

Measuring the ghost of competition: Insights from density-dependent habitat selection on the co-existence and dynamics of lemmings

Douglas W. Morris,^{1*} Douglas L. Davidson¹ and Charles J. Krebs²

¹*Department of Biology, and Faculty of Forestry and the Forest Environment, Lakehead University, Thunder Bay, Ontario P7B 5E1 and* ²*Department of Zoology, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada*

ABSTRACT

When interspecific competitors resolve their co-existence by habitat segregation, their competition might, like a ghost, be invisible because the species occupy separate habitats. Population fluctuations should often bring the species into competition in jointly occupied habitats where their competition can be measured by habitat isodars (lines or planes of density where the expected fitness of individuals is the same in all occupied habitats). We tested the theory by calculating isodars for two species of lemmings with distinct habitat preferences. When population densities are high, both habitats are occupied by both species. But as densities decline, habitat isodars suggest that the joint dynamics of each species pass through a region where each occupies a separate habitat (the ghost of competition). The competition was asymmetrical. The density of collared lemmings in their preferred habitat was reduced as the density of brown lemmings increased in the same habitat. But collared lemmings had no direct competitive effect on brown lemmings. The interspecific effect from brown lemmings was comparable to – possibly even in excess of – intraspecific competition for habitat. The asymmetric competition for habitat yields spectacular new kinds of isolegs categorizing habitat competition between co-existing species. Although current evidence implicates competition, the patterns are also consistent with apparent competition driven by specialized predators. Regardless of whether lemming habitat use reflects true or apparent competition, the associated density-dependent differences in habitat preference are likely to have major consequences for the non-stable dynamics of lemmings and non-linear lemming isoclines.

Keywords: Arctic, co-existence, competition, density dependence, ghost of competition, habitat selection, isocline, isodar, isoleg, lemming.

INTRODUCTION

Differences among species in their ability to harvest and to defend shared resources, in their susceptibility to common predators and parasites, and in their respective life histories are often reflected in differential use of habitat. Habitat selection is, therefore, an effective

* Author to whom all correspondence should be addressed. e-mail: douglas.morris@lakeheadu.ca

mechanism that can mitigate against otherwise negative effects of interspecific competition (Rosenzweig, 1974, 1979, 1981, 1991; Schoener, 1974). In some systems, density-dependent habitat selection allows interspecific competitors to co-exist at equilibrium without any immediate competitive effect because they live in different habitats (the ghost of competition past) (Rosenzweig, 1979, 1981, 1991; Abramsky *et al.*, 1991, 1992, 1994). In others, density-dependent habitat selection reduces *per capita* competition because species become ever more selective in habitat use as the density of their competitor increases (Morris, 1999). In both cases, the estimate of competition, which varies non-linearly with density, will be biased unless the influence of habitat selection is included in the analysis.

Biased estimates of competitive interaction are problematic for at least two reasons. First, they confuse our general understanding of the role of interspecific competition in determining patterns of abundance and distribution among species. Secondly, the apparent absence of competition among habitat selectors may obscure the paramount role that competitive interactions play in reinforcing habitat preferences and their subsequent critical influences on ecological patterns and evolutionary processes. It is thus important to document, with clear field examples, cases where competition is masked by habitat selection, and to demonstrate, for those same examples, that habitat selection is caused by interspecific interactions.

We provide an example where the apparently distinct habitat preferences of two lemming species are reinforced by interactions between the species. We begin with a brief review of the theory of density-dependent habitat selection and the role of habitat selection in creating the ghost of competition. We demonstrate why lemmings are an appropriate choice for testing the theory and develop general field and statistical protocols for the analysis of habitat-dependent competitive interactions. The results from field estimates of lemming densities illustrate that lemming co-existence, at least at high summer densities, depends on competition between species consistent with current interpretations of lemming population regulation. We tackle the interwoven issues of habitat preferences and competitive co-existence. We examine the implications of lemming isopleths and isoclines for our understanding of the role of interspecific competition in ecological communities, and we evaluate the implications of habitat and habitat selection for issues of density dependence. We conclude by examining whether competition or apparent competition is the best current explanation of density-dependent habitat use by co-existing lemmings.

HABITAT-DEPENDENT COMPETITION

Within any given habitat, the expected number of descendants produced by an individual is likely to depend on population density. As the density within a habitat varies, individuals may be able to attain the same or higher fitness in an alternative habitat with a different density (Fretwell and Lucas, 1970). An evolutionarily stable strategy (ESS) of habitat selection will occur when the densities in each habitat are adjusted such that the expected fitness of an individual is the same in each. The densities at the ESS are defined by the habitat isodar (Morris, 1988, 1994), the set of densities in a pair of habitats assuming ideal habitat selection. The isodar intercept corresponds to the density where individuals first begin to use both habitats; the slope reflects the relative differences in density-dependent fitness in the two habitats.

