



# Habitat selection and the scale of ghostly coexistence among Arctic rodents

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Competition between coexisting species existing near their stable equilibrium can be obscured if they occupy separate habitats. Theories of habitat selection promise an ability to reveal the underlying ghost of competition by using isodars to infer the behavioural map of habitat selection. We tested the theory with two years of data on abundance and habitat preference by three Arctic rodent species living at low density along a gradient of wet to dry tundra on Herschel Island in Canada's western Arctic. Generalist brown lemmings exhibited a constant partial preference toward wet tundra whereas specialist collared lemmings and voles occupied the driest and wettest zones respectively. Although both lemming species compete for habitats elsewhere in the Canadian Arctic, isodar analyses suggest that the three species occupy wet and dry habitats independently of one another on Herschel Island. Competition at this large scale may be hidden at low densities, however, if the wet-dry dichotomy is too coarse. Analyses at a finer subdivision of habitat revealed that these species coexist by using different microhabitats. Collared lemmings shifted their niche towards even drier habitat as the abundance of brown lemmings increased. We were thus able to reveal the ghost of competition lurking at large scales through a more refined analysis at smaller scales of density-dependent habitat use.

Guilds of related species with similar morphology and diets, such as rodent herbivores in northern latitudes, should normally compete with one another for limited resources (Morris et al. 2000a, Morris 2005). Competition in such guilds is often thought to be mediated along niche axes corresponding to resources (the  $R^*$  rule, Tilman 1982), predation (the  $P^*$  rule, Holt 1984) or stress (the  $S^*$  rule, Chase and Leibold 2003). Regardless as to root cause, such competing species often resolve their interaction through habitat selection. A particularly intriguing case occurs between pairs of species with distinct preferences for two alternative habitats. It is often possible for such species to occupy only their separate preferred habitat at densities where they coexist in stable equilibrium. The zero-growth isoclines cross where the species live apart and the competition responsible for habitat selection thus becomes, like a ghost, invisible because of it (Rosenzweig 1974, 1979, 1981, Morris 1999a, b). We now know, however, that the ghost can be revealed when natural or experimentally modified densities force individuals to exploit their secondary habitat preference (Morris 1999b, Morris et al. 2000a, b). Regardless, if densities are consistently low, then competition between the species will be invisible because each occupies only its preferred habitat.

Several additional complexities arise in three-species, three-habitat communities where at least 10 different community organizations are possible (Brown 1996). One of

the more intriguing patterns emerges through differences in scale that allow a fine-grained generalist to coexist with two coarse-grained habitat specialists. The generalist persists by exploiting the margins of the specialists' preference. So even though Brown's (1996) model requires three habitats, the species can often exist along a single gradient.

An example of Brown's (1996) three-species solution can be found in northern montane rodents. Chipmunks, *Tamias amoenus*, forage widely with no preference for either the xeric forest occupied by deer-mice, *Peromyscus maniculatus*, or for the more mesic forest favoured by red-backed voles, *Myodes gapperi* (Morris 1996). The chipmunk, in essence, occupies a fine-grained niche in a 'third habitat' nestled between the specialists' more extreme preferences.

Drawing habitat-selection maps to infer competition among three or more interacting species is difficult, but essential if habitat selection theory is to guide our understanding of coexistence in the vast majority of ecological communities. The maps are equally essential as we move from understanding current patterns towards developing insights into evolutionary trajectories associated with impending global habitat change. Our interest in the long-term effects of climate and anthropogenically induced habitat change will often be focused on sparse species whose resources (Turchin et al. 2000, Oksanen et al. 2008), climate (Kausrud et al. 2008), and predators (Reid et al. 1995, Krebs et al. 2003)

maintain populations at low densities. Although individuals may specialize along this complex habitat gradient at low density, the gradient is, in principle, infinitely divisible. Density-dependent interactions that are invisible among sparse species at some large scale might emerge at finer scales of resolution along the habitat cline.

Many of the dynamics of Arctic systems undoubtedly occur at low densities (Boonstra et al. 1998) through a combination of environmental, predation, and stochastic processes. The importance of understanding competition and habitat use at these low densities is underscored by emerging evidence that the once characteristic cycles of many northern herbivores are waning under the weight of climate change (Ims et al. 2008, Kausrud et al. 2008, Post et al. 2009, Gilg et al. 2009, but see Brommer et al. 2010). Although lemming cycles are well documented in Canada's eastern Arctic, populations at some locations in the western Arctic appear to persist at low density (Batzli and Jung 1980, Reid et al. 1995, Krebs et al. 2003). So we concentrated on a small Canadian island in the Beaufort Sea to search for scale-dependent competitive coexistence among three species of small mammals via habitat selection.

We begin by evaluating the possible influences of density-dependent habitat selection on habitat preference, its role in multi-species coexistence, and its dependence on spatial scale. We then use the theory to assess intra- and inter-specific competition for habitat amongst lemmings and tundra voles at coarse and fine scales of habitat use.

## Scale, habitat selection theory and species coexistence

Imagine a pair of species competing exploitatively in a landscape composed of a single habitat gradient. Assume that each species is specialized to use habitat at opposing ends of the gradient where the cline's composite of variables differ significantly from one another. Each species would thus possess a distinct preference for a different habitat. Assume further that each species occupies habitat according to an ideal-free distribution (Fretwell and Lucas 1969). Fitness of each species declines with increasing density. Each species will occupy only its preferred habitat when alone at low density, but will occupy both at higher densities. The density-dependent competition responsible for habitat segregation can be calculated by regression (Rodríguez 1995, Morris et al. 2000a, b) from the system's two-species isodar,

$$N_{2B} = C + bN_{2A} + \alpha N_{1A} - \beta N_{1B} \quad (1)$$

representing the density of species 2 in habitat B such that an individual's fitness there equals its fitness in habitat A ( $N_{ij}$  is the density of species  $i$  in habitat  $j$ ,  $C$  is a constant reflecting quantitative differences between habitats,  $b$  is the slope of species 2's isodar when living alone, and  $\alpha$  and  $\beta$  are the per capita competitive effects of species 1 on individuals of species 2 in habitat A, and of species 1 on 2 in habitat B, respectively, Morris 1987, 1988, 1989, 1999b).

