SPATIAL SCALING IN NORTHERN LANDSCAPES: HABITAT SELECTION BY SMALL MAMMALS

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ABSTRACT

I examined a series of simple and repeated northern landscapes in the Hudson Bay Lowland of Ontario to document regional and local patterns of population abundance of red-backed voles (*Clethrionomys gapperi*). I tested whether a spatially-explicit ecological process, density-dependent habitat selection, could account for population regulation of voles across a range of spatial scales. Over a large regional scale, multiple regression analysis indicated that population density of voles was primarily predicted by location of sampling and measures of microhabitat. Regional abundance patterns, therefore, appear to be independent of nonadditive landscape effects and probably result from large-scale biogeographic influences or differences in average habitat quality between sites. At a local scale, my analysis identified density-dependent habitat selection as a universal process structuring abundance patterns, regardless of regional differences in population density. Habitat selection, at the dispersal and perhaps microhabitat scales, thereby provides a feasible mechanism linking landscape structure directly to population regulation.

Keywords: *Clethrionomys*; density-dependent habitat selection; isodar analysis; landscape ecology; northern wetlands; population regulation; small mammals; spatial scale.

INTRODUCTION

Spatial scaling in the landscape

Much of landscape ecology has focused on the description of spatial patterns found at different scales. There has been relatively little progress, however, linking these patterns to the underlying processes that create them (Allen and Hoekstra 1991, Wiens 1992, Johnson et al. 1992). Part of the difficulty arises because pattern and process are not always coupled to the same spatial scale (e.g. Wiens 1989). Regional differences in population abundance (e.g. Brown and Kurzius 1987, Menge and Olson 1990) illustrate spatial patterns with different conceivable explanations. These regional differences may result from biogeographic effects like geographic dispersal, fluctuation in species' distribution, and climatic differences (e.g. Ricklefs 1987, Menge and Olson 1990, Tonn et al. 1990, Cornell and Lawton 1992). It is also possible that regional abundance patterns are related to some weighted average of regional differences in habitat quality or to variation in the identity and spatial arrangement of available habitat patches at given locations (Dunning et al. 1992).

I address landscape-level variation in population abundance by examining density-dependent habitat selection of red-backed voles (*Clethrionomys gapperi*). I use the term landscape to refer to the matrix of habitats in which a focal habitat is embedded (Dunning et al. 1992). Landscape size differs for different organisms but it can be considered as occupying some spatial scale between the normal home range size for an individual and the regional distribution of the species (Dunning et al. 1992). I explicitly link landscape and the ecological process of habitat selection to identify the spatial scales of habitat heterogeneity influencing red-backed vole populations. My analysis evaluates patterns of population abundance across vast northern landscapes at three basic habitat scales; regional (a large area in which sampling sites are spread over distances of hundreds of kilometres), local (a limited sampling area of several kilometres in which habitat quality and species composition are relatively consistent), and microhabitat (the vegetative and physical composition of census plots). I then examine variation in population density from the perspective of habitat selection to determine if small mammal population abundance within the landscape can be understood in terms of habitat quality, identity, and availability.

The landscape of density-dependent habitat selectors

Density-dependent habitat selection, a primary determinant of relative population densities at the local scale (Rosenzweig 1981, 1987, 1991, Morris 1987a, 1987b, 1988, 1992, Pulliam 1988, Abramsky et al. 1991, Pulliam and Danielson 1991), is likely to be influenced by landscape structure (Danielson 1991, Morris and Brown 1992). Landscape structure refers to the relative amounts of each habitat type in a landscape and the physical layout of those habitats (Dunning et al. 1992). The population density and distribution of an ideal density-dependent habitat selector across habitats will reflect the individual's perception of potential reproductive success in a habitat, discounted by the negative effects of increased density (Morris 1988) and the costs of habitat selection. Because density-dependent habitat selectors choose one habitat relative to others, local population density is believed to depend upon the identity and configuration of neighbouring habitats (Morris 1992, Morris and Brown 1992).

Imagine a matrix of different habitats in which each patch of habitat is much larger than an individual's home range (a habitat patch can be defined as a contiguous area characterized by consistent microhabitat composition). Movement between patches would generally be classified as dispersal and involve relocation of an individual's home range. Individuals moving within the home range would encounter multiple microhabitats during their average daily activity (Morris 1987b). Examples of both scales of habitat selection can be found in previous studies of small mammal habitat use.

The densities of *Peromyscus leucopus* and *Microtus pennsylvanicus* for example, have been explained at the dispersal scale (Morris 1984, 1987c, Adler 1985, 1987). Morris (1984, 1987c, 1989b) regressed population densities of small mammals against microhabitat and "macrohabitat" variables at three geographically separate locations. In all cases, he found that abundance patterns were linked to the "macrohabitat" (dispersal) scale. Habitat selection at the dispersal scale has also been identified with isodar analysis (Morris 1987b, 1987c, 1988, 1989a, 1990, 1992), a technique that documents population densities in replicated pairs of habitat patches. In an experimental setup, Abramsky et al. (1991) used isodar analysis to confirm that *Gerbillus allenbyi* distributed itself equally between two enclosures with identical habitat composition.

Species distributions and population density have also been related to differential microhabitat selection (e.g. Rosenzweig and Winkaur 1969, M'Closkey and Lajoie 1975, M'Closkey 1976, Dueser and Shugart 1978, Price 1978, Ostfeld et al. 1985). Most tests at this "foraging" scale have regressed population density against detailed measures of microhabitat variation (these are most commonly estimated by measures of plant community composition and structure, e.g. Dueser and Shugart 1978, Adler 1987). These measures lack an explicit spatial component, but if population regulation is occurring primarily at the microhabitat scale, the microhabitat measures should explain the majority of variation in animal abundance, regardless of landscape structure or regional location. This protocol does not preclude the possibility that correlation between density and microhabitat are spurious and caused by larger-scale processes (Morris 1984, 1987c).

Recent investigations with *P. maniculatus* in Alberta identify habitat selection at both foraging (microhabitat) and dispersal scales (Morris 1992). Habitat selection at these different spatial scales creates distinctive abundance patterns across the landscape. Habitat selection at the dispersal scale creates abundance patterns associated with the identity and spatial arrangement of habitat patches. Population abundance patterns between replicated pairs of closely connected patches should be similar across the landscape. In contrast, microhabitat selection in a landscape would create population abundance patterns tied only to variation in the average quality of available habitats. Individuals would not recognize patch boundaries, and would distribute themselves according to the availability of preferred microhabitats.

Linking the landscape with ecology: a spatial analysis

Imagine now a series of simple landscapes with a repeated pattern of two alternating habitats. Further, imagine that we have obtained replicated estimates of relative population density in paired habitat patches. Over a large enough geographic area, estimates of density at different sampling locations (regions) would effectively include functionally separate populations, either as spatially distinct entities or as statistically unrelated groups in a continuously occupied region. Although landscape structure would be consistent across the geographic area, the relative qualities of the two habitats would vary, perhaps as a result of regional climatic effects. If within-habitat variability across the region was less than between-habitat variability, and individuals were selecting habitat at the dispersal scale, we may expect to observe similar patterns of relative abundance between the two habitats at each location. At a regional scale, abundance patterns may be relatively independent of landscape effects because of the repeated identity and configuration of the habitat patches. In this case, any regional differences in population density could be attributed to variable habitat quality or some process unrelated to landscape structure.

As a preliminary analysis, multiple linear regression can document general patterns of population abundance in simple landscapes at different spatial scales according to the following model:

$$N = a_o + b_1F_1 + b_2F_2 \ldots + b_nF_n + b_{n+1}H_1 + b_{n+2}L_1$$
$$+ b_{n+3}L_2 \ldots + b_{n+m}L_m + e \qquad (1)$$

where N represents the estimated population density, the F's represent microhabitat factors [determined by summarizing vegetation and physical features with principal components analysis (Adler 1985, 1987, Kershaw and Looney 1985)], H is an indicator variable scored 0 or 1 representing different habitats, the L's are indicator variables for regional location, and e is the normally distributed error variation (modified from Morris 1987c, 1989b). The equation can be solved in a stepwise manner to assess each variable's relative importance in predicting population density (Morris 1987c).

The above analysis provides an estimate of the spatial scales to which average abundance patterns are coupled. The equation can be simplified to include only microhabitat variables to document whether abundance patterns over all scales are closely associated with average habitat quality.

Another approach to the study of spatial scale is isodar analysis. An isodar (Morris 1987a, 1988, 1989a) is a plot of the density of a population in one habitat (habitat 1) against its density in an adjoining habitat (habitat 2). In the case of isodars based on an ideal-free distribution, the expected reproductive success of individuals is assumed to be the same in each habitat (Morris 1987a, 1988, 1989a). The isodar for species A can be estimated by:

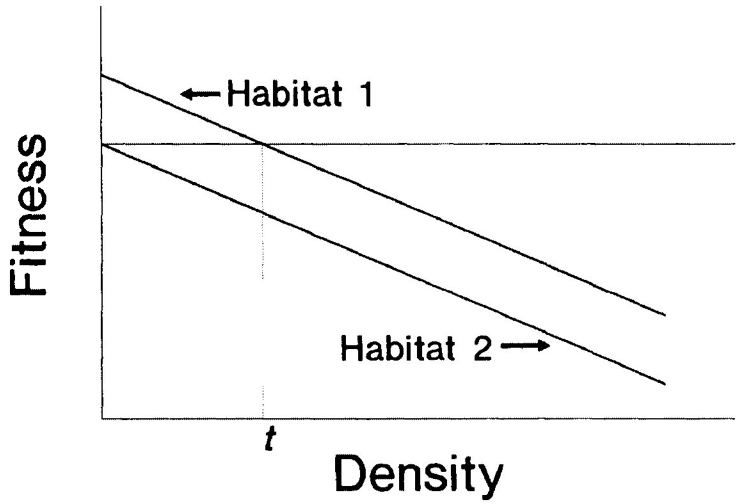
$$N_{A1} = C + b\, N_{A2} \qquad (2)$$

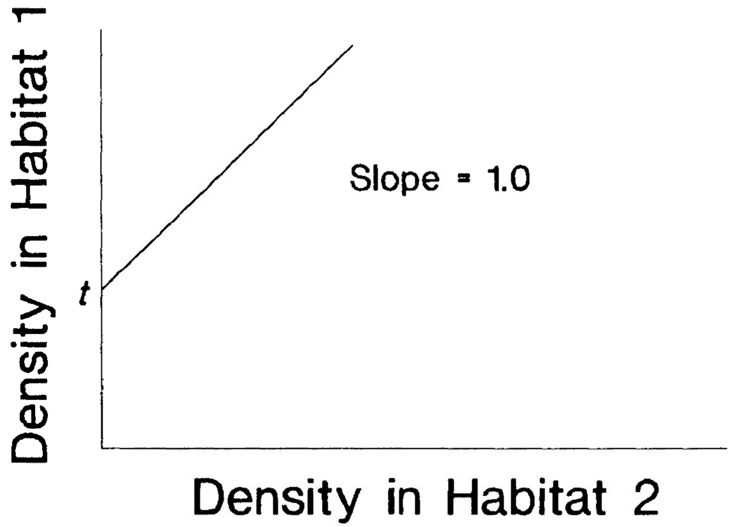
where N_{A1} and N_{A2} are the densities of species A in habitats 1 and 2 respectively, C represents the intercept, and b is the isodar slope (Morris 1987a, 1988, 1989a). To create an isodar empirically, we estimate population density in replicated pairs of habitats, plot the density from one habitat against the other for each pair, and solve by model II regression (Morris 1987a).

Interpretation of the isodar

Density-dependent habitat selection assumes that individuals select habitats in a way that maximizes individual fitness and that fitness declines with density (Fretwell and Lucas 1970, Rosenzweig 1981, Morris 1987a). Consider our landscapes of two adjacent patch types, 1 and 2, where habitat 2 yields a lower maximum fitness (Figure 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 point individuals will expect to achieve equal fitness regardless of which habitat they choose. From this density on, individuals will distribute themselves between habitats such that mean fitness is equal across all occupied patches. Differences in population density between habitats

Figure 1: Hypothetical fitness-density graph (left) and corresponding isodar (right) showing a quantitative difference between habitats. Density-dependent habitat selectors will always choose habitat 1 at low population densities until population size reaches a threshold (t), at which point equivalent fitness can be attained in habitat 2. Parallel fitness-density curves and an isodar slope of one indicate that there is no qualitative difference between habitats (parallel population regulation, Morris 1988).