But the density of individuals within a habitat, and their habitat choice, will also depend on the density of interspecific competitors. The competitive effect is illustrated clearly by the

species' absolute isolegs, lines plotted in the state space of species' densities that represent boundaries between exclusive use of the single preferred habitat and the opportunistic use of that habitat plus at least one more (Rosenzweig, 1979, 1981, 1991). For two species with distinct habitat preferences, the isolegs have positive slopes (Fig. 1). The zone between the isolegs represents the ghost region where interspecific competition causes each species to occupy a different habitat. But the competitive effect cannot be measured in this zone because the species are segregated into different habitats. The average competitive effect, represented by non-linear isoclines, changes with population density as the relative densities of individuals in each habitat vary (Fig. 1). The problem of how to measure competition is exacerbated when the point of stable competitive co-existence also occurs in the zone where each species occupies a separate habitat. The competition responsible for the distinct habitat preferences, like a ghost, becomes invisible because of it. Even so, the population densities of each species can be expected to fluctuate about their jointly determined equilibrium and, occasionally, to cross the isolegs. When they do so, one should be able to plot the isoleg and use its slope to estimate the competitive effect (Morris, 1999).

It is very difficult to plot, precisely, an absolute isoleg even when the investigator possesses data where each species occupies only its preferred habitat as well as data where each occupies one or more additional habitats (e.g. Morris, 1996). All one obtains from the density estimates is the switch in behaviour from selective to opportunistic use of habitat, not the actual location of the boundary (Fig. 1). Fortunately, it is possible to measure the competitive effect by extending the isodar to include interspecific competition. For one species,

$$N_{1A} = C + bN_{1B} \tag{1}$$

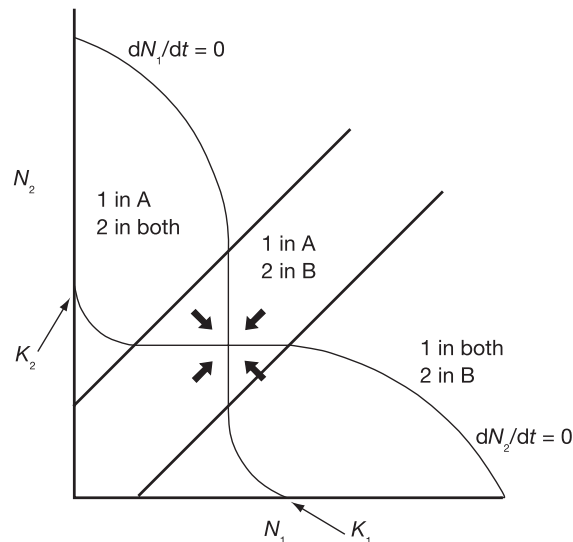


Fig. 1. An example of positively sloped isolegs (bold lines) caused by competition between species 1 and 2 with distinct preferences for habitats A and B. Competitive isoclines (light lines) are necessarily perpendicular in the ghost region because each species is completely segregated by habitat. Isocline slopes vary elsewhere because partial preferences for habitat vary with the joint density of each species (N_i = density in habitat i , K_i = carrying capacity; after Morris, 1999).

where N_{ij} equals the density of species i in habitat j , C is the isodar intercept and b is its slope. Density within a habitat will be reduced by the density of competitors in that habitat plus their joint interactive effects. For two species, equation (1) would be rewritten as:

$$N_{1A} + aN_{2A} + \delta(N_{1A}N_{2A}) = C + b(N_{1B} + \beta N_{2B} + \varepsilon[N_{1B}N_{2B}])$$

A second similar equation for species 2 would yield the two-species isodars

$$N_{1A} = C + bN_{1B} + b\beta N_{2B} - aN_{2A} - \delta(N_{1A}N_{2A}) + b\varepsilon(N_{1B}N_{2B}) \quad (2)$$

and

$$N_{2B} = C' + b'N_{2A} + b'\beta'N_{1A} - a'N_{1B} - \delta'(N_{1B}N_{2B}) + b'\varepsilon'(N_{1A}N_{2A}) \quad (3)$$

respectively, where a and β represent linear habitat-dependent competition coefficients, and δ and ε correspond to the effects of interference between species 1 and 2 (Morris, 1989, 1999). Note that, as in the isoleg, the isodar intercept also represents the switch in behaviour from selective to opportunistic use of habitat. The intercept is changed by the density of interspecific competitors. Thus, the slope of the isoleg corresponds to the sequential isodar intercepts in the presence of the competitor, and one can thereby measure the ghost of competition (Morris, 1999).