The position on a habitat isodar specifies the relative use of different habitats. If two habitats with linear density dependence possess equivalent fitness at low density but differ in carrying capacity, then the relative use of the habitats will

be constant at all population sizes (the linear isodar passes through the origin). If, on the other hand, fitness at low density in one habitat exceeds that in the other, then the use of the 'poorer' habitat will increase with density (the linear isodar will have a non-zero intercept). As the density of competing species increases, it will normally reduce fitness expectations of other species in shared habitats. Each of these density-dependent influences can be detected through isodar analysis (e.g. Eq. 1).

Similar processes should also occur at smaller spatial scales where sites representing continuous variation in preference vary in their contributions to fitness. Selection at this scale could include sites arrayed along single gradients (e.g. productivity), or several (e.g. a mixture of risky foraging sites and relatively safe refuges). Each type of site should occupy a different location along underlying quantitative gradients of microhabitat.

We can anticipate that the quality of such sites will deteriorate with densities of intra-specific and inter-specific competitors. If habitat preference is either directional or asymmetrical along the gradient, a species' mean location on the gradient will vary with density (Fig. 1A). If preference is symmetrical (e.g. Gaussian) along the gradient, niche location will be invariant with density but the variance in microhabitat use will increase (Fig. 1B). The same principle can be applied when habitat selection occurs at larger scales (Fig. 1C–D).

The main point is that one can search for density dependence in habitat use at both coarse (macrohabitat) and fine (microhabitat) scales of resolution. Isodars reveal density dependence when gradients yield clear distinctions between alternative habitats used by more than one species (Fig. 1C–D). When species' distributions do not correspond with clearly divergent habitats, density dependence can be revealed through analyses contrasting the mean and variance of microhabitat characteristics that reflect the underlying gradient. Accordingly, we searched for competition among rodent species occupying wet and dry tundra in northern Canada.

## Methods

### Study area and species

We live-trapped a three-species assembly of arctic small mammals (collared lemmings *Dicrostonyx groenlandicus*, brown lemmings *Lemmus sibiricus* and tundra voles *Microtus oeconomus*) in eight 60 m square trapping grids on Herschel Island (69°36'N, 139°04'W) in Canada's Yukon Territory from July – August 2007 and June – August 2008. Herschel Island (ca 108 km<sup>2</sup>), a part of the Yukon Coastal Plain physiographic region, is rolling tundra elevated up to 180 m a.s.l. (Smits et al. 1988, Lantuit and Pollard 2008). The island's small watersheds are incised by shallow valleys that drain into the sea below. We located trapping grids along two of these small valleys such that each grid spanned wet meadow in the valley bottom and dry upland habitat on the valley margins. The grids were arranged to minimize small-mammal movement between them (all grids were at least 100 m distant from one another). Wet meadows were composed primarily of sedges

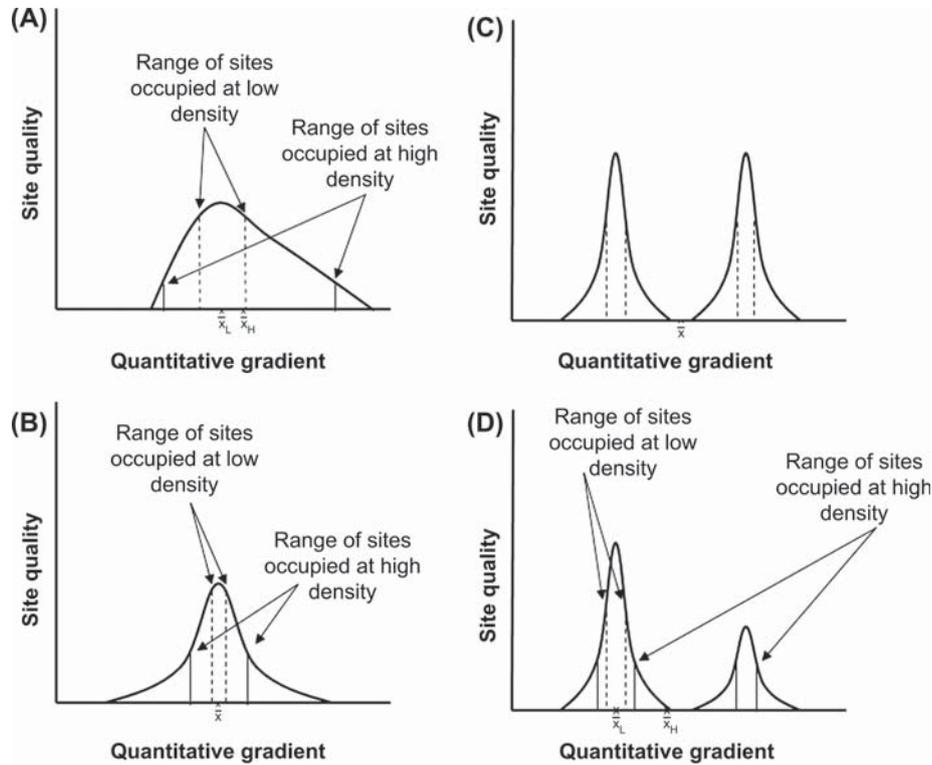


Figure 1. Alternative depictions of microhabitat ‘quality’ that illustrate how niche location can vary (A) or remain constant with density (B). The variance in habitat use increases with density under both scenarios. Each assumes a limited supply of sites that can be measured quantitatively and that individuals choose the highest quality sites available. Scenarios (C) and (D) correspond to the larger-scale alternative where habitats are clearly differentiated along the gradient (niche location constant in (C), varies with density in (D)). Approximate locations of the mean microhabitat along the gradient are indicated by  $\hat{x}_i$  where the subscript denotes low ( $i = L$ ) or high ( $i = H$ ) densities respectively (absence of a subscript indicates that the mean is independent of density).