Fitness
←Habitat 1
Habitat 2→
t
Density


Density in Habitat 1
t
Slope = 1.0
Density in Habitat 2

therefore reflect differences in habitat suitability (see Van Horne 1983, Pulliam 1988, Pulliam and Danielson 1991 for alternative views).

The ideal free distribution (Fretwell and Lucas 1970) in Figure 1 can be redrawn as an isodar by plotting the joint densities in the two habitats for all fitness values. If one constructs an isodar between the habitats using empirical data, a significant regression indicates density-dependent habitat selection. If, on the other hand, the isodar is non-significant, we may conclude that habitat selection, if it occurred at all in that pair of habitats, is independent of density. At the scale of analysis, population regulation would be independent of habitat.

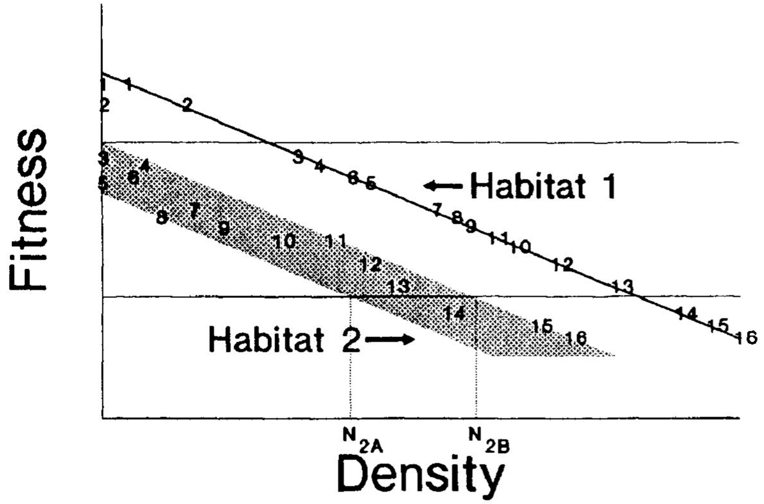
Slopes and intercepts of isodar regressions likely indicate qualitative and quantitative differences in habitat respectively. Quantitative differences in habitat (e.g. differences in productivity) produce isodars whose intercepts are greater than zero, but whose slopes are equal to 1.0 (Morris 1992). Qualitative differences (e.g. differences in habitat structure or kinds of resource) produce isodars whose slopes are different from 1.0 (Morris 1992).

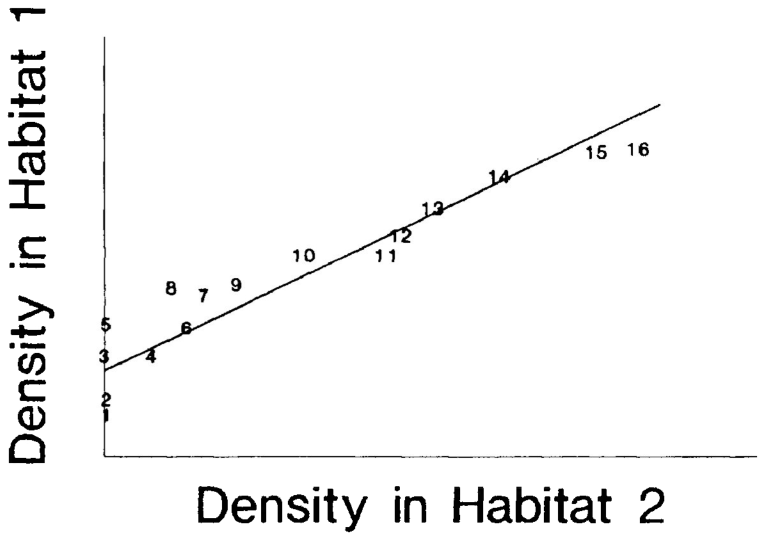
Qualitative and quantitative differences in habitat have profound implications for population regulation by density-dependent habitat selectors (Morris 1992). Quantitative differences alone result in parallel population regulation (Figure 1; Morris 1988) in which one habitat consistently supports a greater density than the other, but density-dependent feedback on reproductive success is the same in both (Morris 1992). Qualitative differences alone suggest that habitats differ in the influence of density-dependence on reproductive success (non-parallel fitness-density curves; Morris 1992).

Divergent regulation, resulting from qualitative differences between habitats, suggests that individuals are probably more efficient at extracting resources in one habitat than in the other. They thereby have a distinct preference for that habitat (Morris 1988) across all densities. Qualitative and quantitative differences combined can result in cross-overs of fitness density curves (Morris 1988).. At low density, one habitat is preferred but at higher densities, preference switches to the second habitat (Morris 1988).

Despite the promise they hold for documenting habitat-related effects on population regulation, applying isodars across landscapes may introduce some difficulties for their interpretation. Most notable is the problem that the relative qualities of habitats may change between landscapes. Variable habitat quality can be represented by a band of fitness-density curves for each habitat (Figure 2; Morris 1987a). This would result in a range of population densities associated with a given level of fitness and, consequently, an increased scatter about the isodar.

Figure 2: One of the difficulties in applying isodars across landscapes may be that habitat quality varies at different locations. This 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_{2A} and N_{2B} identify the range of population densities possible at a given level of fitness in habitat 2.

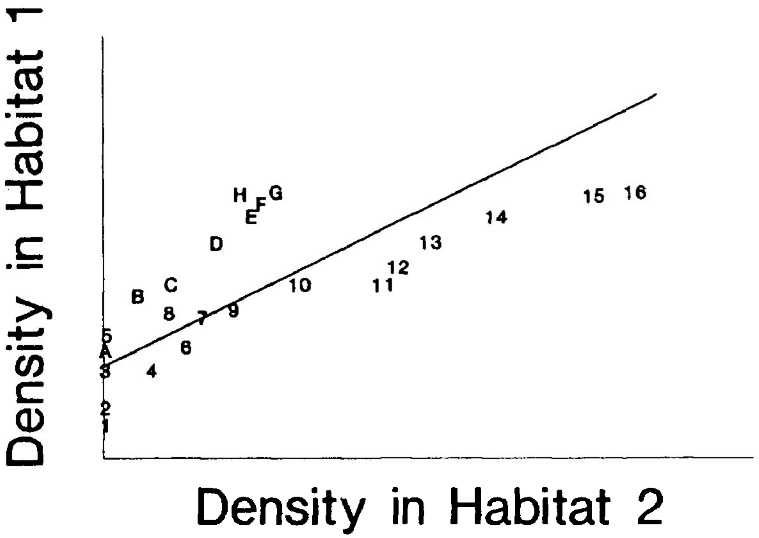

Fitness
← Habitat 1
Habitat 2 →
N_{2A}
N_{2B}
Density

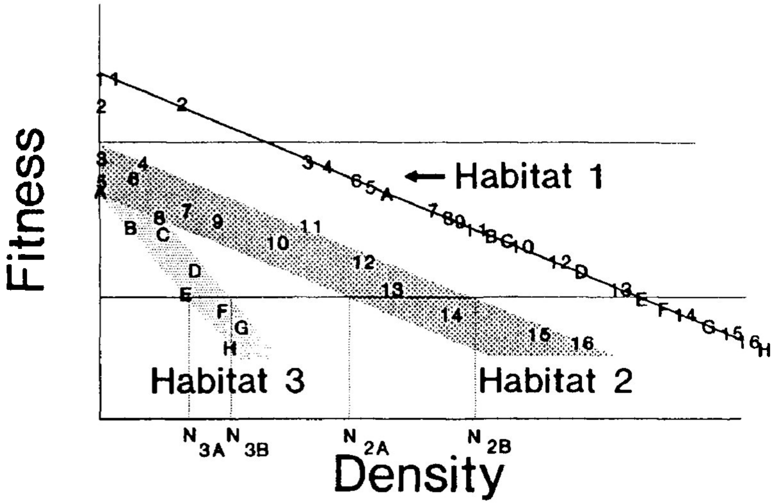

Density in Habitat 1
Density in Habitat 2

In cases of regional comparisons of habitat use, an empirically derived isodar with scatter about the regression line indicates that there is a range of habitat qualities within each habitat type (Figure 2). Patterns in isodar residuals, on the other hand, may identify different fitness-density curves within a "habitat" (Figure 3). By definition this would mean that the individuals had recognized two or more habitats that had been improperly lumped together by the investigator (Morris Unpublished MS a).

I use these features of isodar analysis to document the role of density-dependent habitat selection in population abundance patterns of red-backed voles. The isodars are constructed with paired density estimates from several regions and from habitats with a range of qualities. A statistically significant isodar provides strong evidence that similar processes of density-dependent habitat selection are occurring among the sites. Residual variation suggests, however, that superficially similar habitats may often be recognized as distinct alternatives by the individuals that exploit them.

Figure 3: One of the weaknesses of applying isodars across landscapes may also be one its greatest strengths. An isodar with an unusual pattern of residuals (left) may indicate more than two fitness-density functions (right). By definition this would mean that habitats perceived as different by the organism had been inadvertently lumped into one habitat classification. Corresponding numbers (habitats 1 and 2) and letters (habitats 1 and 3) identify paired habitats. In this example, N_{2A}, N_{2B} and N_{3A}, N_{3B} identify the range of population densities possible at a given fitness in habitats 2 and 3 respectively.


Density in Habitat 1
Density in Habitat 2
1
2
3
A
5
4
6
7
8
9
B
C
D
E
F
H
G
10
11
12
13
14
15
16


Fitness
Density
Habitat 1
Habitat 2
Habitat 3
N_{3A}
N_{3B}
N_{2A}
N_{2B}

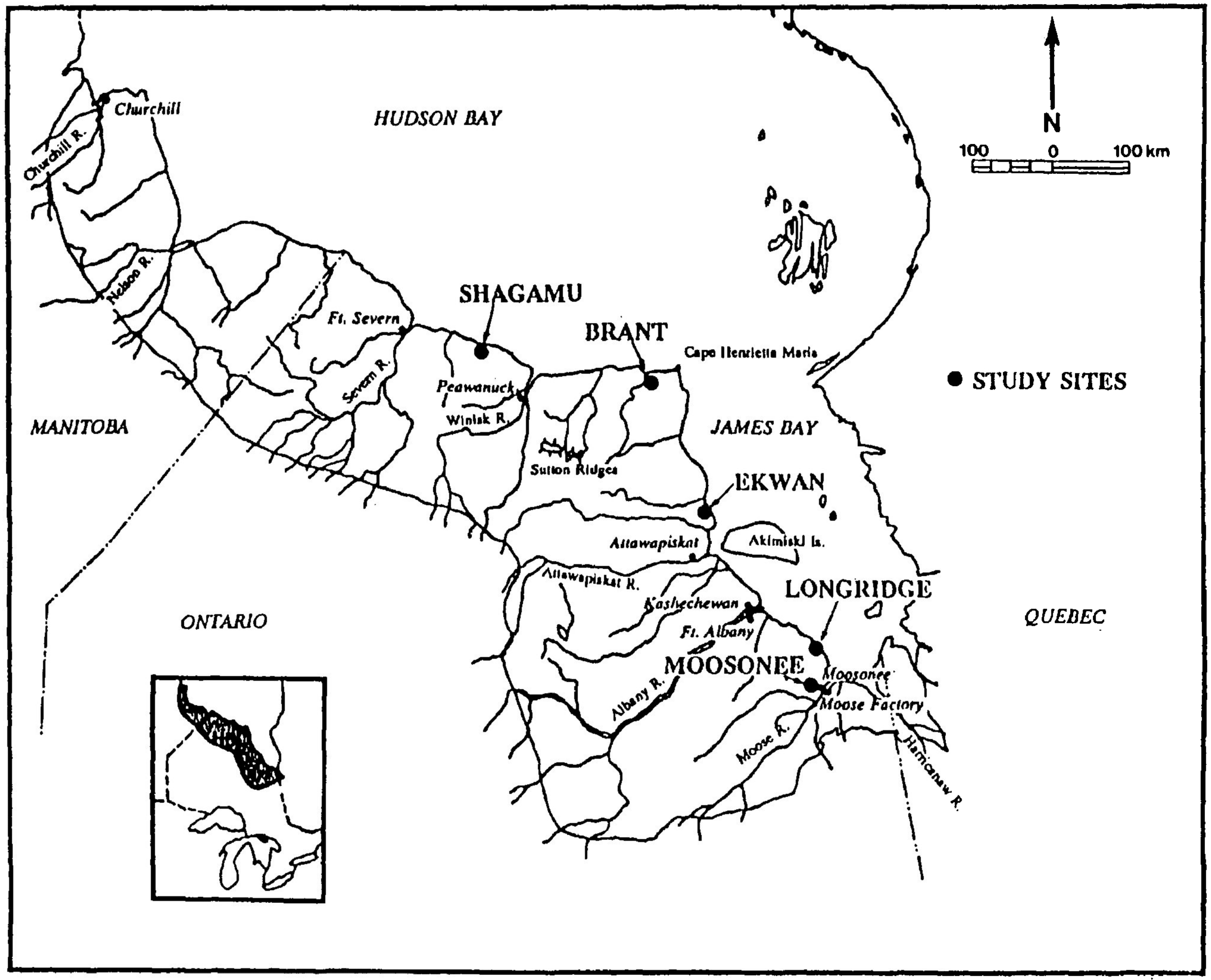
STUDY AREA AND METHODS

I selected the Hudson Bay Lowland to document spatial scaling because it provided a series of landscapes composed of simple and repeated landforms. Alternating habitats of ridge and wetland throughout the coastal region minimize landscape heterogeneity, while a wide range in climate and vegetation ensure regional variability in habitat quality. Red-backed voles are ubiquitous occupants of the region and were commonly found in both habitats.