Interference may also occur within species and cause fitness to decline as a non-linear function of density. One of the ways to incorporate the interference effect is to assume that resource consumption is inversely related to consumer density, that is

$$W_j = R_j/(N_j\varphi_j)^m \quad (4)$$

where W represents fitness, R is the availability of resources, φ is the *per capita* resource demand and m is an interference coefficient specifying the reduction in intake rate with increased density (Hassell and Varley, 1969; Sutherland, 1983; Milinski and Parker, 1991; Morris, 1992, 1994). Equation (4), and its extension to interspecific competition, can be linearized by a logarithmic transformation (Morris, 1992, 1994; Rodríguez, 1995), but it has the undesirable property that *per capita* resource use becomes unrealistically large at low density.

Interference may be better incorporated into isodars using Beddington's (1975) model with a Type II functional response (Holling, 1959) where *per capita* resource consumption in habitat j is given by

$$R_e/N_jT = a_jR_j/(1 + a_jh_jR_j + \theta_jt_j[N_j - 1]) \quad (5)$$

where R_e is the amount of resource consumed by all N foragers, T is the total time allocated to foraging, a is 'searching efficiency', h is handling time per unit resource, θ = encounter rate with other individuals, and t is the time lost from foraging by each encounter. Assuming that harvest rates are equalized between habitats A and B, the single-species isodar for species 1 becomes

$$N_{1A} = ([\omega_{1A}\{1 + \omega_{1B}h_{1B}\} - \omega_{1B}\{1 + \omega_{1A}h_{1A}\}] + \omega_{1B}I_{1A} - \omega_{1A}I_{1B})/\omega_{1B}I_{1A} + (\omega_{1A}I_{1B}/\omega_{1B}I_{1A})N_{1B} \quad (6)$$

where ω_{ij} = the maximum harvest rate ($a_{ij}R_j$) and I_{ij} = interference ($\theta_{ij}t_{ij}$). Following the reasoning leading to equations (2) and (3), and letting the first right-hand term in (6) = k , the isodar for species 1 competing with species 2 is given by

$$N_{1A} = k_1 + (\omega_{1A}I_{1B}/\omega_{1B}I_{1A})N_{1B} + (\omega_{1A}I_{2B}/\omega_{1B}I_{1A})N_{2B} - (I_{2A}/I_{1A})N_{2A} - (\zeta I_{1A})N_{1A}N_{2A} + (\omega_{1A}\zeta/\omega_{1B}I_{1A})N_{1B}N_{2B} \quad (7)$$

where ζ and ξ represent how the combined densities modify competition, and similarly for species 2. Thus, even with interference, isodars may often be linear. Equation (7) assumes that *per capita* interference is independent of population density. If not, a linear isodar could be maintained in models of density-dependent interference by including additional higher-order (e.g. N^2) terms. Both the Hassell/Varley and Beddington models' assumptions of continuous input with instantaneous consumption are likely to apply only to resource use at small spatial scales (Oksanen *et al.*, 1992; Morris, 1994).

Equation (7) demonstrates an interesting paradox, and an intriguing generality for isodar analysis. The effects of intraspecific interference (equation 7) versus exploitation (equation 2) may be indistinguishable in terms of habitat-dependent patterns of population density. It makes no difference, in terms of consumer density, whether the rate of resource acquisition is reduced by consumption (equation 2) or by interference (equation 7). In both cases, however, interspecific interference is likely to emerge through significant interaction terms in the respective isodar equations.

Pre-emptive habitat selection (Pulliam, 1988; Pulliam and Danielson, 1991) where dominant individuals occupy the best available site, regardless of which habitat it occurs in, adds another wrinkle to the analysis because it will frequently produce either curved or non-linear isodars (Morris, 1994). A general test for such effects could be based on isodars constructed by adding sequential terms from the Taylor expansion

$$N_{1A} = C + b_I N_{1B} + b_{II} N_{1B}^2 + b_{III} N_{1B}^3 + \dots \quad (8)$$

with similar equations applying to competition among species. The test presupposes enough variation in density to 'capture' curvilinear or non-linear effects. As noted above, the higher-order terms might also apply to the general interference model.

Although isodars and isolegs both measure density, they are calculated in different ways. Isodars plot densities within a single habitat against those in another. Isolegs plot total densities of one species across a mix of habitats versus those of the other. How, then, do we convert from isodars to isolegs? For certain types of community organization, the solution, in theory, is fairly straightforward. Consider the distinct preference case illustrated in Fig. 1. The absolute isoleg defines the boundary where species 1 and species 2 occupy their preferred habitats only. Thus, from equation (2), the absolute distinct preference isoleg of species 1 is given by

$$N_{1A} = C + b\beta N_{2B}$$

If one knows the proportion of the total area covered by each habitat, the isoleg can be converted easily to total density.