(*Eriophorum* spp., *Carex* spp.) and grasses (e.g. *Arctagrostis latifolia*) with a few small shrubs (*Salix* spp.), whereas dry habitat was dominated by *Dryas integrifolia*, forbs (e.g. *Saxifraga* sp., *Lupinus arcticus*), and mixed lichens. Each grid was oriented to yield the most equal representation of each habitat. All grids contained more dry stations than wet ones, reflecting the overall composition and distribution of the dry and wet habitat mosaic on the island.

We trapped lemmings during three 3-day periods in each year. We placed a single Longworth live-trap, containing cotton and one or more pieces of apple, at each of the 25 stations (15 m spacing) on each grid following two days of pre-baiting with open locked traps. Each trap was protected from direct sunshine and precipitation by a small wooden board. Traps were unlocked in the morning over the next three consecutive days and checked 5 h and 10 h later before being locked open until the following morning. We identified each captured animal to species, marked it with a unique ear-tag, and recorded its age (juvenile or adult), mass, body-length, and sex before release at the point of capture.

We censused animals biweekly in 2007 and at three-week intervals in 2008. We estimated population density in each habitat on a grid separately for 2007 and 2008 by calculating the relative abundance of each species (the number of different individuals captured in a habitat divided by the number of stations in that habitat and the number (3) of sampling periods (no. of individuals station<sup>-1</sup> period<sup>-1</sup>). Low densities

prevented us from assessing variation among trapping periods within a year.

Our approach assumes that enumeration provides an unbiased estimate of relative abundance, and that our estimate within a habitat over the season represents the potential for competition. Bias in minimum-number-alive estimates of density is slight if ‘trappability’ (probability of a living individual appearing in a trap sample) is high (Hilborn et al. 1976, Efford 1992). Bias appears to be low on Herschel Island because 91% of all animals known alive from one trapping period to another were captured during each period. We are unable to confirm whether animals captured during a single period were residents in that habitat and grid, but we are certain that they were present. Regardless, there was no significant difference in habitat use between animals captured during one period and those captured during two or more (*Lemmus*,  $\chi^2 = 1.52$ , DF = 1,  $p = 0.22$ ; *Dicrostonyx*, Fisher’s exact test, odds ratio = 2.71,  $p = 0.34$ ; there were too few recaptures of *Microtus* for analysis).

We measured 16 habitat variables at each station in 2007 in order to ‘ordinate’ habitat along the dominant mesic to xeric cline in our study grids (Table 1). All variables were comparable to those previously identified as significant predictors of the two tundra habitats (Morris et al. 2000a). Variables included ‘cover’ by habitat classes (collected at points separated by 1 m along a randomly oriented 10 m

Table 1. Varimax rotated principal component (PC) coefficients of 11 habitat variables measured at 200 stations on eight grids on Herschel Island in Canada's Yukon Territory.

Variable*	PC 1	PC 2	PC 3
Maximum hummock height	0.84	-0.09	0.05
Number of hummocks	0.75	-0.40	-0.20
Proportion cover by water	-0.63	0.07	-0.05
Proportion cover by <i>Equisetum</i> and mosses	-0.56	-0.38	0.31
Proportion cover by grass and sedge	-0.01	0.82	-0.04
Maximum shrub height	-0.13	0.72	0.29
Proportion of vegetation cover	-0.49	0.67	0.26
Proportion cover by shrubs	0.04	0.03	0.82
Proportion cover by lichens	0.20	-0.08	-0.67
Proportion cover by <i>Dryas</i>	0.22	-0.52	-0.53
Absolute difference in hummock height	0.15	0.29	0.43

\*five variables failed data screening for the PC analysis (proportions of cover by debris, forbs and mud; and absolute differences in shrub height and in the number of hummocks).

transect centred on each station), maximum height of shrubs (in each of two hemispheres of 5 m radius centred on the station), total vegetation cover (mean of two observer estimates of cover that could conceal a lemming from vision in each hemisphere), as well as the mean number and mean maximum height of hummocks along each half of the 10 m transect. We also included an estimate of variation in shrub and hummock heights (absolute difference in the two maxima) as well as variation in the number of hummocks along the two segments of the 10 m transect. We completed the habitat assessment by estimating the proportions of area within a 5 m radius of each station belonging to dry and wet habitat.

## Analysis

We used principal components (PC) analysis (FACTOR routine, SPSS-16) to extract composite summary variables describing habitat variation on our grids. We deleted all variables with representation in fewer than 5% of the 200 samples (eight grids, 25 stations in each grid), highly collinear variables, as well as those that were unrelated to any other variable (Table 1). We transformed all proportions (arcsine-square root transformation), but this did not improve the distribution of any variable. We then entered the PC scores into a discriminant function (DF) analysis (SPSS-16) to classify stations into two separate classes along the xeric-mesic axis represented by the PCs. We selected only those stations that we classified in the field as pure dry (*Dryas*) habitat ( $n = 56$ ) or pure wet (grass-sedge) habitat ( $n = 40$ ) to represent two reference classes for the DF analysis (Morris et al. 2000a). We used the DF scores of the remaining 104 'ungrouped' stations to classify each as either dry or wet.

