (dbh $\geq 30$ mm):<br>Number of each species<br>Diameter at breast height (dbh) of each tree<br>Saplings (dbh $< 30$ mm):<br>Number of each species<br>Seedlings (stem diameter $< 3$ mm): Number of each species |   |
| $25 \text{ m}^2$    | Shrubs: Percentage cover and average height, by species  | Wood, rock, pebble, soil, water:<br>Percentage cover<br>Mat depth:<br>1 estimate in each of 4 corners |
| $0.125 \text{ m}^2$ | Small shrubs, herbs, grasses, sedges, mosses, lichens:<br>Percentage cover, by species   | Soil, rock, pebble, wood:<br>Percentage cover<br>Mat depth:<br>1 estimate in each quadrat             |

TABLE 3. Variables used in principal components analysis of vegetation and physical characteristics of habitats. All variables were calculated from pooled measures at the four central stations of each plot.

| Variable | Description   |
|----------|---|
| LMAT     | Log <sub>10</sub> (mean mat depth)  |
| EMNI     | Arcsine square root(mean percentage cover by <i>Empetrum nigrum</i> )       |
| MOSS     | Arcsine square root(mean percentage cover by mosses)                        |
| SEDGE    | Arcsine square root(mean percentage cover by sedges)                        |
| SPHAG    | Arcsine square root(mean percentage cover by sphagnum)                      |
| VAVI     | Arcsine square root(mean percentage cover by <i>Vaccinium vitis-idaea</i> ) |
| LITTER   | Arcsine square root(mean percentage cover by litter)                        |
| VSAPL    | Volume of <i>Shepherdia canadensis</i>                                      |
| VLEGR    | Volume of <i>Ledum groenlandicum</i>  |
| VMYGA    | Volume of <i>Myrica gale</i>  |
| AWOOD    | Arcsine square root(mean percentage cover by wood)                          |
| AVSHT    | Mean height of shrub cover  |
| SPIGL    | Square root(number of <i>Picea glauca</i> trees)                            |
| SSPIGL   | Square root(number of <i>Picea glauca</i> saplings)                         |
| SLALA    | Square root(number of <i>Larix laricina</i> trees)                          |
| SSLALA   | Square root(number of <i>Larix laricina</i> saplings)                       |
| LTBAS    | Log <sub>10</sub> (total basal area of all trees)                           |

wetland) may have been simplistic, and that the rodents were recognizing additional habitats (e.g., Fig. 3).

*Habitat sub-division—Steps 7 and 8a(i).*—We performed cluster analyses (Norušis 1990a: Procedure CLUSTER, UPGMA method [unweighted pair-group method using arithmetic averages]) to search for discontinuities in microhabitat composition within ridge and wetland habitat classifications. Clusters, based on habitat principal components (PCs) for all plots included in the isodar, were used to identify additional habitats for subsequent isodar analysis (Steps 8a(ii)–8b).

## RESULTS

### *Small-mammal captures*

Small-mammal communities were primarily composed of red-backed voles (*Clethrionomys gapperi*)

TABLE 4. Small-mammal densities (minimum number known alive during the last of three trapping rounds) in ridge and wetland habitats at three coastal sites in the Hudson Bay Lowland, 1990–1991. Cg = *Clethrionomys gapperi*, Mp = *Microtus pennsylvanicus*, Sa = *Sorex arcticus*, Sc = *Sorex cinereus*, Zh = *Zapus hudsonius*, Pm = *Peromyscus maniculatus*.

| Location         | Habitat | Small-mammal species |    |    |    |    |    |
|------------------|---------|----------------------|----|----|----|----|----|
|                  |         | Cg                   | Mp | Sa | Sc | Zh | Pm |
| Shagamu (1990)   | Ridge   | 18                   | 7  | 0  | 0  | 0  | 0  |
|                  | Wetland | 4                    | 18 | 0  | 3  | 1  | 0  |
| Ekwan (1990)     | Ridge   | 88                   | 0  | 0  | 7  | 2  | 0  |
|                  | Wetland | 69                   | 7  | 4  | 4  | 3  | 0  |
| Longridge (1991) | Ridge   | 5                    | 6  | 2  | 8  | 16 | 1  |
|                  | Wetland | 0                    | 16 | 6  | 2  | 15 | 0  |