In practice, we can anticipate complications. Imagine that we are estimating the density of a species that occupies two habitats at different densities, and that we calculate average densities in plots of equal area. If the plots differ in habitat composition, the isoleg data (average density within each plot) will vary with the proportional representation of habitats; the isodar data (density within a habitat) will not.

One can imagine more complicated scenarios. Consider the case of distinct preferences where the density of species 1 is reduced by competition from species 2 in both habitats, but where species 2 is uninfluenced by species 1. The respective isolegs are given by

$$N_{1A} = C + b\beta N_{2B} - aN_{2A}$$

and

$$N_{2B} = C'$$

We note that the isoleg of species 1 is positive when the density of species 2 in its preferred habitat is less than C' ($N_{2A} = 0$), and that the isolegs cross at $N_{2B} = C'$, $N_{1A} = C + b\beta C'$. Beyond that point, the slope of species 1's isoleg declines as the density of species 2 increases in habitat A. To calculate the rest of species 1's isoleg, one needs to know not only the proportional representation of the two habitats, but also the expected density of species 2 in each habitat (the intraspecific isodar for species 2). Significant interaction terms will compound the problem further. It may be best, therefore, to evaluate intra- and interspecific competition in terms of the isodars, and to use caricatures of the isolegs to help interpret the density- and habitat-dependent competitive interactions.

DENSITY-DEPENDENT INTERACTIONS BETWEEN ARCTIC LEMMINGS

Dicrostonyx groenlandicus (collared lemming) and *Lemmus trimucronatus* (brown lemming) cohabit tundra throughout much of the North American Arctic (e.g. Jarrell and Fredga, 1993). Both species are legend for multi-annual fluctuations in abundance (Elton, 1942; Krebs, 1964; Oksanen, 1990; Stenseth and Ims, 1993; Chitty, 1996). Despite differences in diet (Batzli and Jung, 1980; Batzli and Pitelka, 1983; Rodgers and Lewis, 1986a), the two lemming species appear to compete for space. Large brown lemmings specializing on graminoids and moss are thought, at high density, to exclude by competition the smaller and subordinate shrub and forb specialist *Dicrostonyx* from jointly preferred moist habitats (reviewed in Rodgers and Lewis, 1986b). Associated with their differences in diet, the two species appear to have distinct habitat preferences along a moisture gradient, with *Dicrostonyx* living in drier areas and *Lemmus* occupying the wet end of the moisture continuum (Watson, 1956; Krebs, 1964; Batzli *et al.*, 1983; Rodgers and Lewis, 1986b; Batzli, 1993; Pitelka and Batzli, 1993).

Dicrostonyx and *Lemmus*, in areas where they are the only abundant rodents, represent an excellent system with which to test ideas about competitive ghosts and co-existence. Distinct-preference competitors may frequently co-exist in the ghost region between their diverging isolegs (Fig. 1). Even if they do not, their isoclines will necessarily be warped into non-linear forms by habitat selection (Morris, 1999). The 'simple' two-species system that we analyse here avoids complications that may arise in more diverse assemblages.

The dramatic differences in diet and habitat suggest that competition between lemmings, if it occurs, is likely to be mediated via interference rather than through exploitation of shared resources (reviewed by Rodgers and Lewis, 1986b). We predict that the lemming isodars should thereby include significant interaction terms between species. Our interest in whether lemmings compete or not is directed at our ability to detect that competition with isodars, and to infer its effect on their resulting isolegs and competitive isoclines.

Competition between lemming species should not be seen as a mutually exclusive alternative to their possible regulation by predators (e.g. Hanski *et al.*, 1993; Hanski and Henttonen, 1996). A specialist predator whose habitat selection mimics that of its prey, could make it difficult to differentiate between true competitive effects and apparent competition (Holt, 1977, 1984; Holt and Kotler, 1987; Holt and Lawton, 1994). The presence of

the predator in one habitat could simply reduce the density of one prey species and allow a second to increase in abundance. Alternatively, if predatory risk correlates positively with prey density, an abundance of one prey species in its preferred habitat could reduce the habitat's preference to the second prey species. Reduced density of the putative competitor would correspond to less predatory risk and increased relative preference for that habitat by the second species. But competitive and apparently competitive scenarios both produce 'prey' isoclines (e.g. Holt *et al.*, 1994; Morris, 1996) that represent the net effects of each species' density on that of the other. Any interpretations that we may make about their interspecific effects from isodars and isolegs will hold. Thus, the implicit inclusion of competitive and apparently competitive effects is more a strength of isodars than it is a weakness. Nevertheless, we are able to infer the underlying mechanisms because apparent competition yields a set of unique predictions that can be evaluated in ancillary or subsequent tests (see below).