The study was conducted over a large geographic scale, encompassing 700 km along the coasts of both Hudson and James Bays in the Hudson Bay Lowland of Ontario (HBL) (Figure 4). The HBL is one of the largest continuous wetlands in the world (324,000 km^2) and remains relatively undisturbed. Isostatic uplift has created repeated landscapes of raised beach ridges interspersed with low-lying wetlands (Pielou, 1991).

The Hudson Bay coast has a climate that is heavily influenced by the cooling effects of the bay. Ridges are characterized by open sub-arctic tundra with sparse tree (*Picea glauca*) distribution. Wetlands range from open fen to shrub-covered fen (*Betula spp.*, *Salix spp.*). The James Bay coast has a more temperate climate and is characterized by boreal forest vegetation. Ridges are generally covered with mature spruce-lichen forest (*Larix laricina, P. glauca, P. mariana)*. Wetlands are more

Figure 4: Map showing sampling locations in the Hudson Bay Lowland.


HUDSON BAY
N
100 0 100 km
Churchill
Churchill R.
Nelson R.
Ft. Severn
Severn R.
SHAGAMU
BRANT
Cape Henrietta Maria
Peawanuck
Winisk R.
● STUDY SITES
MANITOBA
Sutton Ridges
JAMES BAY
EKWAN
Attawapiskat
Akimiski Is.
Attawapiskat R.
Kashechewan
LONGRIDGE
Ft. Albany
QUEBEC
ONTARIO
MOOSONEE
Moosonee
Moose Factory
Albany R.
Moose R.
Harricanaw R.

variable, ranging from open sedge fen (*Carex spp.*, *Scirpus spp.*) to sparse black spruce (*P. mariana*) and tamarack (*L. laricina*) forest with deep sphagnum and moss cover.

Small mammals were censused and plant communities quantified from May to September 1990 and again during the same period in 1991. Two coastal sites were sampled each year; one on the James Bay and one on the Hudson Bay coast. This gave a total of four coastal sites over the two year period. A fifth site near the southern limit of James Bay was sampled both years.

Site Descriptions

Shagamu (1990) (55°49'N 86°37'W)

This most northwestern site was characterised by closely packed ridge systems. Two parallel 1200 m transects, separated by approximately 1 km, were initiated at right angles to and approximately 3 km from the Hudson Bay coast. Ridge habitats had increasing tree cover with increasing distance from the coast. They ranged from open tundra, with lichen (*Cladonia spp.*) and moss ground cover, and few, small shrubs (*Empetrum nigrum, Ledum groenlandicum, Rhododendron lapponicum, Salix spp., Shepherdia canadensis*), to open spruce-lichen forest (*P. glauca*) with similar shrubs in the understorey. Wetlands similarly varied from open fen with low sedges (*Carex spp.*, *Eleocaris spp.*) to shrub covered (*Betula spp.*, *Salix spp.*), tall-sedge fen.

Brant River (1991) (55°03'N 82°50'W)

Inland approximately 10 km and near the point where James and Hudson Bay meet, the Brant River location is a virtually treeless, sub-arctic tundra. The region is primarily a watery plain with large but widely spaced ridges of irregular pattern and smaller ridge systems surrounded by wetland. Transects began on opposite sides of a lake and ran in opposite directions for 800 and 2400 m respectively. One of the transects traversed a principal ridge formation. Here, ridges were large and open with little vegetation (*Betula spp., E. nigrum, R. lapponicum*) above the lichen mat (*Cladonia spp.*). Wetlands were open, short-sedge fen (*Carex spp., Scirpus spp.*) with few shrubs. The second transect crossed a matrix of low but similar ridge habitat, and hummocky sedge wetland, some of which was covered in shrub (*Betula glandulosa, Salix spp.*).

Ekwan (1990) (53°27'N 82°10'W)

The ridge system here was tightly packed with mature spruce-lichen forests on ridges located within 500m of the coast. Parallel transects began on the first heavily forested ridge and ran inland for approximately 900 and 1400 m respectively. They were separated by a large stream and about 1 km distance. Ridges on both transects were heavily covered with spruce-lichen woodland, some with a large component of sphagnum and shrub (*Betula spp., L. groenlandicum, Salix spp.*) away from the centre of the ridge. Wetlands of one transect were a mix of open, sedge-covered bog and fen (*Carex spp., Scirpus spp.*), and tamarack fen (*L. laricina, P. mariana, Betula* *spp., Salix spp.*). Wetlands of the second transect were primarily black spruce forest with deep sphagnum and moss cover.

Longridge (1991) (51°49'N 80°41'W)

The two transects at this site encompassed two different ridge systems. One transect was 1700 m long, and composed of relatively wide, low ridges covered in tamarack, black and white spruce forest (*L. laricina, P. glauca, P. mariana*) with a ground cover of moss. Wetlands were tamarack bogs with relatively heavy shrub cover (*Betula spp., Salix spp.*). The most coastal ridge-wetland in this system and all of the plots on the other transect were more coastal in nature. This second transect was 1300 m long. Ridges had a very shallow ground cover of mosses and herbaceous plants on a gravel substrate. Wetlands were open sedge fens with some shrub cover (*Salix spp.*). Ridges of the second transect ranged from open and shrub covered to mature white spruce-balsam poplar forest (*P. glauca, Populus balsamifera, Juniperus communis, Ribes oxyacanthoides, S. canadensis,*).

Moosonee (1990 and 1991) (51°15'N 80°41'W)

Moosonee lacked the distinctive ridge-wetland pattern of the other sites. A single transect was located in a relatively homogeneous black spruce-tamarack fen (*L. laricina, P. mariana*) with an ericaceous shrub layer (*L. groenlandicum, S. canadensis*) and moss ground cover. Two of the Moosonee plots were densely covered by speckled alder (*Alnus incana*).

For 3 of the 4 coastal sites, two live-trap and vegetation transects separated by approximately 1 km were set perpendicular to the orientation of the ridge - wetland landscape. Each traversed a series of progressively older ridges with increasing distance from the coast. An irregular pattern of ridge habitats prevented this design at one of the Hudson Bay sites (Brant River) where the two transects were set on opposite sides of a small lake. Transect lengths varied because of the relative packing of habitats at different locations. Four pairs of plots were trapped along each transect at all coastal sites. A pair consisted of a plot on ridge habitat and one in wetland habitat separated by 100 m. The same ridge or wetland was never sampled more than once. The southern James Bay site near Moosonee had only one transect of 8 plots, which was set in relatively homogeneous black spruce-tamarack fen.

Plots at all sites were 60 X 60 m and consisted of a 4 X 4 array of Longworth live traps set with 20 m spacing. This sampling regime provided 1,152 individual trapping stations and 11,520 trap nights.

Small Mammal Trapping

Three sampling periods were equally spaced at six-week intervals during each field season (May 15 - June 20, June 21 - July 31, August 1 - September 15). Traps were set on one transect at a time for a period of three consecutive nights and were checked at dawn and dusk each day. All soiled traps were washed with detergent and rinsed in warm water before being reset. Only data from the final census, the period of highest rodent density at all locations, were used in the spatial analyses. Including data from all three seasons would have complicated the analyses with autocorrelated density estimates.

All captured mammals were individually marked. Relative density of each small-mammal species was estimated as the total number of different individuals caught on each grid (minimum number known alive (MNA); Hilborn et al. 1976). Although Efford (1992) demonstrated that MNA provides inaccurate absolute density estimates, the isodar analyses require only precise relative densities. Information recorded for each capture included station of capture, species, ID number, age, sex and reproductive condition, weight, body and tail lengths. Age was estimated as juvenile or adult based on mass (*C. gapperi* juvenile$<$20 g) and pelage. Animals found dead in the traps were sent to the Royal Ontario Museum in Toronto as voucher specimens.

Habitat Analysis

A series of nested quadrats (50m^2, 25m^2, and 0.125m^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 1). All trees within the largest quadrat (50m^2) were identified to species, counted, and diameter at breast height (DBH) measured with callipers. Saplings and seedlings in this quadrat were identified to species and counted. Shrubs were sampled in a 25m^2 quadrat and classified on the basis of species, percent cover, and height. Average

Table 1: Vegetation and physical sampling regimen for each quadrat.

QUADRAT	VEGETATION ESTIMATES	PHYSICAL ESTIMATES
50m^2	Trees (DBH > 30mm): Number of each species Diameter at Breast Height (DBH) Saplings (DBH < 30mm): Number of each species Seedlings (Stem Diameter < 3mm): Number of each species	
25m^2	Shrubs: Percent cover and average height by species	Wood, rock, soil, water: Per cent cover Mat depth: 1 estimate in each of 4 corners
0.125m^2	Small shrubs, herbs, grasses, sedges, mosses, lichens: Percent cover by species	Soil, rock, pebble, wood: Per cent cover Mat depth: 1 estimate in each quadrat

shrub height was calculated using the mean height and relative proportion of each species, and shrub volume was calculated by converting percent cover estimates in 25m^2 to area and multiplying by average height for the species. Percent cover was also estimated for wood, rock, soil, and water in the 25m^2 quadrat. Cover estimates of grasses, sedges, herbaceous plants, lichens and mosses, soil, rock, pebble, and wood were made within a 0.125m^2 quadrat placed at a randomly selected distance along a 5m transect, centred on the station. The mat, a layer consisting of moss and undecomposed organic matter, was measured in the NW corner of the 0.125m^2 quadrats and in each of the 4 corners of the 25m^2 quadrat. Mat depth was taken as the depth to which a metre stick could be pushed into the substrate.

Variables describing vegetation and physical measures were summarized by Principal Components Analysis (PCA) (SPSS-PC+, Procedure FACTOR; Norušis 1990a). Only those variables that were represented at more than 5% of plots and which had an approximately normal distribution after transformation were retained for use in subsequent analyses (Table 2). In all cases, data from the four stations within a sampling plot were pooled to give one estimate of each variable per plot. Variables which met the criteria included arcsine square-root transformed estimates of percent cover for common ground species, litter, and wood; estimates of volume for common shrub species; estimates of average shrub height; square root transformed counts of trees and saplings by species; and a measure of total basal area of trees determined by a logarithmic transformation of a total DBH for all trees.

Table 2: Variables used in principal components analysis of vegetation and physical characteristics of habitats. All variables were calculated from pooled measures at the 4 central stations of each habitat.