TABLE 5. Principal component (PC) loadings for habitat variables in the Hudson Bay Lowland (see Table 3 for description of variables). High PC1 scores are associated with forest-covered ridges, whereas the lowest scores represent wetter, open sedge habitats. PC2 primarily describes a gradient from wet areas with many trees and shrubs to more open, dry areas. PC3 distinguishes habitats with deep mats and short shrubs from habitats with tall shrubs and litter-covered substrate.

| Variable | PC1   | PC2   | PC3   |
|----------|-------|-------|-------|
| LTBAS    | 0.92  | 0.17  | 0.06  |
| SPIGL    | 0.90  | 0.05  | 0.11  |
| AWOOD    | 0.79  | -0.02 | -0.05 |
| SPHAG    | 0.78  | 0.06  | 0.04  |
| SSPIGL   | 0.68  | 0.20  | -0.10 |
| VAVI     | 0.60  | -0.09 | 0.38  |
| SEDGE    | -0.59 | 0.14  | 0.40  |
| VLEGR    | 0.35  | 0.16  | 0.08  |
| SSLALA   | 0.19  | 0.86  | 0.01  |
| VMYGA    | 0.05  | 0.77  | -0.10 |
| SLALA    | 0.41  | 0.73  | 0.12  |
| VSAPL    | 0.14  | 0.68  | -0.11 |
| LMAT     | -0.06 | 0.66  | 0.55  |
| MOSS     | -0.49 | 0.59  | 0.13  |
| EMNI     | 0.13  | -0.34 | 0.23  |
| LITTER   | -0.24 | -0.06 | -0.86 |
| AVSHT    | 0.21  | 0.42  | -0.67 |

with fewer meadow voles (*Microtus pennsylvanicus*) and meadow jumping mice (*Zapus hudsonius*), but there was a great deal of variation among sites (Table 4). Shrews (*Sorex cinereus*, *S. arcticus*) were relatively common at most sites, and *Zapus* were important community members at Longridge. *C. gapperi* was the only species consistently found at relatively high densities and in both ridge and wetland habitat.

### *Microhabitat*

Principal components analysis extracted three orthogonal components accounting for 60.2% of the common variation among the 17 habitat variables (Table 5). Additional components were excluded, as none accounted for more than 8% of the common variation.

### *Confirmation of habitat divisions*

Ridges and wetlands were clearly different in microhabitat composition (DFA [discriminant function analysis]  $\chi^2 = 58.62$ ,  $df = 2$ ,  $P < 0.01$ ). Of 24 pairs of habitats, only one ridge and one wetland plot were misclassified by the discriminant function analysis. PC1 and PC2 were the only components to enter the stepwise solution, indicating that ridges and wetlands were primarily discriminated on the basis of relative amounts of tree and shrub cover in the different moisture regimes (Fig. 5).

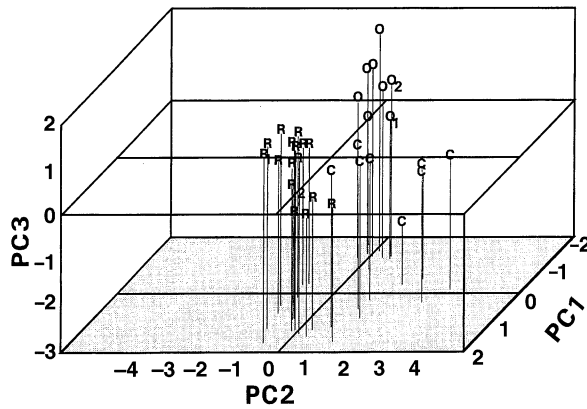


FIG. 5. Habitat structure of ridges (R), covered wetlands (C), and open wetlands (O), plotted in principal components (PC) space. The division of wetlands into open and covered was based on cluster analysis of microhabitat principal components (Tables 3 and 5). The two pairs of plots that were "outliers" in the initial isodar (see Fig. 6) are identified with subscripts (four points).

*Isodar analysis*

Geometric mean regression of densities in ridge vs. those in wetland habitats was significant ( $F = 5.9$ ,  $df = 1, 14$ ,  $P = 0.03$ ; Table 6) consistent with density-dependent habitat selection by *C. gapperi* (Fig. 6). A nonsignificant intercept (1.97, 95% confidence interval = -1.74-5.68) and a slope not significantly different from one (1.09, 95% confidence interval = 0.57-1.61) suggested that, for red-backed voles, the two habitats function as one (equal preference for ridge and wetland). Two potential, but nonsignificant, "outliers" (Fig. 6) and a low  $R^2$  (0.30) suggested, however, that this isodar may provide an incomplete description of habitat selection by *C. gapperi* in the Hudson Bay Lowland (HBL).