METHODS

We censused collared and brown lemmings in 12 trapping grids near Walker Bay on the Kent Peninsula of Canada's Northwest Territories (68°21'N, 108°05'W) during a widespread lemming outbreak in July 1996. Each 60 × 60 m grid bisected dry hummock heath from adjacent wet meadows. Hummock habitat was dominated by prostrate and a few taller shrubs (*Salix arctica*, *S. reticulata*, *Dryas integrifolia*, *S. lanata*, *Betula glandulosa*), and by varying numbers of forbs (e.g. *Saxifraga cernua*, *Hedysarum mackenzii*), sedges and grasses. Wet meadows (that also contain low hummocks) were dominated by sedges (*Eriophorum* spp., *Carex* spp.) and grasses with fewer shrubs (*S. arctica*, *S. lanata*) than dry hummocks. Each grid was selected for analysis only if fresh evidence of both species (*Dicrostonyx* burrows, *Lemmus* runways or faeces) was present within or adjacent to the grid. Within the constraints of the tundra mosaic, each grid was oriented to yield a more or less equal representation of each habitat.

We placed a single Longworth live-trap baited with one or more pieces of apple plus cotton nesting at the 25 stations (15 m spacing) on each grid. Following 2 days of pre-baiting, we checked the traps at approximately 5 h intervals during the 10–12 h they were open on each of 3 consecutive days. We identified each lemming to species, recorded its age (juvenile or adult), mass and sex, and marked it with a unique eartag before releasing it at the capture point.

We estimated population density in each habitat on a grid as the number of different individuals captured in a habitat divided by the number of stations belonging to that habitat. We determined the number of stations in dry and wet habitats by the classification probabilities of a discriminant function analysis on composite habitat variables. We measured the habitat variables at all stations. One observer (D.W.M.) recorded 'cover' by habitat classes (Table 1) at points separated by 1 m along a randomly oriented 10 m transect centred on each station. We calculated the proportional representation of each cover class at every station. We measured the maximum height of shrubs in two hemispheres of 5 m radius centred on the station, as well as the mean number and mean maximum height of hummocks along each half of the 10 m transect. We estimated the variance among shrubs and hummocks by calculating the absolute difference in their maximum height between the separate estimates. We did the same for the number of hummocks along the two segments of the 10 m transect. We created reference classes for each habitat by classifying the

Table 1. Varimax rotated principal component coefficients of habitat variables collected in 12 grids, including wet and dry tundra, occupied by two lemming species in northern Canada

Variable	PC1	PC2	PC3	PC4
Proportion cover by shrubs <0.25 m tall	0.79	0.06	-0.35	0.13
Mean number of hummocks	0.71	0.32	0.28	0.24
Mean maximum height of hummocks (cm)	0.68	0.30	0.38	0.21
Proportion cover by mud or water	-0.56	-0.02	-0.18	0.10
Absolute difference in shrub height	0.44	0.01	0.08	-0.05
Proportion cover by grasses or sedges	-0.37	-0.77	-0.06	-0.14
Proportion cover by <i>Dryas</i>	-0.13	0.75	0.23	-0.03
Proportion cover by lichens	0.08	0.72	-0.09	-0.07
Proportion 'hummock' within 5 m	0.53	0.64	0.23	0.20
Proportion cover by shrubs ≥ 0.25 m tall	0.06	0.05	0.83	-0.01
Mean maximum height of shrubs (cm)	0.45	0.17	0.74	0.06
Absolute difference in number of hummocks	0.07	0.06	0.04	0.78
Absolute difference in hummock height	-0.01	-0.02	-0.01	0.78

proportion of area within a 5 m radius as belonging to hummock (as opposed to wet) habitat.

We extracted the composite variables from principal components analysis (PCA) (Norušis, 1992a) on all variables (excluding those habitat classes represented in fewer than 5% of the 300 samples, arcsine and logarithmic transformations did not improve the distribution of any variable). We selected only those stations that we classified as pure hummock or pure wet habitat to represent two groups for discriminant function analysis (Norušis, 1992a). We calculated the classification probability of the remaining stations and defined as hummock all stations with a probability greater than 0.5. All others were classified as wet.

We used the density estimates as input variables in a multi-species isodar analysis of competitive interaction (Morris, 1989; Ovadia and Abramsky 1995; Rodríguez, 1995). We had planned to analyse the data by model II multiple regression (McArdle, 1988; Rodríguez, 1995), an approach that uses the p th principal component (smallest eigenvalue) to represent the axis orthogonal to the structural equation for the regression. Bootstrap estimates of the standard errors or confidence intervals of the regression coefficients (e.g. Efron and Tibshirani, 1986) test for statistical significance. In some cases, including the randomized resampling of our data on lemming densities, the final eigenvalues are nearly identical and close to zero. The resulting PCA coefficients are not unique (e.g. Anonymous, 1991) and are likely to produce biased estimates of the isodar coefficients.