VARIABLE	DESCRIPTION
LMAT	$\log_{10}$(average mat depth)
EMNI	arcsine square root (average per cent cover by *Empetrum nigrum*)
MOSS	arcsine square root (average per cent cover by mosses)
SEDGE	arcsine square root (average per cent cover by sedges)
SPHAG	arcsine square root (average per cent cover by sphagnum)
VAVI	arcsine square root (average per cent cover by *Vaccinium vitis-idaea*)
LITTER	arcsine square root (average per cent cover by litter)
VSAPL	volume of *Shepherdia canadensis*
VLEGR	volume of *Ledum groenlandicum*
VMYGA	volume of *Myrica gale*
AWOOD	arcsine square root (average per cent cover by wood)
AVSHT	average height of shrub cover
SPIGL	square root (number of *Picea glauca* trees)
SSPIGL	square root (number of *Picea glauca* saplings)
SLALA	square root (number of *Larix laricina* trees)
SSLALA	square root (number of *Larix laricina* saplings)
LTBAS	$\log_{10}$(total basal area of all trees)

Statistical Analysis

Microhabitat and spatial scale I used the principal component scores in three stepwise Canonical Discriminant Function Analyses (DFA) (SPSS-PC+, Procedure DSCRIMINANT; Wilks' method; Norušis 1990b), to reconfirm habitat and site designations. The first DFA verified that ridges and wetlands were significantly different in terms of microhabitat composition. I then examined ridges and wetlands with two separate DFA's to estimate the amount of variation present within- as compared to between-sites.

Using Equation 1, I assessed the relative significance of different habitat scales in determining variation in red-backed vole population densities. The principal components, as well as indicator variables for habitat and location, were analyzed by stepwise multiple regression (Equation 1; SPSS-PC+, Procedure REGRESSION; Norušis 1990a).

Habitat quality I regressed densities of *C. gapperi* against the microhabitat components (SPSS-PC+, Procedure REGRESSION; Norušis 1990a) to determine if abundance was directly related to habitat quality, regardless of region or habitat. I then repeated the analysis for ridges and wetlands separately to assess within-habitat variation in quality on population density of red-backed voles.

Isodar analysis I calculated isodars (Equation 2) with geometric mean regression (Krebs 1989, p. 458-464) using population density estimates at paired sampling plots. Low population densities at some plots presented a challenge for the isodar analyses. Eight pairs of plots had no *C. gapperi* captures during the three trapping rounds. They were not included in the isodar analysis. It could not be determined with certainty whether these plots simply represented very low population densities in both habitats, or whether they represented habitats which were incapable of supporting *C. gapperi* populations.

Some unusual density combinations were detected by the first isodar analysis. I investigated the possibility that these resulted from a misclassification of habitat into only two divisions (ridge and wetland) when, in fact, the rodents were recognizing additional habitats (e.g. Figure 3). I performed cluster analysis (SPSS-PC+, Procedure CLUSTER; UPGMA-unweighted pair-group method using arithmetic averages; Norušis 1990a) to identify possible discontinuities in microhabitat composition within ridge and wetland habitat classifications. Large discontinuities in microhabitat would suggest that my initial classification of habitat may have been overly simplistic. Clusters were based on habitat PC's for all plots included in the isodar.

I constructed new isodars using the habitat classification produced by the cluster analysis. Part of my interpretation of these isodars required that I look for possible convergence or divergence of habitat composition between ridge and wetland habitats. I attempted to determine whether there was a significant relationship between the population density in a pair of habitat patches and the relative similarity of their microhabitat composition. I calculated the euclidean distance in PC space between ridge and wetland for each pair of plots (SPSS-PC+, Procedure CLUSTER; Norušis 1990a). I then regressed the combined population density for each habitat pair against their euclidean distance (SPSS-PC+, Procedure REGRESSION; Norušis 1990a) to determine if convergence or divergence in habitat composition could explain convergence or divergence in population density.

RESULTS

Small Mammal Captures

Small mammal communities were primarily composed of red-backed voles (*C. gapperi*) and meadow voles (*M. pennsylvanicus*), but there was a great deal of variation between sites (Table 3). Shrews (*Sorex cinereus*, *S. arcticus*) were relatively common at most sites, and meadow jumping mice (*Zapus hudsonius*) were important community members at Longridge. Except for the capture of one meadow jumping mouse in 1991, species composition at the Moosonee site was constant in both years, but the densities of all species varied (Table 3).

Table 3: Small mammal densities (minimum number known alive during final trapping round) in ridge and wetland habitats at 5 coastal sites in the Hudson Bay Lowland. Cg=*Clethrionomys gapperi*, Mp=*Microtus pennsylvanicus*, Sa=*Sorex arcticus*, Sc=*Sorex cinereus*, Zh=*Zapus hudsonius*, Pm=*Peromyscus maniculatus*.

LOCATION	HABITAT	Cg	Mp	Sa	Sc	Zh	Pm
Shagamu (1990)	Ridge	18	7				
	Wetland	4	18		3		
Brant River (1991)	Ridge		1				
	Wetland		14				
Ekwan (1990)	Ridge	88			7	2	
	Wetland	69		4	4	3	
Longridge (1991)	Ridge	5	6	2	8	16	
	Wetland		16	6	2	15	
Moosonee (1990)	Wetland	52			2		
Moosonee (1991)	Wetland	24			30		

C. gapperi was the only species consistently found at relatively high densities and in both ridge and wetland habitat. It was, therefore, the only species used in further analyses of habitat selection. I used data only from the Shagamu, Ekwan, and Longridge sites. Brant River was excluded because *C. gapperi* was absent at that site. Moosonee was also eliminated as these plots lacked the distinctive ridge-wetland pattern of the coastal locations.

Microhabitat

Principal components analysis extracted three orthogonal components accounting for 60.2% of the common variation among the 17 habitat variables (Table 4). PC1 described a gradient from open-sedge fen to heavily forest-covered ridges. PC2 represented a cline from open, dry habitats with some tree cover to heavily tree-covered wet areas with many shrubs. PC3 primarily differentiated typically coniferous habitats with deep mats from more deciduous habitats with shallow mats and litter-covered substrate (Appendix 1). Additional components were excluded as none accounted for more than 8% of the common variation.

Ridges and wetlands were clearly different in microhabitat composition (DFA, $\chi^2=58.62$, df=2, $P<.01$). 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 analysis indicating that ridges and wetlands were primarily distinguished on the basis of relative amounts of tree and shrub species

Table 4: PC loadings for the habitat variables. High PC1 scores are associated with forest-covered ridges while 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 more typically boreal habitats with deep mats and relatively short shrubs from more deciduous habitats with litter-covered substrate.

VARIABLE	**PC 1**	**PC 2**	**PC 3**
LTBAS	.92	.17	.06
SPIGL	.90	.05	.11
AWOOD	.79	-.02	-.05
SPHAG	.78	.06	.04
SSPIGL	.68	.20	-.10
VAVI	.60	-.09	.38
SEDGE	-.59	.14	.40
VLEGR	.35	.16	.08
SSLALA	.19	.86	.01
VMYGA	.05	.77	-.10
SLALA	.41	.73	.12
VSAPL	.14	.68	-.11
LMAT	-.06	.66	.55
MOSS	-.49	.59	.13
EMNI	.13	-.34	.23
LITTER	-.24	-.06	-.86
AVSHT	.21	.42	-.67

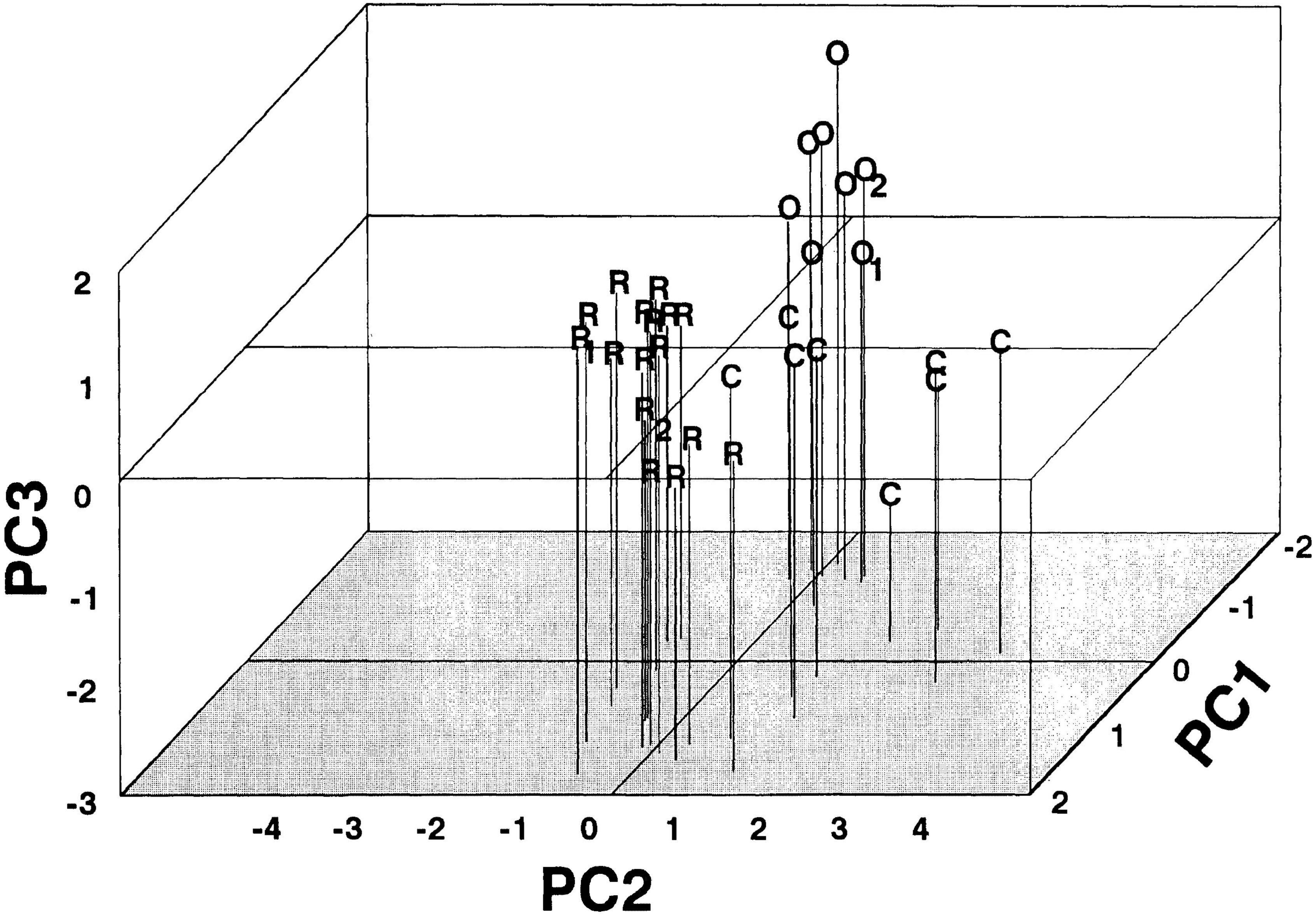
living in different moisture regimes. Relative to wetlands, PC loadings for ridges were generally higher for PC1 and lower for PC2 (Figure 5).

Significant differences in microhabitat composition within ridge and wetland also existed between sites. Twenty-one of 24 ridge plots were correctly classified to their appropriate site (DFA - two discriminant functions: DF_1, $\chi^2=46.98$, df=6, $P<.01$; DF_2, $\chi^2=8.65$, df=2, $P=.01$), demonstrating that habitat structure of ridges differed more between sites than within. Between-site differences were also significantly greater than within-site differences for wetland habitats. Seventeen of 24 were correctly assigned to their appropriate site (DFA - two discriminant functions: DF_1, $\chi^2=23.77$, df=6, $P<.01$; DF_2, $\chi^2=6.46$, df=2, $P=.04$).

Spatial Scale

Stepwise multiple regression analysis assessing the influence of site (regional location), habitat (patch type), and microhabitat, on the population density of *C. gapperi* (Equation 1), was highly significant ($F=44.9$, df=2,45, $P<.01$; Table 5). Population abundance was significantly related to regional location. Densities at Ekwan were higher than elsewhere ($P<.01$, $R^2=0.60$). Microhabitat (PC1) also influenced population density, improving the fit of the regression ($R^2=0.67$). Red-backed vole abundance was higher in tree-covered areas than in open areas. No other variables entered the analysis. *C. gapperi* density varied primarily with regional location and was modified locally by microhabitat composition (PC1).

Figure 5: Habitat structure of ridges (R), covered wetlands (C), and open wetlands (O), plotted in PC space. The two pairs of plots that were 'outliers' in the initial isodar are identified with subscripts (4 points).