*Habitat sub-division*

The two unusual density combinations corresponded to Ekwan plots in which the wetland had unusually low population densities relative to neighboring ridge habitat. Is it possible that the "outliers" represent an additional habitat type? We performed two cluster analyses with the PC scores, one within ridges and one within wetlands, to assess this possibility.

From the resulting dendrograms we identified three habitats: ridge, open wetland, and covered wetland (Fig. 7). Open and covered wetlands are distinguished by the relative amount of tree and shrub cover present. The wetlands are not only different from each other, they are also different from each other relative to the ridges (Fig. 5). This relative difference may be recognized by habitat-selecting red-backed voles.

*Isodar analysis of three habitats*

We reanalyzed density-dependent habitat selection by calculating two different isodars based on the three-

TABLE 6. The relationships (isodars) of *Clethrionomys gapperi* population density in ridge habitat to its density in wetland habitat. The isodar of ridge vs. wetland was the initial regression (Fig. 6) that included 16 habitat pairs. Isodars of ridge vs. open wetland (Fig. 8) and ridge vs. covered wetland (Fig. 8) include eight habitat pairs each. The wetland habitats were divided into two groups based on a cluster analysis of microhabitat composition. All isodars were significant.

| Source                              | df | MS     | P     |
|-------------------------------------|----|--------|-------|
| Isodar of ridge vs. wetland         |    |        |       |
| Regression                          | 1  | 167.27 | 0.029 |
| Residual                            | 14 | 28.12  |       |
| Isodar of ridge vs. open wetland    |    |        |       |
| Regression                          | 1  | 373.30 | 0.001 |
| Residual                            | 6  | 10.93  |       |
| Isodar of ridge vs. covered wetland |    |        |       |
| Regression                          | 1  | 94.52  | 0.001 |
| Residual                            | 6  | 2.25   |       |

habitat division. The first corresponded to tree- and shrub-covered wetlands vs. their paired ridges, the second to open wetlands vs. their paired ridges. Despite small sample sizes ( $n = 8$ ) both isodars were highly significant ( $P < 0.001$ ), with no unusual residuals. Vole density ( $N_{Cg}$ ) in covered wetlands was closely related to vole density in adjoining ridges ( $F = 42.1$ ,  $df = 1, 6$ ,  $R^2 = 0.88$ ; Table 6, Fig. 8),

$$N_{Cg \text{ Ridge}} = 1.96 + 0.58N_{Cg \text{ Covered Wetland}} \quad (2)$$

A similar result occurred between open wetlands and their adjoining ridges ( $F = 34.15$ ,  $df = 1, 6$ ,  $R^2 = 0.85$ ; Table 6) but the regression was strongly influenced by the two points corresponding to high densities at Ekwan (Fig. 8),

$$N_{Cg \text{ Ridge}} = 1.87 + 2.83N_{Cg \text{ Open Wetland}} \quad (3)$$

The isodar intercept was significantly different from

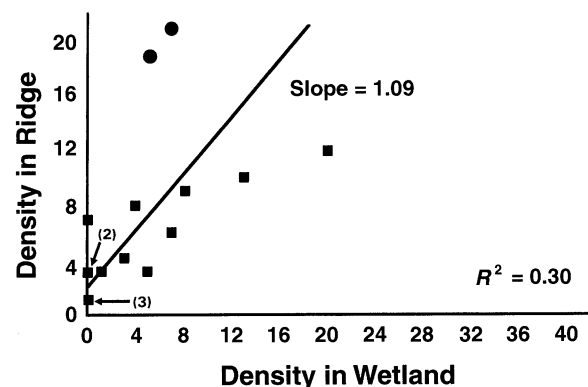


FIG. 6. Isodar of *Clethrionomys gapperi* demonstrating equal preference for ridge and wetland (i.e., one habitat). Numbers in parentheses denote multiple points with the same coordinates. Note the unusual residuals resulting from two density combinations marked with ●. These two points suggest that *C. gapperi* may be recognizing more than the two categories of habitat analyzed here.