We therefore adopted a hybrid technique where we evaluated, for each species, the statistical significance of density-dependent habitat selection and habitat-dependent competition by stepwise linear regression. We used the density of *Dicrostonyx* in hummock and the density of *Lemmus* in wet meadows as dependent variables, and the corresponding densities in each habitat as predictors (e.g. equations 2 and 3) in two different analyses. We confirmed the resulting solutions by backward elimination (both performed in MINITAB). Our sample sizes were insufficient to include higher-order single-species terms in the isodar. Recall, however, that the two-species interactions implicitly assume interference and allow us to evaluate its role in interspecific habitat selection (Morris, 1989).

The densities of each species were centred and standardized before calculating interaction terms (Montgomery and Peck, 1982; Rodríguez, 1995). Note that the standardization procedure removes the mean densities from the interaction. The interactions have high positive values when the densities of both species are either high or low. The interactions are low (negative) when the density of one species is low (negative standardized value) and that of the other is high.

Our intent was to produce an empirical model of those variables influencing the density of each species in its preferred habitat. We analysed the reduced data set with PCA and calculated the two model II equations as our best estimate of the structural relationship for collared and brown lemming isodars. To convert from isodars to isolegs, we computed model II regressions predicting the density on each grid (isoleg) from the density in each habitat (isodar).

We explored the role that demography might play in competitive interactions by examining patterns of habitat use between adult and juvenile lemmings. Significant differences in habitat preference between the two age classes would reveal an important role for demography in habitat selection and lemming co-existence.

We returned to Walker Bay between 22 June and 4 July 1997 to re-trap all grids during the low densities following a precipitous decline in lemming abundance over winter. We plotted these data along with those from 1996 to illustrate the isolegs of both species.

RESULTS

Thirteen habitat variables contributed to four principal components accounting for 63% of the common variance in habitat (Table 1). The first component described a gradient extending from wet areas covered by sedges and grass to stations with many tall hummocks covered by low shrubs (mostly *Salix arctica*). The second ranged from sedge- and grass-covered stations to dry stations covered by *Dryas* and lichens. The third component varied from stations with many low shrubs, to those with many tall shrubs, while the fourth described stations varying from those with high variance in the nature of hummocks to stations with low variance. Each component thus described a different cline associated with sedge- versus hummock-dominated habitat.

The discriminant function analysis distinguishing between wet meadow and hummock stations was highly significant ($\chi^2_4 = 238.02$, $P < 0.0001$) and correctly classified each of the 130 stations used in the analysis as belonging to either wet or hummock habitat. The classification of the remaining 170 'ungrouped' stations was also impressive (Fig. 2). Equal numbers of stations were classified in the extremes of the two habitat classes (128 wet, 128 hummock). The remaining 44 stations were more or less evenly distributed along the wet-hummock gradient. The analysis confirms our initial selection of two more or less distinct habitat types as well as our ability to sample each habitat equally, even though the number of stations on a grid classified to a particular habitat varied. The proportional representation of grids dominated by each type of habitat was almost identical: four pairs of grids were composed of mirror-image proportions of wet meadow versus hummock habitat; one of the two remaining pairs differed by one station (9 wet versus 10 dry); the final two were slightly biased to wet habitat, with 15 and 14 stations respectively.

Collared and brown lemmings were also equally abundant in our samples (261 and 264 captures respectively). Both species existed on all grids except the one with the greatest cover by *Eriophorum* sedges, where *Lemmus* was captured. We found signs of *Dicrostonyx* in a dry