We incorporated the relative abundance estimates into stepwise multiple linear regressions (SPSS-16, probability to enter = 0.05, probability to remove = 0.1), to determine the set of candidate variables influencing the abundance of each species in its preferred habitat. We excluded data where one of the lemming species was absent on the grid, as well as data where the target species and its putative competitors were absent in the target species' preferred habitat ( $n = 2$

for *Dicrostonyx*, 3 for *Lemmus*, and 8 for *Microtus* over the 16 grid  $\times$  year combinations; inclusion of 'zero' densities can bias the isodar). We used geometric mean regression (package "lmodel2"; Legendre 2001) in R software (R Development Core Team 2009) to describe density-dependent habitat selection and habitat-dependent competition among the three species (Morris et al. 2000a, b). We calculated two separate regressions using the abundance of *Dicrostonyx* in its preferred dry habitat, and the abundance of *Lemmus* in the wet meadows, as dependent variables. The predictor variables were the corresponding abundances of the target species in the second habitat as well as appropriate interactions between *Lemmus* and *Dicrostonyx* (that influence lemming habitat use elsewhere in the Canadian arctic, Morris et al. 2000a). We did not include the *Lemmus*  $\times$  *Dicrostonyx* interaction in wet habitat, or interactions with *Microtus*, because collared lemmings and voles rarely occupied any location other than their preferred end of the gradient, and because there is no evidence of interference between voles and lemmings when they occur at low densities (Saetnan et al. 2009). We standardized the abundances of each lemming species in dry habitat before calculating interaction terms in order to remove the confounding effects of mean densities (Rodríguez 1995, Morris et al. 2000a).

The abundances of all rodents were low at Herschel Island (Table 2). *Microtus* was present in only eight of the 16 grid  $\times$  year combinations and seldom occupied the dry end of the gradient. *Dicrostonyx* was rarely captured in wet habitat. So we treated *Lemmus* and *Dicrostonyx* abundances in dry habitat as continuous variables in the *Dicrostonyx* isodar, and *Lemmus* in wet, *Lemmus* in dry, and *Dicrostonyx* in dry as continuous variables in the *Lemmus* isodar analyses. We converted *Microtus* abundance in wet habitat to a bi-variate presence-absence indicator variable in order to determine the effect of voles on *Lemmus* abundance. Indicator variables overcome problems associated with the dichotomous selection or rejection of a habitat by sparse species while still allowing us to interpret the role of each species' habitat use on the habitat selection of others.

Our analyses assume that rodent abundances within a habitat during one year are independent of those in the previous year. The assumption is reasonable provided that habitat selection operates more quickly than does population dynamics, and that carry-over effects are absent. Although we expect time-lagged dynamics, our 'speed of habitat selection' assumption appears valid because the scale of habitat on our Herschel Island plots is sufficiently small so that individuals can quickly alter habitat use with expanding density. Carry-over effects would thus occur only if the same individuals were captured in both years. None of the animals captured in 2007 was captured again in 2008.

We were concerned that the wet-dry dichotomy might be too coarse to detect inter-specific competition and that coexistence might occur through a finer subdivision of habitat. We addressed this concern with two stepwise discriminant function analyses. The first compared *Lemmus* and *Microtus* microhabitat selection in wet habitat, the second *Lemmus* versus *Dicrostonyx* microhabitat choice in dry habitat. These analyses determined whether the pairs of species living in the two macrohabitats at each end of the gradient occupied significantly different positions (microhabitats). We weighted

Table 2. Total number of captures (number of different individuals) and relative abundance estimates (no. of individuals station<sup>-1</sup> period<sup>-1</sup>) of lemmings and voles living in dry (a total of 55 stations) and wet habitats (a total of 145 stations) in eight census grids on Herschel Island, Yukon Territory, Canada.

Species	Total number of captures				Relative abundances			
	2007		2008		2007		2008	
	Dry	Wet	Dry	Wet	Dry	Wet	Dry	Wet
<i>Dicrostonyx</i>	147 (50)	9 (6)	26 (20)	1 (1)	0.11	0.05	0.05	0.01
<i>Lemmus</i>	63 (23)	58 (34)	18 (12)	14 (7)	0.05	0.22	0.03	0.05
<i>Microtus</i>	1 (1)	51 (22)	10 (8)	41 (21)	0.002	0.15	0.02	0.1

the occurrence of each set of microhabitat values at a station by the number of captures of each species. The data for a station with two captures, for example, were duplicated in the data set. A station with one capture was included once only. The weighting assumes that the frequency of captures at a station correlates with that species' preference for microhabitat.

Differences in microhabitat use can be caused either from inter-specific competition or by independent preferences. Thus, we searched for competition's signal emerging from significant discriminant functions assessing species differences in microhabitat with 12 linear mixed models (2 macrohabitats  $\times$  2 species  $\times$  3 PCs; sampling grids were treated as a random effect). We evaluated, for each principal component, whether a species' PC score (niche location) in a macrohabitat depended on its abundance and on the abundance of its putative competitors. The effect of inter-specific competition might emerge only through interference, so we also included standardized two-species interaction terms in the analyses. We reasoned that a significant model would confirm intra- and/or inter-specific competition over microhabitat, whereas a non-significant outcome would demonstrate that differences among species on the habitat gradient were independent of abundance and species interactions over the range of population sizes observed on Herschel Island.

We were concerned that any significant patterns might represent epiphenomena associated with annual differences in abundance and distribution. Consequently, we included 'year' as an additional variable in our overall model of niche location. Neither 'year', nor interaction terms, contributed significantly to any of the 12 models we tested. So we limit our assessment of niche location to the parsimonious models which included only the densities of each species.

## Results

### Most stations were classified as either dry or wet habitat

Eleven of the 16 habitat variables passed our screening criteria and contributed to three principal components accounting for 59.6% of the common variance in habitat (Table 1). Each component described a different gradient associated with wet versus dry habitats. The first component represented a cline ranging from stations in dry hummocks to wet stations dominated by sparse *Equisetum* and mosses surrounding small pools of water. The second component identified a gradient from stations with tall shrubs and dense grass and sedge cover to areas with *Dryas*-covered hummocks. The third component extended from areas dominated by shrubs

in undulating hummocks to flat, dry stations covered with lichen and *Dryas*.

The majority of trapping stations classified into extremes of wet versus dry habitat (Fig. 2). Ninety-two of the 96 reference stations used in the analysis were classified correctly as belonging to either wet or dry habitat ( $\chi^2 = 121.4$ ,  $p < 0.001$ ). Dry habitat was approximately three times more common than wet (73% dry vs 27% wet). Even so, the proportion of wet stations varied between a high of 60% (one grid) to a low of 12% (two grids).