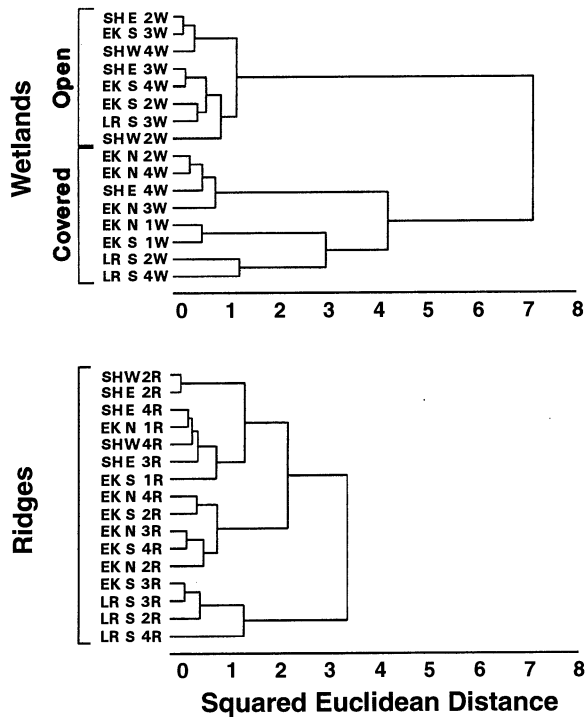
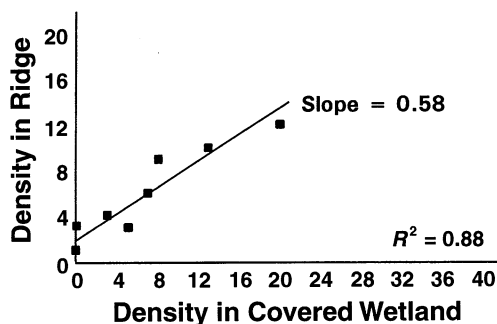


FIG. 7. Dendrograms showing results of cluster analyses. Clustering was based on the squared Euclidean distances between sample plots in PC space. Wetlands divided into two main clusters: those that were relatively open and those that were more heavily shrub and tree covered (see Fig. 5). Compared with wetlands, ridges were relatively homogeneous in microhabitat composition. Consequently, ridges were not divided into separate classifications. Individual plots are identified by site (EK = Ekwan, LR = Longridge, SH = Shagamu), transect (North, South, East, West), and plot number. Plot numbers increase with increasing distance from the coast.

zero (95% confidence interval = 0.29–4.15) for ridges with covered wetlands and not significantly different from zero (95% confidence interval = -1.35–6.02) for ridges with open wetlands. There was also a striking



difference in the slope of the isodars. Habitat distributions were dramatically different for ridges paired with open wetlands (slope >1; 95% confidence interval 1.74–3.92) vs. those paired with covered wetlands (slope <1; 95% confidence interval = 0.34–0.74). Red-backed voles in the HBL recognize not two, but at least three, separate habitats.

## DISCUSSION

The isodar analyses illustrate that at least three habitat types appear to influence spatial population regulation by red-backed voles in the Hudson Bay Lowland (HBL). We initially speculated that there were two. Landsat thematic maps (1:250,000 scale) of the same areas (Ontario Centre for Remote Sensing, Ontario Ministry of Natural Resources, Toronto, Ontario, Canada) identify up to seven thematic classifications for those same habitats and up to 13 thematic classifications when habitats with zero density of *Clethrionomys gapperi* are included. Satellite images of habitat do not correspond to those of red-backed voles. This result emphasizes our main point—habitat must be mapped with ecological criteria.

The isodars also illustrate that the same forms of habitat-dependent population regulation can act across huge geographical scales. In the HBL, habitat selection alone is a major factor influencing population regulation of red-backed voles. The influence of habitat selection must be evaluated before invoking higher-scale effects such as landscape composition and structure (Danielson 1992).