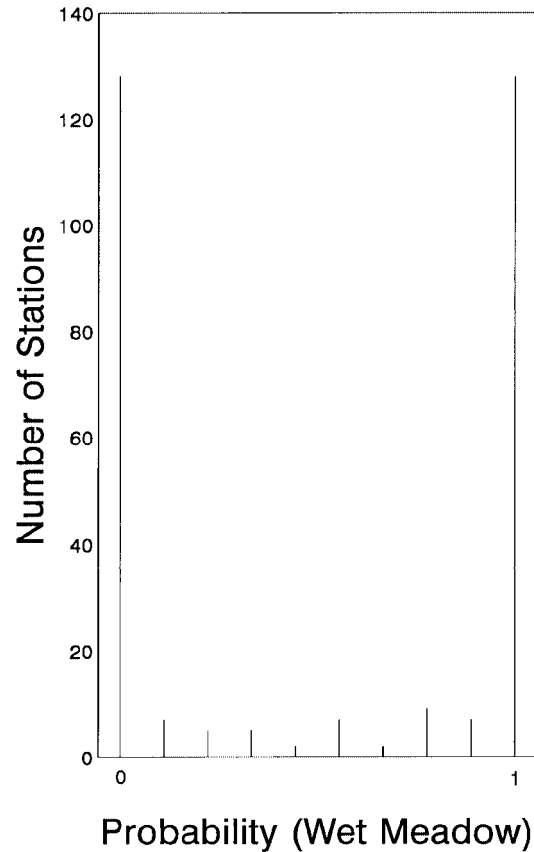


Fig. 2. The bimodal probabilities (based on discriminant function scores) that live-trap stations belonged to 'wet' habitat illustrate two clear habitats occupied by brown and collared lemmings.

section of this grid and included it in our isodar analysis based on the assumption that the density of *Dicrostonyx* was close to the zero density we recorded. Subsequent analyses that deleted this grid were similar to those that included it.

Lemming populations declined drastically over winter in 1997 and we recorded only 24 lemming captures in 1997 (all *Dicrostonyx*), with a trapping effort equal to that of 1996. Collared lemmings occurred on five of the 12 grids.

Dicrostonyx exhibited a distinct preference for hummock (mean density [individuals per station] in hummock = 0.8; mean density in wet = 0.27), whereas *Lemmus* had a distinct preference for the wet habitat (mean density in wet = 0.63; mean density in hummock = 0.31). The density of collared lemmings in hummock habitat was negatively related to the density of brown lemmings in that habitat (Table 2; *Dicrostonyx* density in hummock = 1.18 minus 1.59 *Lemmus* density in hummock minus 0.76 standardized interaction between *Lemmus* and *Dicrostonyx* in meadow; model II solution, all coefficients significant at $P < 0.05$; adjusted $R^2 = 0.497$). The interspecific effect from brown lemmings in the wet-meadow habitat depended on the joint densities of the two species. The significant multiple regression does not include the density of *Dicrostonyx* in the wet meadow; the

Table 2. Significant isodar summaries evaluating competition in wet-meadow and hummock habitats between two lemming species occupying a tundra mosaic in northern Canada

Species	Source	d.f.	SS	<i>F</i>	<i>P</i>
<i>Dicrostonyx</i> in hummock	Regression	2	2.47	6.45	0.018
	Error	9	1.72		
	Total	11	4.19		
<i>Lemmus</i> in meadow	Regression	1	1.55	34.19	<0.001
	Error	10	0.45		
	Total	11	2.00		

residual variation accounted for by *Dicrostonyx* density-dependent habitat selection was marginally significant, however ($b = 0.74$, $F_{3,8} = 2.86$, $P = 0.13$), indicating weak density-dependent habitat selection by collared lemmings (Fig. 3).

Brown lemming density in its preferred wet-meadow habitat was negatively influenced by the interaction with collared lemmings in that habitat (Table 2; *Lemmus* density in wet meadow = 0.54 minus 0.64 standardized interaction between *Lemmus* and *Dicrostonyx* in meadow; model II solution, both coefficients significant at $P < 0.001$; adjusted $R^2 = 0.751$).