### Small mammal densities declined through time

Small mammals were twice as abundant in 2007 as they were in 2008 (Table 2). The proportion of *Dicrostonyx* and *Lemmus* declined between years, but increased for *Microtus*. *Lemmus* occupied both habitats in each year. Except for one grid in 2007, and four grids in 2008, *Microtus* was restricted to wet habitat. The opposite pattern (four grids in 2007, one grid in 2008) restricted *Dicrostonyx* to dry habitat.

### *Lemmus* is a density-dependent habitat selector

On average, *Lemmus* were nearly five times as abundant in wet habitat as they were in dry (*Lemmus* isodar; abundance in wet =  $-0.03 + 4.88$  abundance in dry, geometric mean regression (95% CI for the slope = 3.42 and 6.96, and for the intercept =  $-0.11$  and 0.02;  $F_{1,11} = 25.71$ ,  $p < 0.001$ , Fig. 3)). No other variables were statistically significant.

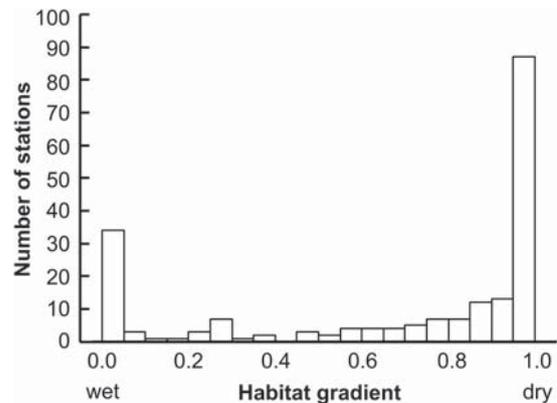


Figure 2. The frequency of different habitat classes revealed by the classification probabilities of a discriminant function analysis contrasting pure wet versus pure dry stations on Herschel Island, Yukon Territory, Canada. Most stations clustered together at the two extremes of the wet-dry habitat gradient. Dry stations were approximately three times more abundant than wet ones.

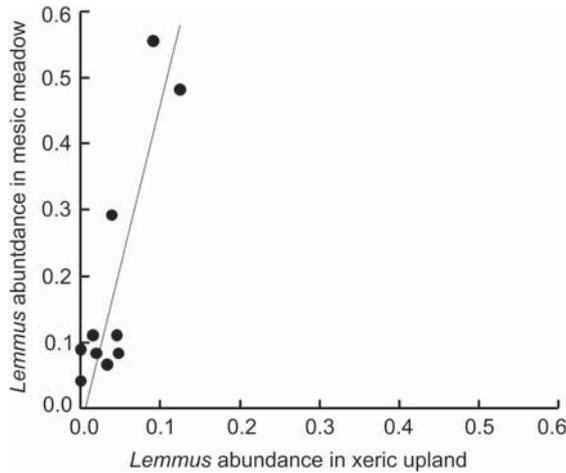


Figure 3. The *Lemmus* habitat isodar illustrates a constant preference for wet habitat over dry.

### Herschel Island small mammals did not compete for wet versus dry habitat

The abundances of *Dicrostonyx* and presence of *Microtus* had no significant effect on the *Lemmus* isodar. The ‘isodar regression’ for *Dicrostonyx* was not significant ( $p = 0.77$ ) and *Microtus*, when present, was restricted mostly to wet habitat. We interpret these results as evidence that (1) the distinct preferences of *Dicrostonyx* for dry habitat, and of *Microtus* for wet (Table 2), were independent of population density, and (2) that inter-specific competition had no influence on habitat selection at this ‘large’ scale.

### The three species coexist by partitioning four habitats

The isodar analyses document a constant partial preference for wet habitat by *Lemmus*. *Dicrostonyx* at Herschel Island is thus able to coexist with *Lemmus* through its distinct preference for dry habitat. But *Microtus* coexistence cannot be reconciled easily because it shares preference with *Lemmus* for wet habitat where the two species should compete. The wet-dry dichotomy may nevertheless be too coarse to capture competition occurring at finer subdivisions of habitat.

*Lemmus* and *Microtus* in wet habitat were indeed captured at stations with significantly different microhabitat attributes

( $\chi^2 = 56.52$ ,  $DF = 6$ ,  $p < 0.001$ ,  $n = 164$ ; 14 microhabitat variables passed screening criteria, six variables retained, Table 3). We repeated the analysis using the same variables without weighting stations by captures to verify that the results were not caused by our weighting criteria. That analysis also confirmed separate microhabitat use ( $\chi^2 = 4.28$ ,  $DF = 1$ ,  $p = 0.038$ ,  $n = 49$ ; one variable significant).

*Lemmus* and *Dicrostonyx* were likewise captured in different microhabitats in the dry end of Herschel’s wet-dry gradient ( $\chi^2 = 104.58$ ;  $DF = 6$ ,  $p < 0.001$ ,  $n = 254$ ; six significant variables, 15 variables passed screening, Table 3). The DF analysis using the same variables without weighting by captures also revealed microhabitat separation by *Dicrostonyx* and *Lemmus* ( $\chi^2 = 24.82$ ,  $DF = 2$ ,  $p < 0.001$ ,  $n = 113$ ; two significant variables). Five of the retained variables were common to both weighted analyses (cover by grass and sedge in the dry habitat ‘replaced’ cover by shrubs in the wet habitat). The overlap in discriminating variables suggests that both pairs of species discriminate their use of individual sites at different wet and dry extremes along the same underlying gradient.

We confirmed existence of a single gradient by superimposing the electivities (calculated using Ivlev’s index, Krebs 1989) of each rodent species along the mesic-xeric gradient represented by the DF probabilities that we used to classify wet versus dry habitats (Fig. 2). Electivities standardize the data relative to the availability of different habitat classes along the gradient.