PC3
2
1
0
-1
-2
-3
PC2
-4
-3
-2
-1
0
1
2
3
4
PC1
-2
-1
0
1
2
O
O
O
O
O2
O
O
O1
C
C
C
C
C
C
C
R
R
R
R1
R
R
R
R
R
R
R2
R
R
R
R

Table 5: Analysis of the relative significance of different habitat scales in determining variation in *C. gapperi* population densities. Analysis was by stepwise multiple regression of *C. gapperi* density with microhabitat PC's, and indicator variables for habitat and regional location. The indicator variable distinguishing Ekwan from other sites (EKWAN-IV) and PC1 were the only variables to enter the stepwise analysis.

Step	Variable	b	Cumulative R Square
1	EKWAN-IV	7.80	0.60
2	PC1	1.54	0.67

ANOVA

Source	df	Mean Square	P
Regression	2	477.26	< 0.001
Residual	45	10.63	

Habitat Quality

Stepwise regression of *C. gapperi* density with microhabitat components was highly significant ($F=16.1$, $df=2,45$, $P<.01$; Table 6), indicating habitat quality's influence on population abundance. Large residual variation ($R^2=0.42$) suggested, however, that density was related to more than just average habitat quality. Results were similar for microhabitat within wetlands ($F=13.0$, $df=2,21$, $P<.01$, $R^2=0.55$; Table 6) and within ridges ($F=8.20$, $df=2,21$, $P<.01$, $R^2=0.44$; Table 6). In all cases, PC1 and PC3 were the only variables to enter the stepwise analysis. Higher population densities were found in habitats with denser tree cover (PC1) and deeper mats (PC3).

Entry of PC3 into the analysis of habitat quality points to a potential interaction between regional location, average habitat quality, and population density. In the analysis of spatial scale (Equation 1) the indicator variable distinguishing Ekwan from other regional locations appears to have masked the influence of PC3 on population density. Ekwan plots generally had larger values of PC3 and higher population densities than other regional locations (Appendices 1 and 2).

Isodar Analysis

Geometric mean regression of densities in ridge versus those in wetland habitats was highly significant ($F=5.9$, $df=1,14$, $P=.03$; Table 7) confirming the role of density-dependent habitat selection in determining local population densities of *C.*

Table 6: The relationship between *C. gapperi* population density and habitat quality. Analysis was by stepwise multiple regression of *C. gapperi* density with PC's describing habitat composition. An analysis was performed for ridge and wetland habitats combined, as well as for each habitat separately.

RIDGE AND WETLAND

Step	Variable	b	Cumulative R Square
1	PC1	2.89	0.27
2	PC3	2.10	0.42

ANOVA

Source	df	Mean Square	P
Regression	2	299.22	< 0.001
Residual	45	18.54	

WETLAND

Step	Variable	b	Cumulative R Square
1	PC1	4.76	0.43
2	PC3	1.69	0.55

ANOVA

Source	df	Mean Square	P
Regression	2	161.67	< 0.001
Residual	21	12.46	

RIDGE

Step	Variable	b	Cumulative R Square
1	PC3	2.79	0.30
2	PC1	2.99	0.44

ANOVA

Source	df	Mean Square	P
Regression	2	179.30	0.002
Residual	21	21.86	

Table 7: The relationship of *C. gapperi* population density in ridge habitat to density in wetland habitat. The isodar of ridge versus wetland was the initial regression that included 16 habitat pairs. Isodars of ridge versus open wetland (Figure 10) and ridge versus covered wetland (Figure 9) include 8 habitat pairs each. The wetland habitats were divided into two groups based on a cluster analysis of microhabitat composition. All isodars were highly significant.

ISODAR OF RIDGE vs. WETLAND

Source	df	Mean Square	P
Regression	1	167.27	0.029
Residual	14	28.12	

ISODAR OF RIDGE vs. OPEN WETLAND

Source	df	Mean Square	P
Regression	1	373.30	0.001
Residual	6	10.93	

ISODAR OF RIDGE vs. COVERED WETLAND

Source	df	Mean Square	P
Regression	1	94.52	0.001
Residual	6	2.25	

gapperi (Figure 6). A non-significant 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 equal preference for ridge and wetland habitat. Two potential, but non-significant, 'outliers' (Figure 6) and a low R^2 (0.30), suggested, nevertheless, that this isodar may provide an incomplete description of habitat selection in this system. Was it possible that these two 'outliers' identified a problem with my division of habitat patches into ridge and wetland?

The two unusual density combinations corresponded to Ekwan plots in which the wetland had unusually low population densities relative to neighbouring ridge habitat. Interestingly, these two wetlands were misclassified by site in the DFA that compared within- and between-site microhabitat differences for wetlands. Two possibilities suggest themselves:

1. If the same process of habitat selection operates in all plots, then the unusual density differences of the Ekwan wetlands may simply reflect unusual differences in microhabitat. This does not appear to be the case. Microhabitat differences between ridge and wetland (measured for each pair as the euclidean distance between habitats in PC space) were no greater for these pairings than for others (Table 8).
2. The 'outliers' represent a third habitat type that modifies spatial population regulation. I performed two cluster analyses, one within ridges and one within wetlands, to assess this possibility. From the resulting dendrograms I identified three habitats; ridge, open wetland and covered wetland (Figures 7 and 8).

Figure 6: Isodar of *C. gapperi* population densities demonstrating equal preference for ridge and wetland habitat. Numbers in brackets denote multiple points with the same coordinates. Note the two unusual density combinations marked with '+'. These two points suggest that *C. gapperi* may be recognizing more than two categories of habitat.

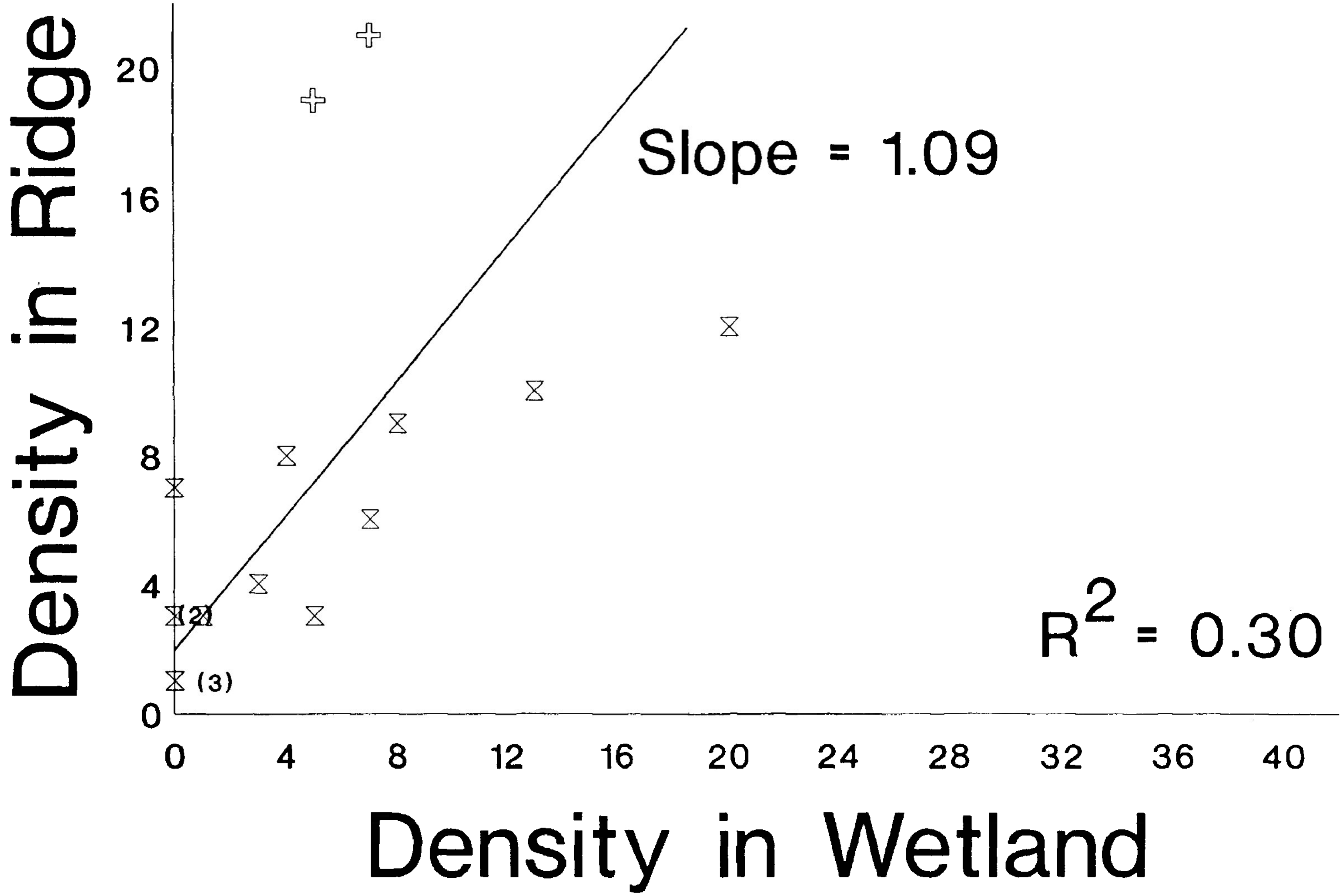

Density in Ridge
20
16
12
8
4
0
(2)
(3)
Slope = 1.09
R^2 = 0.30
0
4
8
12
16
20
24
28
32
36
40
Density in Wetland

Table 8: Red-backed vole densities and euclidean distances in PC space for all pairs of plots used in the isodar analyses. Wetlands are classified as either open or covered based on results of cluster analysis. N_{Ridge} and $N_{Wetland}$ are the estimated population densities of *C. gapperi* in each habitat. Apparent outliers from the initial isodar are marked with asterisks (*).

SITE	TR	PLOT NO.	N_{RIDGE}	$N_{WETLAND}$	WETLAND TYPE	EUCLIDEAN DISTANCE
Shagamu	W	2	1	0	Open	1.21
Shagamu	W	4	7	0	Open	2.67
Shagamu	E	2	3	0	Open	1.64
Shagamu	E	3	3	1	Open	2.37
Shagamu	E	4	4	3	Covered	1.94
Ekwan	N	1	3	5	Covered	3.19
Ekwan	N	2	10	13	Covered	1.88
Ekwan	N	3	9	8	Covered	1.04
Ekwan	N	4	12	20	Covered	2.14
Ekwan	S	1	6	7	Covered	3.66
Ekwan*	S	2	19	5	Open	3.38
Ekwan	S	3	8	4	Open	2.89
Ekwan*	S	4	21	7	Open	2.71
Longridge	S	2	3	0	Covered	2.72
Longridge	S	3	1	0	Open	2.35
Longridge	S	4	1	0	Covered	2.44

Figure 7: Dendrogram showing results of cluster analysis on wetland microhabitat. Clustering was based on the squared euclidean distances between plots in PC space. Wetlands divided into two main clusters, those that were relatively open (upper cluster) and those that were more heavily shrub and tree covered (lower cluster). 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.