Our procedure assumes that density differences among sampling plots represent different stages of natural population fluctuations. It is also possible that the isodars simply reflect geographic patterns in abundance. This does not seem likely in our study. Fig. 9 illustrates the two original isodars together with data from the first and second trapping rounds at Ekwan, the site with highest overall densities (these data were

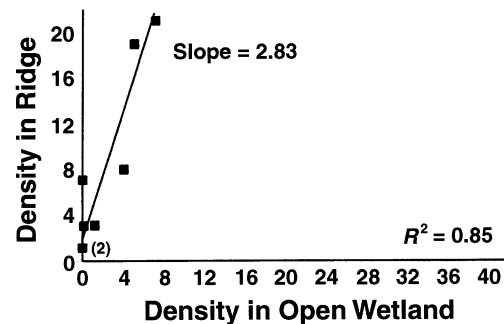


FIG. 8. Isodars of covered and open wetlands. The significant non-zero intercept for covered wetlands indicates that red-backed voles preferentially select ridges over covered wetlands at low population densities. The isodar slope significantly <1 reveals a crossover in habitat suitability and preference at higher densities. The isodar slope for open wetlands is significantly >1, indicating that red-backed voles preferentially occupy ridges over open wetlands across all population densities. The "(2)" denotes two points with the same coordinates. Note that the open-wetland isodar is strongly influenced by two points at high density.



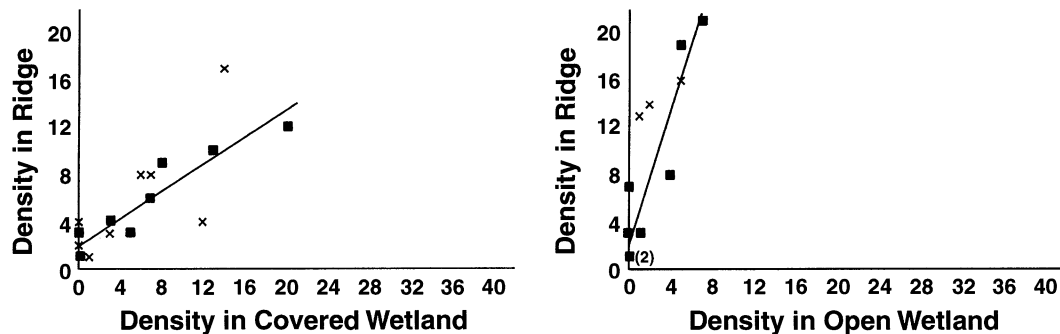


FIG. 9. Ekwon data from first and second trapping rounds (×) superimposed onto the isodars for open and covered wetlands (■). The "(2)" denotes two points with the same coordinates. The new data points were not included in the isodar regressions.

not incorporated into the isodar regressions, to avoid autocorrelation). The additional data are consistent with the interpretation that the two isodars characterize habitat selection by red-backed voles along the coast of the HBL.

Another potential problem lies with the scale dependence of habitat selection. The protocol we use here does not identify the spatial scale of habitat selection; it only confirms, through isodar analysis, whether habitat selection is active at the scale of analysis. If the investigator identifies habitats at too small a spatial scale, individuals may be incapable of differentiating between patches (Morris 1992), and no consistent pattern of habitat use will emerge. On the other hand, population regulation may be independent of habitat selection when habitat patches are significantly larger than the mean linear dispersal distance of the study organisms (Morris 1992). It may frequently be advisable to modify our protocol to include a preliminary assessment of the scales of habitat selection (e.g., Morris 1992).

Perhaps the most controversial aspect of our analysis is the underlying assumption of ideal habitat selection. Our choice of assuming an ideal free distribution to illustrate isodar analysis may frequently be violated (e.g., Van Horne 1983, Pulliam 1988, Kennedy and Gray 1993). All probable forms of ideal density-dependent habitat selection are likely, nevertheless, to generate isodars (Morris 1994, 1995, Rodriguez 1995). The possibility of nonlinear isodars may complicate interpretation. Isodars and their residuals must always be carefully assessed to ascertain whether such nonlinearities exist. None was apparent in our study.

Our approach has been designed for relatively simple landscapes with few obvious habitats. We suspect that it should work in any set of repeated landscapes or for any set of paired plots in a single landscape. It will be interesting to find out how many different types of habitat functionally influence population regulation in other landscapes. Some patch-based models (e.g., Pulliam 1988, Danielson 1991, 1992, Pulliam and Danielson 1991, Wiens et al. 1993) consider only two or

three major habitat groupings in a landscape: source, sink, and unusable habitat. Each habitat identified in our study encompassed a broad range of structural and floristic variation (Fig. 6) and Landsat thematic classifications. Apparently complex landscapes may be relatively simple in the number of habitats recognized by density-dependent habitat selectors.

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