As expected, *Microtus* specialized on the extreme wet microhabitat and *Dicrostonyx* specialized on the extreme dry microhabitat (Fig. 4a–b). *Lemmus* on Herschel Island is a habitat generalist with a pronounced bias toward wet habitat (Fig. 3, 4c). We interpret these patterns to represent four different habitats exploited by the three species. *Lemmus* uses two, moderately wet and moderately dry, that are significantly different from the extremely wet stations occupied by *Microtus*, and the extraordinarily dry stations preferred by *Dicrostonyx* (Fig. 5).

### *Lemmus* displaced *Dicrostonyx*’s niche toward drier habitat

The niche locations (PC scores) of *Lemmus* and *Microtus* were not correlated with either intra-specific or inter-specific abundances in the wet habitat ( $p > 0.05$  in all the analyses, Table 4). The niche location of *Lemmus* was similarly

Table 3. Means (and SE) of variables documenting significant microhabitat separation between *Lemmus* and *Microtus* in wet habitat, and between *Lemmus* and *Dicrostonyx* in dry habitat (as revealed by stepwise multiple discriminant function analysis), in eight census grids on Herschel Island, Yukon Territory, Canada.

Variable	Wet habitat		Dry habitat	
	<i>Lemmus</i>	<i>Microtus</i>	<i>Lemmus</i>	<i>Dicrostonyx</i>
Proportion cover by <i>Dryas</i>	0.01 (0.004)	0.003 (0.002)	0.18 (0.01)	0.34 (0.01)
Maximum hummock height	7.55 (0.84)	7.13 (0.56)	17.51 (0.47)	14.37 (0.22)
Log <sub>10</sub> number of hummocks	0.37 (0.04)	0.29 (0.03)	0.69 (0.01)	0.72 (0.01)
Proportion cover by <i>Equisetum</i> and mosses	0.12 (0.01)	0.14 (0.01)	0.08 (0.02)	0.05 (0.005)
Absolute difference in hummock height	5.29 (0.60)	6.41 (0.72)	6.64 (0.63)	3.88 (0.24)
Proportion cover by shrubs	0.27 (0.02)	0.38 (0.02)		
Proportion cover by grasses and sedges	0.27 (0.02)	0.13 (0.01)		

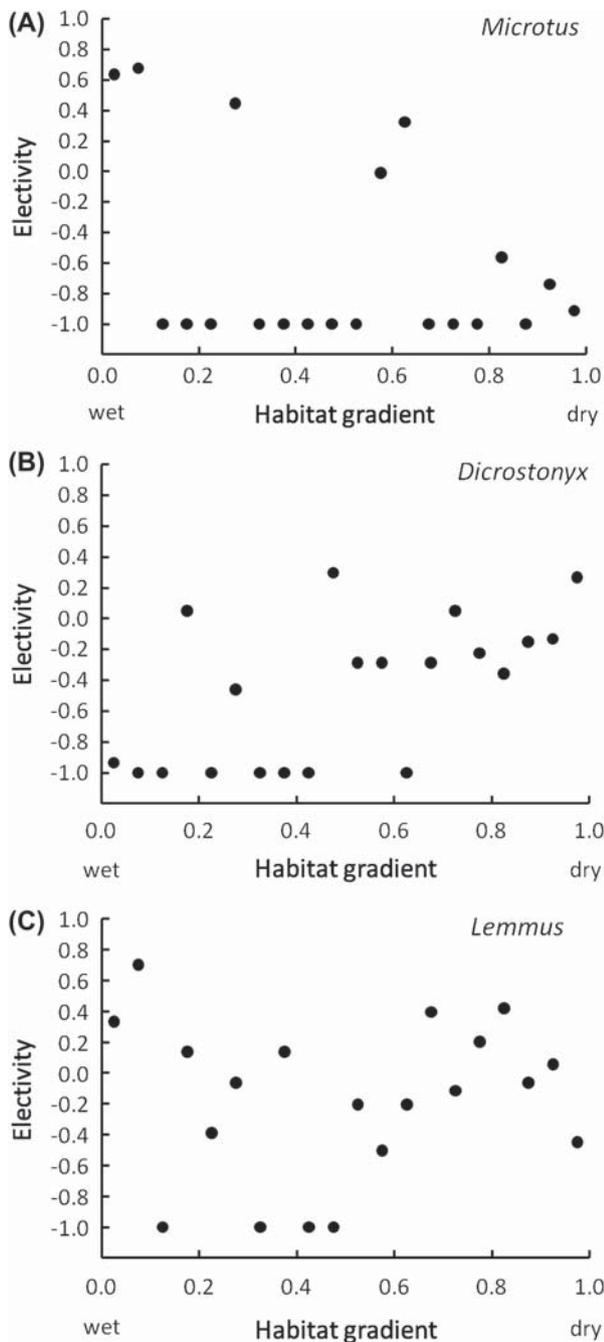


Figure 4. Microhabitat preference by three rodent species, as estimated by Ivlev's index of electivity, in eight census grids on Herschel Island, Yukon Territory, Canada. *Microtus* preferred wet habitat (a), whereas *Dicrostonyx* preferred dry (b). Generalist *Lemmus* occupied a range of wet to dry patches sandwiched between the specialists' preferences at opposite ends of the gradient (c). Please note that some low electivities in the middle of the gradient reflect the absence, or near absence, of habitat categories to occupy (Fig. 2).

independent of its abundance. *Lemmus*' niche scores along the third component (*Dryas* to shrub) increased with *Dicrostonyx* abundance in dry habitat (Table 4), but this displacement toward wetter microhabitat was confounded by year (*Dicrostonyx* abundance in dry habitat was significantly higher in 2007 than in 2008, Mann-Whitney U test;