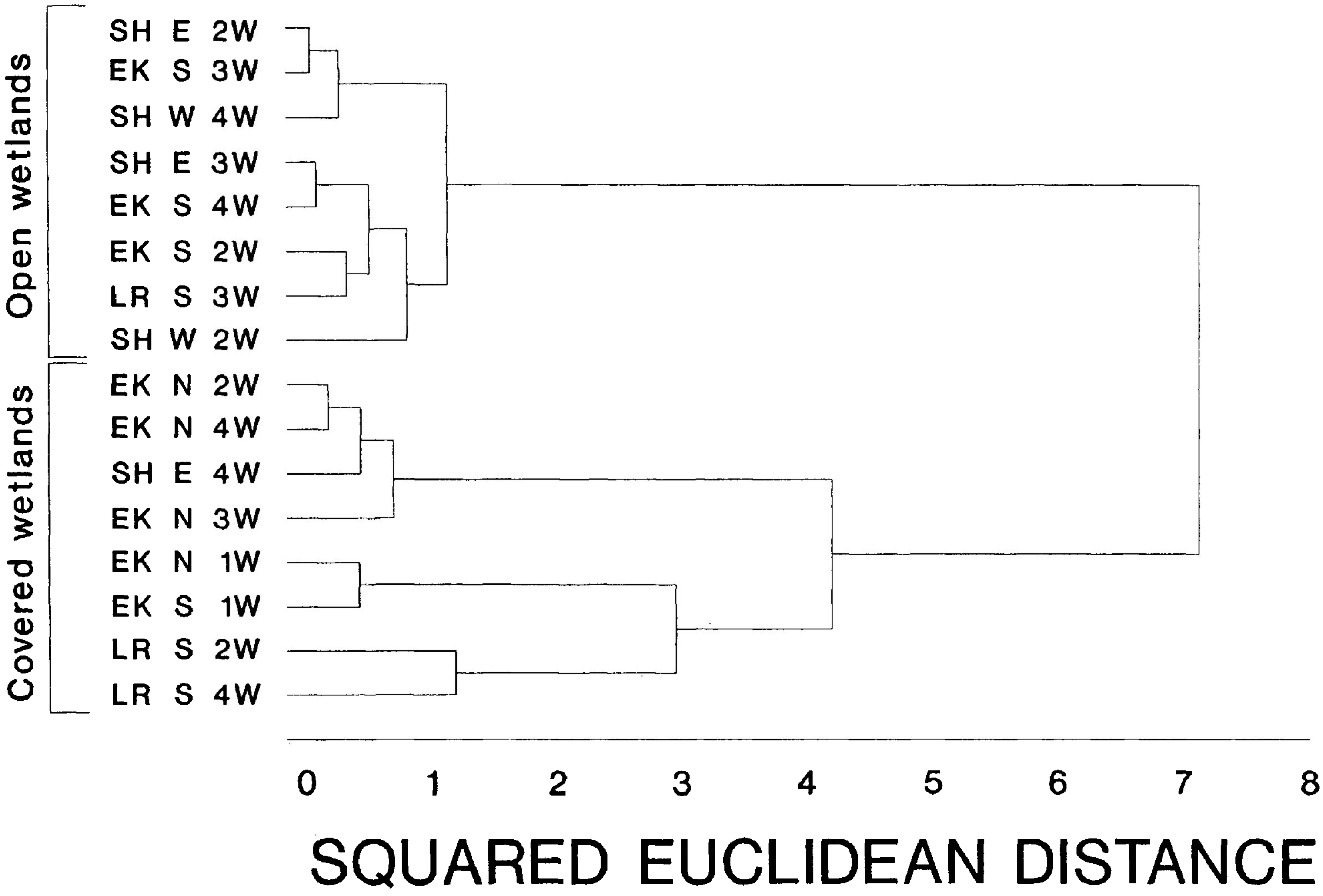
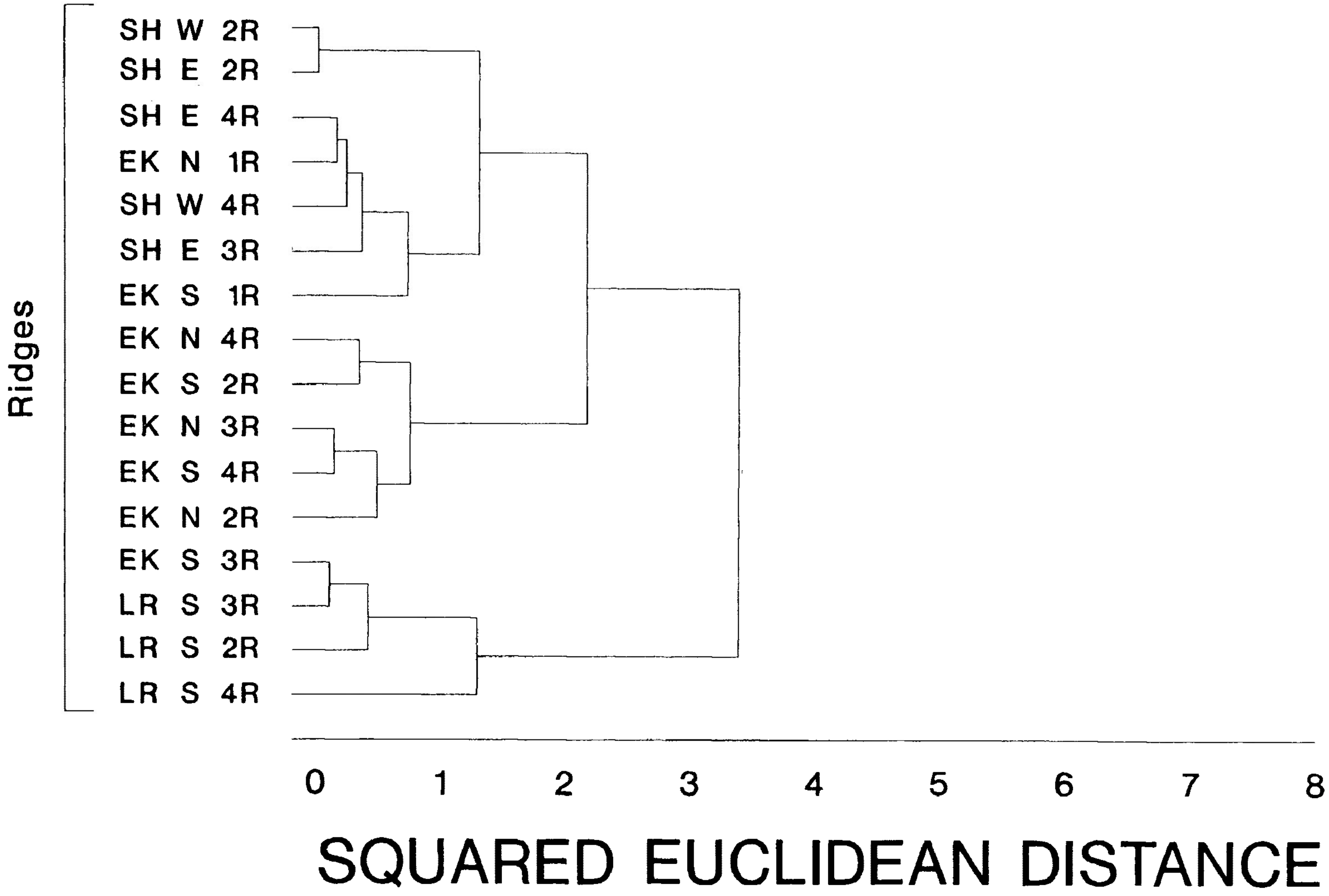

Open wetlands
Covered wetlands
SH E 2W
EK S 3W
SH W 4W
SH E 3W
EK S 4W
EK S 2W
LR S 3W
SH W 2W
EK N 2W
EK N 4W
SH E 4W
EK N 3W
EK N 1W
EK S 1W
LR S 2W
LR S 4W
0
1
2
3
4
5
6
7
8
SQUARED EUCLIDEAN DISTANCE

Figure 8: Dendrogram showing results of cluster analysis on ridge microhabitat. Clustering was based on the squared euclidean distances between plots in PC space. 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.


Ridges
SH W 2R
SH E 2R
SH E 4R
EK N 1R
SH W 4R
SH E 3R
EK S 1R
EK N 4R
EK S 2R
EK N 3R
EK S 4R
EK N 2R
EK S 3R
LR S 3R
LR S 2R
LR S 4R
0
1
2
3
4
5
6
7
8
SQUARED EUCLIDEAN DISTANCE

Open and covered wetlands are not only different from each other, they are also different from each other relative to the ridges (Figure 5). This relative difference, if recognized by habitat selecting red-backed voles, would suggest the possibility of a second type of habitat-dependent population regulation occurring within the lowland landscapes.

Three habitats

I reanalysed density-dependent habitat selection by calculating two different isodars in the three-habitat division. The first corresponded to tree and shrub covered wetlands versus their paired ridges, the second to open wetlands versus their paired ridges. Despite small sample sizes ($n=8$), both isodars were highly significant ($P<.01$). Vole density in covered wetlands was tightly related to vole density in adjoining ridges ($F=42.1$, $df=1,6$, $R^2=0.88$; Table 7, Figure 9):

$$N_{Cg\ \mathrm{Ridge}} = 1.96 + 0.58\ N_{Cg\ \mathrm{Covered\ Wetland}}. \tag{3}$$

A similar result occurred between open wetlands and their adjoining ridges ($F=34.15$, $df=1,6$, $R^2=0.85$; Table 7) but the regression line was strongly influenced by the two points corresponding to high densities at Ekwan (Figure 10):

$$N_{Cg\ \mathrm{Ridge}} = 1.87 + 2.83\ N_{Cg\ \mathrm{Open\ Wetland}}. \tag{4}$$

The isodar intercept was significant (95% confidence interval=0.29-4.15) for ridges with covered wetlands and non-significant (95% confidence interval=-1.35-6.02) for ridges with open wetlands. It is probable, however, that both intercepts

Figure 9: Isodar of covered wetlands. The isodar slope significantly less than one and its significant non-zero intercept indicate qualitative and quantitative differences between the ridge and wetland habitats. This isodar is consistent with cross-over population regulation (Morris 1988).