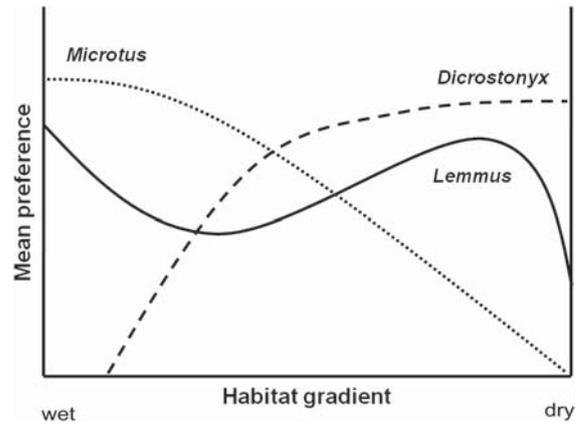


Figure 5. A summary of preferences by three rodent species living along a habitat moisture gradient on Herschel Island, Yukon Territory, Canada. Lines summarize the data in Fig. 4. *Microtus* has a clear preference for wet habitat whereas *Dicrostonyx* prefers the dry end of the gradient. *Lemmus* has relatively high preference for wet patches, reduced preference for intermediate habitat, and similarly reduced preference for the driest end of the gradient (Fig. 4c). Lines as follows: *Lemmus* = solid curve, *Microtus* = dotted curve, *Dicrostonyx* = dashed curve.

$n = 16$ ,  $U = 55.5$ ,  $p = 0.014$ ). *Dicrostonyx* shifted its niche in dry habitat toward the drier end of the first component with increasing *Lemmus* abundance while simultaneously shifting toward the wetter end as its own density increased (Table 4). The collared lemming's niche was thus displaced towards drier microhabitat by increasing abundance of brown lemmings, but towards the wetter end of the gradient when its own abundance increased in dry habitat (Fig. 6).

## Discussion

'When we reach the Arctic regions, or snow-capped mountains, or absolute deserts, the struggle for life is almost exclusively with the elements.' (Darwin 1859, p.69)

Three species of rodents coexist at low densities along a wet-dry continuum on Herschel Island. Only one of the species, the relatively generalized *Lemmus*, is a density-dependent habitat selector at the wet versus dry habitat scale. Brown lemmings maintain a constant partial preference toward wet tundra whereas specialist collared lemmings and voles occupy the driest and wettest zones respectively. The distinct coarse-grained habitat preferences of each species at these low densities are not caused by inter-specific competition. Competition surfaces at a finer scale of resolution, however, where *Dicrostonyx*'s preference for dry habitat is reinforced by increasing *Lemmus* abundance. But we detected no similar effect between *Lemmus* and *Microtus* at the wet end of the gradient.

Although *Lemmus* and *Microtus* diets overlap, *Lemmus* is more specialized on monocots (and mosses) than is *Microtus* in Alaska (Batzli and Jung 1980, Batzli and Lesieutre 1995), and there is little evidence for competition between the two genera in Norway (Saetnan et al. 2009). We conclude that these genera exist independently of one another at low

Table 4. Results of the 12 linear mixed models evaluating the effects of intra- and inter-specific competition on niche location (PC scores) of the three rodent species occupying wet and dry habitats on Herschel Island, Yukon Territory, Canada.

Models	Estimate ( ± SE)				F-value			p-value		
	PC1	PC2	PC3	DF	PC1	PC2	PC3	PC1	PC2	PC3
<i>Microtus</i> in wet habitat										
Mw	2.46 (2.43)	-2.13 (1.99)	-0.03 (1.03)	1.83	1.02	1.12	0.23	NS	NS	NS
Lw	0.68 (0.81)	-1.09 (1.20)	-0.32 (0.56)	1.83	0.70	0.82	0.01	NS	NS	NS
<i>Lemmus</i> in wet habitat										
Lw	1.67 (1.83)	-0.18 (0.93)	-1.18 (1.08)	1.62	0.83	0.04	0.62	NS	NS	NS
Mw <sup>1</sup>	0.66 (0.71)	-0.05 (0.37)	-0.33 (0.42)	1.62	0.87	0.02	1.19	NS	NS	NS
<i>Lemmus</i> in dry habitat										
Ld	-3.32 (2.73)	0.13 (3.35)	-5.11 (3.85)	1.71	1.48	0.01	1.74	NS	NS	NS
Dd	-0.72 (1.08)	0.60 (1.34)	-5.56 (1.65)	1.71	0.44	0.02	11.36	NS	NS	**
<i>Dicrostonyx</i> in dry habitat										
Dd	-1.65 (0.76)	-0.19 (1.15)	-2.81 (1.78)	1.163	4.66	0.03	2.46	*	NS	NS
Ld	-3.24 (1.12)	-2.67 (2.10)	-3.27 (3.02)	1.163	8.35	1.61	1.17	**	NS	NS

Dd: abundance of *Dicrostonyx* in dry habitat. Ld: abundance of *Lemmus* in dry habitat. Lw: abundance of *Lemmus* in wet habitat. Mw: abundance of *Microtus* in wet habitat. NS: not significant at  $\alpha = 0.05$ . \*:  $0.05 > p \geq 0.01$ ; \*\*:  $0.01 > p \geq 0.001$ . 1: bi-variate indicator variable.

densities such as those observed on Herschel Island (and near Atkasook, Batzli and Jung 1980). *Lemmus* and *Dicrostonyx*, on the other hand, compete for wet and dry tundra at similar latitude in Canada's central arctic (Morris et al. 2000a), *Lemmus* on Herschel Island competes intra-specifically for habitat, and *Dicrostonyx*'s dryland niche varies with both *Lemmus* and intra-specific abundance. *Dicrostonyx*'s habitat preference is thus influenced at least as much by inter-specific competitors as it is by its own abundance. Brown and collared lemmings have dramatically different diets (Rodgers and Lewis 1986), and each species uses foods that are unpalatable to the other (e.g. tannins in willow leaves, a main food source for collared lemmings, inhibit growth in *Lemmus*; alkaloids and phenolics in the sedges preferred by *Lemmus* reduce growth in *Dicrostonyx*, Batzli and Jung 1980). Our evidence of competition for microhabitat thus suggests, as have several other studies (Pitelka 1973, Batzli and Jung 1980, Batzli 1983, Morris et al. 2000a), that competition between lemmings is mainly through interference.