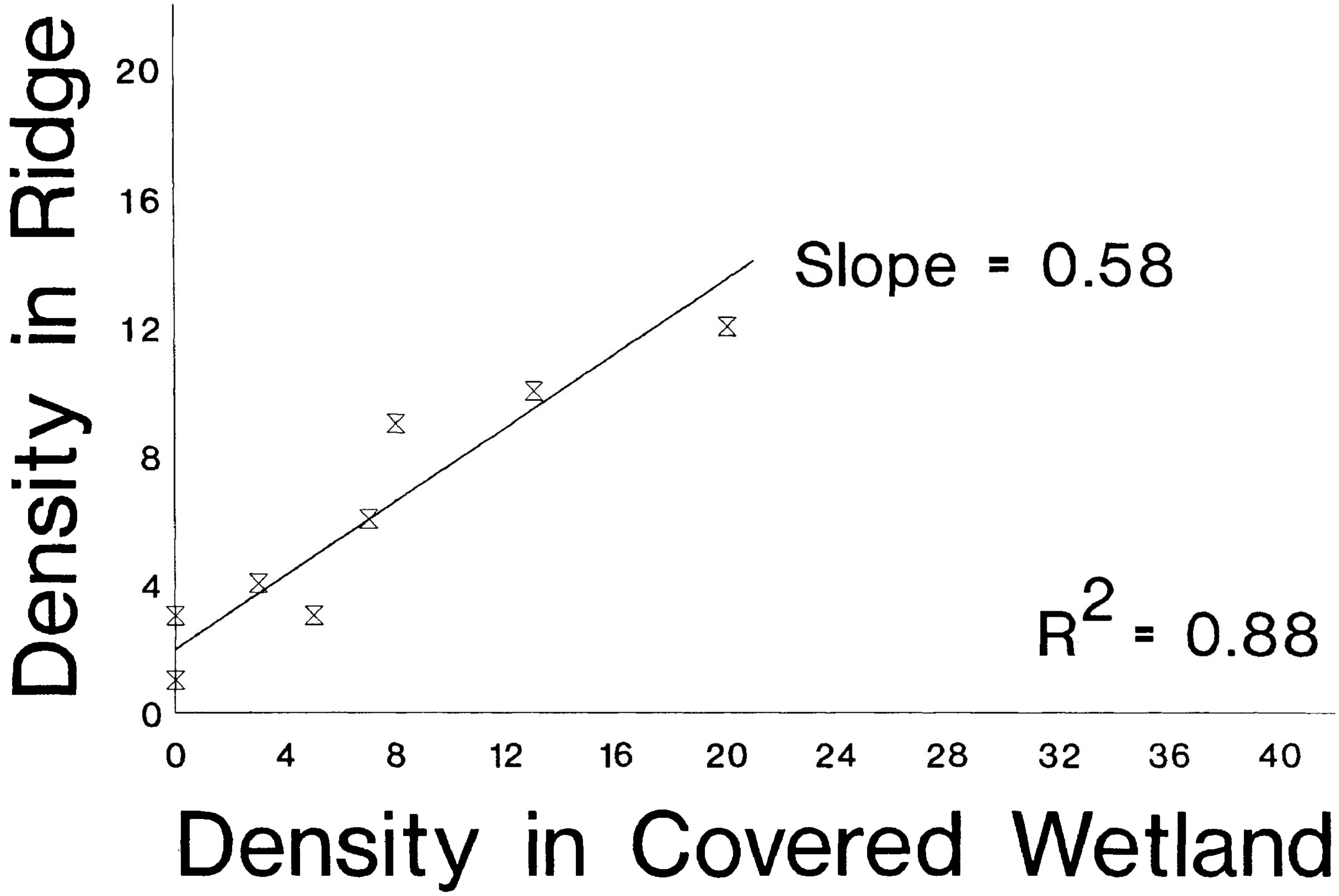
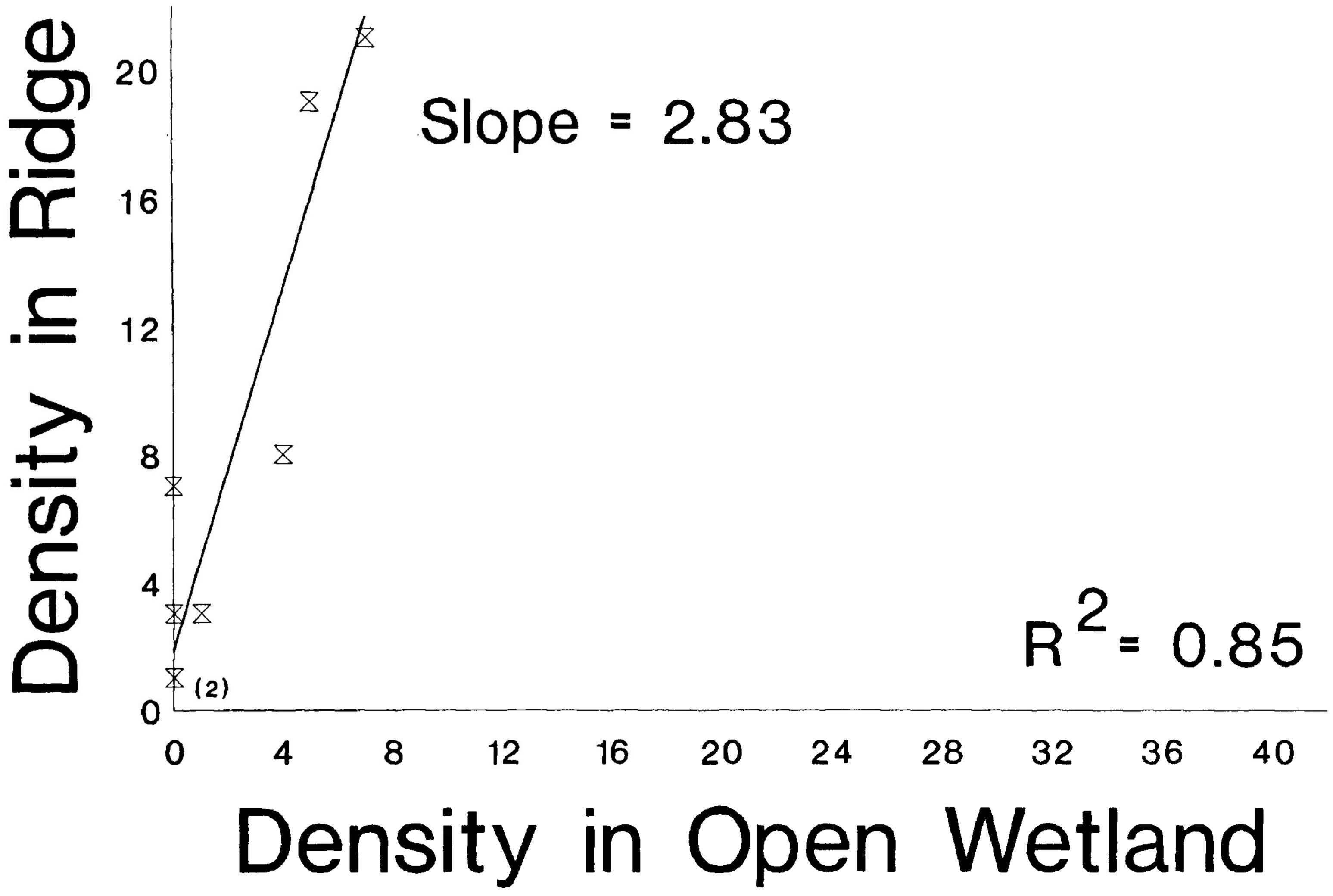

Density in Ridge
20
16
12
8
4
0
0
4
8
12
16
20
24
28
32
36
40
Slope = 0.58
R^2 = 0.88
Density in Covered Wetland

Figure 10: Isodar of open wetlands. The isodar slope significantly greater than one and its non-significant non-zero intercept indicate qualitative differences between the ridge and wetland habitats. (2) denotes two points with the same coordinates. Note that the isodar regression is strongly influenced by two points at higher density. The isodar is consistent with divergent population regulation (Morris 1988).


Density in Ridge
Density in Open Wetland
Slope = 2.83
R^2 = 0.85
(2)
0
4
8
12
16
20
0
4
8
12
16
20
24
28
32
36
40

have biological significance. There were only two instances out of 72 paired density estimates, in which a red-backed vole was present in a wetland plot while the population density estimate was zero for the corresponding ridge (Appendix 2). It appears that *C. gapperi* consistently selects ridge over wetland at low population density (Figures 9 and 10). The striking difference in the slope of the isodars, indicates that as population density increases, density-dependent habitat selection becomes dramatically different for paired habitats with open wetlands versus those with covered wetlands. The isodar of ridges with open wetlands is consistent with divergent population regulation (slope greater than one; 95% confidence interval 1.74-3.92), whereas the isodar with covered wetlands signifies cross-over population regulation (slope less than one; 95% confidence interval=0.34-0.74).

It is possible that these apparent forms of population regulation could be artifacts of microhabitat variation within habitat classifications. A ridge with more tree cover, for example, may be able to support a higher density of red-backed voles than an 'average' ridge. If both ridges are paired with wetlands of similar microhabitat composition, there would be a greater difference in population density between the tree-covered ridge and its wetland than between the 'average' ridge and its wetland. When plotting the isodar in this case, the choice of habitats would appear to diverge at high density. Divergent regulation could therefore result from a divergence in microhabitat between ridge and wetland while cross-over regulation could result from a convergence in microhabitat.

Using euclidean distances in PC space, I estimated microhabitat similarity between corresponding ridges and wetlands. In the case of cross-over regulation, regression of combined population density for each habitat pair against their euclidean distance was not significant (F=0.76, df=1,6, P=.42). Cross-over regulation was independent of a convergence in microhabitat. Divergent regulation was, however, apparently associated with divergence in microhabitat composition (F=5.93, df=1,6, b=10.74, P=.051).

DISCUSSION

It is evident from my spatial analysis across simple and repeated landscapes, that population density of red-backed voles is related to habitat at different spatial scales. Population-level abundance patterns were best documented by density-dependent habitat selection at the local scale while regional and microhabitat scales modified the local patterns.

Average habitat quality was a partial predictor of population density across locations, but it did not fully account for abundance patterns at the population level (Table 6). This suggests that microhabitat selection probably modifies population density patterns of *C. gapperi* but that microhabitat selection is not the primary process regulating population density in a landscape. It is also possible that habitat quality correlations were spurious and resulted from consistent microhabitat differences between sites and between habitat types.

The fact that both the open wetland and covered wetland isodars were highly significant underscores the importance of investigating local-scale processes of population regulation. The isodars help confirm that density-dependent habitat selection is an important factor in the local-scale population dynamics of *C. gapperi*. Because the isodars were constructed with paired estimates of population densities from different regional locations, we can conclude that the same forms of population regulation appear to be acting across landscapes, and across a wide range of population densities. This may be the key scale for understanding the interaction between landscape structure and population regulation.

Divergent regulation, documented in the isodar of ridges with open wetlands, suggests that populations in open wetlands have a lower intrinsic rate of increase and a smaller carrying capacity than those in ridges. Morris (1992) identified this form of regulation for populations of *P. maniculatus* in prairie and badland habitats of Alberta. The isodar slope greater than one indicates a qualitative difference between ridge and open wetland habitats (Morris 1988). But it is also possible that apparent divergent population regulation was simply an artifact caused by divergence in microhabitat composition between ridges and open wetlands. Regression analysis of combined ridge and wetland density with euclidean distances between habitat PC's, provided tentative evidence (P=.051) that larger overall population sizes were generally associated with habitat pairs which were structurally more dissimilar in terms of microhabitat. This is of particular importance because the isodar regression was strongly influenced by two points at high population density. It is difficult, therefore, to unambiguously translate the isodar into the context of population regulation, but it is evident that red-backed voles preferentially select ridges over open wetlands across all population densities.

The isodar of ridges with covered wetlands suggests cross-over population regulation (Morris 1988). At low population density, the non-zero intercept identifies a quantitative difference in perceived fitness rewards between habitats. This difference becomes less and less detectable with increasing population density, to the point that there is reversal, or cross-over, in habitat suitability. Cross-over results from a qualitative difference between habitats, indicated by a slope significantly less than one. In contrast with the divergent isodar, there was no evidence of convergence or divergence in habitat composition within the habitat pairs. It is likely that ridges have a higher intrinsic rate of increase at low density, but a smaller carrying capacity than covered wetlands. Abramsky et al. (1990) identified a similar pattern with two desert gerbil species (*G. pyramidum* and *G. allenbyi*).

It seems clear from the isodars that individuals are, to some extent, recognizing and responding to ridges and wetlands as distinct habitats. Population density in ridges is consistently related to population density in wetlands, despite significant variation in microhabitat at different regional locations. This suggests that red-backed voles respond to common landscape features in similar ways.

Regional variation in population abundance was primarily predicted by a regional indicator variable (Equation 1), suggesting that density patterns may be linked to regional-scale biogeographic effects (e.g. Ricklefs 1987, Menge and Olson 1990, Tonn et al. 1990, Cornell and Lawton 1992). The apparent absence of *C. gapperi* in the sub-arctic tundra at Brant River emphasizes this point. Thus, regional climatic differences may have important influences on regional abundance patterns in the Hudson Bay Lowland. Average habitat quality, measured as microhabitat of census plots, also differed between sites and was a predictor of population density at the regional scale. At least in this series of repeated landscapes, regional-scale population dynamics can probably be explained as some combination of large-scale biogeographic influences and regional differences in average habitat quality.

It appears that regional variation in population abundance resulted in large density differences within habitat types, thereby masking the significance of local-scale habitat effects. This could help explain why the initial regression analysis (Equation 1) failed to identify habitat type (ridge or wetland), as a significant predictor of red-backed vole density. My analysis of habitat use at the regional scale probably identified average habitat differences between landscapes (Danielson 1991) which masked the potential effects of the identity and arrangement of habitat patches within landscapes (Danielson 1991, Dunning et al. 1992).

My analysis of population abundance in red-backed voles highlights the importance of documenting ecological patterns at an appropriate spatial scale. In this case, population regulation appears to be acting between habitat patches within landscapes. Although processes occurring at other scales influence abundance patterns, density-dependent habitat selection provides a feasible mechanism that directly links population regulation with habitat.

Habitat-dependent population regulation emphasizes the potential importance of landscape structure on local-scale patterns of population abundance, beyond a simple weighted average of the sum of landscape components (Danielson 1992, Dunning et al. 1992). My isodar analysis demonstrates, for example, that population density of red-backed voles in ridge habitat is a function of population density in neighbouring wetland habitat, which, in turn, is a function of the wetland habitat's identity (either open or covered).

This finding lends support to Pulliam and Danielson's (1991) conclusion that landscape composition significantly influences a species' population dynamics. It does not test for the importance of nonadditive landscape effects (sensu Pulliam and Danielson 1991, Danielson 1992, Dunning et al. 1992) because the relatively consistent nature of landscapes at the three sites analyzed in the HBL made comparative study impossible. Substantiating the effects of landscape composition on population dynamics requires a field test that compares population dynamics in landscapes with different relative abundances of each type of habitat. This may be a profitable next step.

Isodars, habitat, and population regulation across landscapes

In a simple and repeated series of northern landscapes, I have demonstrated that population-abundance patterns of red-backed voles represent an interaction of processes occurring over a range of spatial scales. Large disparities in abundances between locations appeared to result from biogeographic effects and habitat differences. Despite regional variation in abundance, isodar analysis demonstrated that density-dependent habitat selection was a significant process unifying local-scale patterns of population density. Significant correlations between population density and microhabitat provide tentative evidence that microhabitat choice may also influence habitat selection at the population level. It appears that individuals from populations spread across hundreds of kilometres, in conditions ranging from sub-arctic tundra to boreal forest, and from early to late stages of primary succession, are recognizing and responding to common landscape features in a similar way. At least in the Hudson Bay Lowland, the process of density-dependent habitat selection regulates *C. gapperi* populations between habitats, suggesting that landscape structure may play a critical role in the determination of local-scale abundance patterns.