Niche displacement, and hence the competition that we observed on Herschel Island, varies with rodent density. If densities remain low, then the Herschel Island rodent

community would appear to confirm Darwin's general view that competition is reduced in highly unproductive environments. This conclusion must be reconciled with clear evidence of competition between lemmings elsewhere, and with the coexistence of one habitat generalist with two specialized species on Herschel Island.

One possibility is that rodent densities are maintained at low levels on Herschel Island by other species (e.g. predators and parasites) or climate. Although a possible explanation for their mostly independent coexistence, this hypothesis would appear insufficient to explain why the three species maintain distinct preferences along the habitat gradient. This interpretation is also inconsistent with evidence that relatively sparse and low-quality diets can maintain low densities of these rodents in a similar community in Alaska (Batzli 1983).

A second option is that habitat preferences, and accompanying independent coexistence, reflect independent niche evolution toward separate habitat optima. This hypothesis may explain *Microtus* preference for wet microhabitats. *Microtus* occupy wet tussocks in the central arctic and overlap with lemmings only along the northern limits of the vole's geographic range. The hypothesis is much more difficult to reconcile with the more extensive geographical overlap between the two lemming species and their documented competition for habitat elsewhere (Morris et al. 2000a).

A third possibility is that rodent populations on Herschel Island may irrupt towards much higher densities than those we observed during our study period. If competition for habitat emerges only at higher densities, then it could reinforce habitat preferences such that competition would mostly disappear at low population size. Our current data are insufficient to test for this ghostly hypothesis, but we suspect that it is unlikely because rodent densities on Herschel Island were even lower in 2009 than in the two years of our study (Morris et al. 2010), and a four-year study on the same three-species microtine community near Atkasook, Alaska also failed to document either high densities or cyclical dynamics (Batzli and Jung 1980).

It seems far more likely that a combination of factors interact to maintain habitat preferences and independent existence at the scale of wet versus dry habitats in

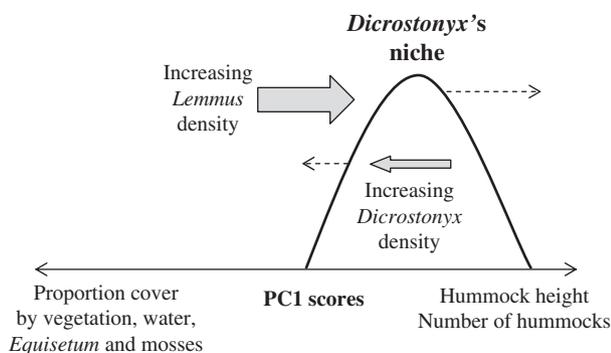


Figure 6. A summary of *Dicrostonyx*'s niche shift along the first PC in response to increasing densities of brown and collared lemmings in dry habitat. The right and left extremes of the PC gradient indicate drier and wetter microhabitat respectively. The size and length of arrows illustrate the impact of competition on *Dicrostonyx*'s niche shift.

Herschel Island's rodent-herbivore guild. Least weasels *Mustela nivalis* and avian predators are common on Herschel Island and might help to constrain rodent population sizes as they do in other parts of the western arctic (Reid et al. 1995). Habitat preferences honed by adaptation elsewhere, often in the presence of inter-specific competition, can thereby express themselves without invasion from competing strategies. Each species occupies its own adaptive peak along the habitat gradient and seldom reaches densities where fitness is depressed to that available in other habitats. Never being exposed to those habitats, each species retains its habitat preference.

The multi-factorial explanation is consistent with concepts of adaptive landscapes (Wright 1931) that rise and sink with population density, and change shape with the frequency of habitat use by intra- and inter-specific competitors (Rosenzweig 1978, 1995, Brown 2001, Morris 2003, Vincent and Brown 2005, Morris et al. 2010). Individual peaks and valleys ebb and flow with the relative abundances (frequency dependence) of nearby species. Peaks and valleys in adaptive landscapes vary with scale (Brown 1996) and the wet-dry dichotomy typically used to assess Arctic-rodent coexistence appears too coarse (flat) to detect inter-specific competition at low densities. When densities are low in relatively flattened adaptive landscapes, micro-niche displacement, such as that exhibited by *Dicrostonyx* in dry habitat, is more likely to emerge from competition than is habitat selection at the larger 'isodar scale'. A specialist species restricted to its minor fitness 'peak' on such a habitat gradient can expand its use to both ends of the habitat cline only if its mean fitness is positive across the gradient between them.

On Herschel Island, relatively low abundance of *Lemmus* with a constant preference to wet habitat can easily depress *Dicrostonyx*'s population growth rate below replacement at the wet end of the gradient. *Lemmus*' occupation of wet and moderately wet microhabitats depresses the fitness experienced by *Dicrostonyx*, an effect exacerbated by the low frequency of intermediate sites along the habitat gradient. When *Lemmus* density increases, a constant proportion of the additional animals occupies dry habitat where microhabitat preference is skewed toward 'moist' sites that would otherwise be suitable for *Dicrostonyx*. *Dicrostonyx* responds by playing to its strength and shifts its niche toward even drier habitat. *Dicrostonyx*'s niche contraction in the face of population pressure from *Lemmus* is resisted, however, by reverse pressure for niche expansion caused by its own increasing density.

Although the story of rodent coexistence on Herschel Island may appear complicated, our interpretation is buoyed by the existence of theory that links, explicitly, the spatial dynamics of populations, competition among species, and the strategies of habitat selection by fitness-maximizing individuals. The isodars, and concepts of niche contraction and expansion embedded in those theories, provide the necessary insights to understand coexistence across habitat scales and stand ready to reveal the ghosts of competition wherever they might appear.

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