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APPENDIX 1

Habitat description of all trapping plots

The following table identifies each plot by site, transect (TS), habitat type, and plot number (NO). Principal component scores are provided for all plots except Brant River and Moosonee which were excluded from the PCA. Habitat descriptions indicate general conditions of the plot.

TS	HABITAT	NO	PC1	PC2	PC3	HABITAT DESCRIPTION
SHAGAMU (1990)						
W	Ridge	1	-0.50	-1.23	0.31	Open tundra: few trees and shrubs
W	Wetland	1	-1.39	-0.16	1.08	Open sedge fen: wet, low sedge
W	Ridge	2	-0.38	-1.11	0.06	Open tundra: some small trees and shrubs
W	Wetland	2	-1.27	-0.31	0.29	Open sedge fen: wet with some shrubs
W	Ridge	3	0.31	-1.08	0.50	Open tundra: low, moist, some trees
W	Wetland	3	-0.67	0.76	-0.54	Open sedge fen: tall sedge, some shrubs
W	Ridge	4	0.64	-0.96	0.34	Mature spruce-lichen forest
W	Wetland	4	-1.48	0.03	1.62	Open sedge fen: some shrubs
E	Ridge	1	-0.28	-0.81	0.32	Open tundra: few trees, some shrubs
E	Wetland	1	-1.27	-0.26	0.94	Open sedge fen: wet, low sedge, some shrubs
E	Ridge	2	-0.45	-0.95	0.07	Open tundra: low, moist, some trees and shrubs
E	Wetland	2	-1.40	-0.08	1.09	Open sedge fen: hummocky, tall sedge, some shrubs
E	Ridge	3	0.46	-1.24	0.76	Sparse spruce-lichen woodland
E	Wetland	3	-1.32	0.32	0.74	Open sedge fen: hummocky, tall sedge, many shrubs
E	Ridge	4	0.21	-0.76	0.54	Mature spruce-lichen forest
E	Wetland	4	0.18	1.13	0.13	Tree and shub covered fen: tall sedge

TS	HABITAT	NO	PC1	PC2	PC3	HABITAT DESCRIPTION
BRANT RIVER (1991)						
W	Ridge	1				Open tundra: hummocky, few shrubs
W	Wetland	1				Open sedge fen: hummocky, low sedge, few shrubs
W	Ridge	2				Open tundra: moist, some sedge and shrubs
W	Wetland	2				Open sedge fen: low sedge, few small shrubs
W	Ridge	3				Open tundra: some shrubs
W	Wetland	3				Open sedge fen: wet, tall sedge, many shrubs
W	Ridge	4				Open tundra: some sedge and shrubs
W	Wetland	4				Open sedge fen: low sedge, some shrubs
E	Ridge	1				Open tundra: very few shrubs
E	Wetland	1				Open sedge fen: hummocky, low sedge
E	Ridge	2				Open tundra: very few shrubs
E	Wetland	2				Open sedge fen: hummocky, moist, some shrubs
E	Ridge	3				Open tundra: few shrubs
E	Wetland	3				Open sedge fen: low sedge, some shrubs
E	Ridge	4				Open tundra: hummocky, some sedge
E	Wetland	4				Open sedge fen: hummocky, wet

TS	HABITAT	NO	PC1	PC2	PC3	HABITAT DESCRIPTION
EKWAN (1990)						
N	Ridge	1	0.55	-0.56	0.61	Mature spruce-lichen forest: some mossy areas
N	Wetland	1	0.29	2.57	0.04	Heavily shrub covered fen: deep moss cover
N	Ridge	2	0.87	-0.42	0.91	Mature spruce-lichen forest
N	Wetland	2	0.80	1.39	0.44	Tree and shrub covered fen: wet with deep moss
N	Ridge	3	1.45	0.05	0.86	Mature spruce-lichen forest: areas of deep moss
N	Wetland	3	1.19	0.88	0.30	Tree and shrub covered fen: deep moss cover
N	Ridge	4	1.24	-0.91	0.87	Mature spruce-lichen forest
N	Wetland	4	0.53	1.09	0.59	Tree and shrub covered fen: sedges
S	Ridge	1	0.83	-0.46	0.01	Mature spruce-lichen forest: areas of deep moss
S	Wetland	1	1.21	0.64	0.17	Tree and shrub covered bog: wet
S	Ridge	2	1.74	-0.71	1.12	Mature spruce-lichen forest: areas of deep moss
S	Wetland	2	-1.21	0.64	0.17	Open sedge fen: some shrubs
S	Ridge	3	1.25	0.39	-0.14	Mature spruce-lichen forest: areas of deep moss
S	Wetland	3	-1.29	0.05	1.18	Open sedge fen: hummocky, some shrubs and trees
S	Ridge	4	1.30	-0.13	0.55	Mature spruce-lichen forest: areas of deep moss
S	Wetland	4	-1.29	0.61	0.81	Open sedge fen: wet, some shrubs

TS	HABITAT	NO	PC1	PC2	PC3	HABITAT DESCRIPTION
LONGRIDGE (1991)						
N	Ridge	1	-0.22	-0.82	-2.30	Shrub and tall sedge, gravel substrate
N	Wetland	1	-0.83	-0.71	0.07	Open supertidal sedge fen: low sedges, legumes
N	Ridge	2	-0.83	-0.73	-2.12	Heavily shrub covered: low shrub
N	Wetland	2	-0.93	-0.65	-0.67	Open sedge fen: tall and low sedges, some shrubs
N	Ridge	3	1.32	-0.70	-1.74	Early stage spruce-poplar forest: many shrubs
N	Wetland	3	-0.82	-0.76	-0.01	Open supertidal sedge fen: tall and low sedges
N	Ridge	4	0.49	-0.39	-1.00	Mature spruce-poplar forest: some shrubs
N	Wetland	4	-0.91	-0.08	-2.38	Shrub covered sedge fen: tall sedges
S	Ridge	1	1.25	-0.86	-0.78	Mature spruce-poplar forest: few shrubs
S	Wetland	1	-0.70	-0.60	-2.74	Supertidal sedge fen: tall and low sedges
S	Ridge	2	1.28	-0.18	-0.47	Mature spruce-moss forest: few shrubs
S	Wetland	2	-0.34	1.66	-1.67	Tree and shrub covered swamp: wet
S	Ridge	3	1.47	0.42	-0.38	Mature spruce-moss forest: many shrubs
S	Wetland	3	-0.78	0.27	0.28	Open sedge bog: wet, some shrubs
S	Ridge	4	1.59	1.19	0.05	Mature spruce-tamarack forest: many shrubs
S	Wetland	4	-0.54	2.12	-0.70	Tamarack covered swamp: many shrubs, tall sedge

TS	HABITAT	NO	PC1	PC2	PC3	HABITAT DESCRIPTION
MOOSONEE (1990 AND 1991)						
S	Wetland	1				Dense alder thicket swamp: many trees
S	Wetland	2				Shrub covered fen: deep moss
S	Wetland	3				Shrub covered fen: deep moss
S	Wetland	4				Shrub covered fen: deep moss, some trees
S	Wetland	5				Shrub covered fen: deep moss, some trees
S	Wetland	6				Mature spruce-moss forest: many shrubs
S	Wetland	7				Shrub covered fen: deep moss
S	Wetland	8				Shrub covered fen: deep moss

APPENDIX 2

Small mammal population densities by plot and trapping round

The following table identifies population densities (Minimum Number known Alive) of all small mammal species captured in the Hudson Bay Lowland. Densities are provided by species for each trapping round on the basis of site, transect (N,S,W,E), habitat type (R or W), and plot number (1,2,3,4). All plots correspond with those described in Appendix 1.

SHAGAMU (1990)

SPECIES	1R	1W	2R	2W	3R	3W	4R	4W
TRANSECT W								
FIRST TRAPPING ROUND								
No captures								
SECOND TRAPPING ROUND								
Clethrionomys gapperi							2	
Microtus pennsylvanicus								
THIRD TRAPPING ROUND								
Clethrionomys gapperi							7	
Microtus pennsylvanicus				4			2	5
TRANSECT E								
FIRST TRAPPING ROUND								
Microtus pennsylvanicus		1		2				
SECOND TRAPPING ROUND								
Clethrionomys gapperi			3		3	2		2
Microtus pennsylvanicus		2			1			
Zapus hudsonius					1			
THIRD TRAPPING ROUND								
Clethrionomys gapperi			3		3	1	4	3
Microtus pennsylvanicus		2		2	5	1		3
Sorex cinereus						1		2
Zapus hudsonius				1				

BRANT RIVER (1991)

SPECIES	1R	1W	2R	2W	3R	3W	4R	4W
TRANSECT W								
FIRST TRAPPING ROUND								
No captures								
SECOND TRAPPING ROUND								
No captures								
THIRD TRAPPING ROUND								
Microtus pennsylvanicus						6		7
TRANSECT E								
FIRST TRAPPING ROUND								
No captures								
SECOND TRAPPING ROUND								
No captures								
THIRD TRAPPING ROUND								
No captures								

EKWAN (1990)

SPECIES	1R	1W	2R	2W	3R	3W	4R	4W
TRANSECT N								
FIRST TRAPPING ROUND								
Clethrionomys gapperi	2		3					
SECOND TRAPPING ROUND								
Clethrionomys gapperi	3	3	4	12	8	7	17	15
Sorex cinereus				1				
Tamiasciurus hudsonicus								
THIRD TRAPPING ROUND								
Clethrionomys gapperi	3	5	10	13	9	8	12	20
Microtus pennsylvanicus				1				1
Sorex cinereus		2						
Zapus hudsonius				2				
TRANSECT S								
FIRST TRAPPING ROUND								
Clethrionomys gapperi	4							
SECOND TRAPPING ROUND								
Clethrionomys gapperi	8	6	14	2	13		16	5
Zapus hudsonius				1				
THIRD TRAPPING ROUND								
Clethrionomys gapperi	6	7	19	5	8	4	21	7
Microtus pennsylvanicus		2		1				2
Sorex arcticus				4				
Sorex cinereus	1	2			5			
Zapus hudsonius	1	1			1			

LONGRIDGE (1991)

SPECIES	1R	1W	2R	2W	3R	3W	4R	4W
TRANSECT N								
FIRST TRAPPING ROUND								
Zapus hudsonius								2
SECOND TRAPPING ROUND								
Clethrionomys gapperi								
Microtus pennsylvanicus						2		
THIRD TRAPPING ROUND								
Microtus pennsylvanicus	3							1
Sorex cinereus	2		3		1		2	1
Peromyscus maniculatus					1			
Zapus hudsonius	3		4	1	1		6	6
TRANSECT S								
FIRST TRAPPING ROUND								
Clethrionomys gapperi								
SECOND TRAPPING ROUND								
Clethrionomys gapperi							2	
Zapus hudsonius								
Tamiasciurus hudsonicus	1							
THIRD TRAPPING ROUND								
Clethrionomys gapperi			3				1	
Microtus pennsylvanicus		3				3	3	1
Sorex arcticus				4	2			2
Sorex cinereus								
Zapus hudsonius	2	2		3				2

MOOSONEE (1990)

SPECIES	1W	2W	3W	4W	5W	6W	7W	8W
FIRST TRAPPING ROUND								
Clethrionomys gapperi			6	2		2		6
Tamiasciurus hudsonicus						1		1
SECOND TRAPPING ROUND								
Clethrionomys gapperi	1			3	1	2		2
Tamiasciurus hudsonicus	1				1	3		
THIRD TRAPPING ROUND								
Clethrionomys gapperi	6	5	6	14	8	4	4	5
Sorex cinereus		1					1	
Zapus hudsonius					-			
Tamiasciurus hudsonicus		1				1		2

MOOSONEE (1991)

SPECIES	1W	2W	3W	4W	5W	6W	7W	8W
FIRST TRAPPING ROUND								
Clethrionomys gapperi		3				3		
SECOND TRAPPING ROUND								
Clethrionomys gapperi	3	2	6	5	5			
Sorex cinereus			1					
Tamiasciurus hudsonicus						2		
THIRD TRAPPING ROUND								
Clethrionomys gapperi	3	2	5	9	2		1	2
Sorex cinereus	9	3	1	3	3	3	6	2
Tamiasciurus hudsonicus	1							