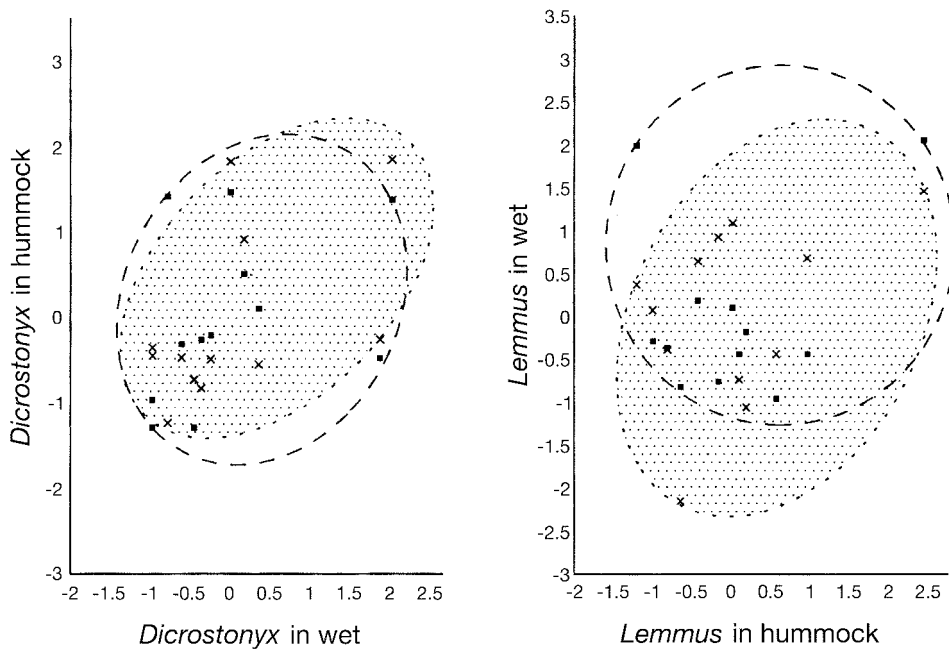


Fig. 3. The reduction in variance accomplished by each species' 'best-fit' isodar is illustrated by superimposing partial regression scores (standardized values from model I regressions; indicated by 'x' and the stippled ellipses) on the mean-centred and standardized densities of each species in each habitat (indicated by solid squares and dashed ellipses). Density-dependent habitat selection is revealed for both lemming species.

Otherwise, *Dicrostonyx* had no effect on *Lemmus* density. The density of brown lemmings in hummock habitat was not a significant predictor of *Lemmus* density in wet meadows ($b = 0.3$, $F_{2,9} = 1.44$, $P = 0.26$). Thus, brown lemming density in wet meadows can vary from being low or high when collared lemming density is low in the wet habitat. It is apparent that the co-existence of the two lemming species, at least during population irruptions, is partly predicated on an interspecifically reinforced differential use of tundra habitats.

We explored the fit of the isodar regressions by superimposing partial regression plots (the standardized residuals from the significant stepwise analyses) on graphs of mean-centred and standardized lemming densities in the two habitats (Fig. 3). The graphs represent each species' single-species' isodar controlling for interspecific effects. Despite the significant isodars, considerable residual variation remains in lemming density. Yet it is clear that, even for *Lemmus*, there is a trend towards a positive correlation between the density in the preferred habitat and its density in the alternative one (weak density-dependent habitat selection).

Overall lemming density on the grid as a whole was significantly correlated with the density in each habitat (Table 3). But, when all data were considered, *Lemmus* density on entire grids was not significantly correlated with its density in hummock habitat ($r = 0.2$). *Lemmus* was absent from hummocks on one grid with very high *Lemmus* density. Most brown lemmings on this grid were juveniles (23 of 28 individuals), which preferentially occupy wet habitat (see below) and are less likely to have direct negative interactions than adults. The number of juvenile *Lemmus* on this grid was more than twice the number on any other, and the ratio of juveniles to adults was also greater than on any other sample grid. Recognizing these aberrant differences, we removed the grid from our analysis and repeated the regression to reveal a significant correlation between average *Lemmus* density and its density in hummock habitat (Table 3). Removal of this grid had no discernible effect on the correlation between total *Lemmus* density and its density in the wet habitat ($r = 0.94$ for 12 grids, $r = 0.93$ for 11 grids).

The significant interaction terms in the isodar equations suggest a role for interference on habitat choice, a view that is also consistent with many interpretations of lemming population regulation (e.g. Stenseth and Ims, 1993; Chitty, 1996). Aggressive interactions should asymmetrically favour large adults over small juvenile lemmings, and the demographic structure of a population could be crucial in understanding interspecific interactions for habitat between species.

Table 3. Relationships between lemming density (number per trap-station) on a sample grid (total N) and the corresponding density in each of hummock and wet-meadow habitats (model II regression)

Total <i>Dicrostonyx</i> density = $0.05 + 0.53$ <i>Dicrostonyx</i> density in hummocks $F_{1,10} = 15.88$; $P = 0.003$; adjusted $R^2 = 0.58$
Total <i>Dicrostonyx</i> density = $0.15 + 1.19$ <i>Dicrostonyx</i> density in wet meadows $F_{1,10} = 13.9$; $P = 0.004$; adjusted $R^2 = 0.54$
Total <i>Lemmus</i> density = $0.06 + 0.82$ <i>Lemmus</i> density in hummocks $F_{1,9} = 18.28$; $P = 0.002$; adjusted $R^2 = 0.63$
Total <i>Lemmus</i> density = $-0.04 + 0.7$ <i>Lemmus</i> density in wet meadows $F_{1,10} = 83.4$; $P < 0.001$; adjusted $R^2 = 0.88$

Our sample size was too small to incorporate demographic variables in the isodar analyses. Two alternative analyses seemed plausible. First, we could analyse data on adults and juveniles separately for each species' isodar; secondly, we could search for possible demographic influences by contrasting habitat use between juveniles and adults of each species. We rejected the first option because it would necessarily exclude the demographic interaction that may be necessary to understand habitat-dependent competition between the two species. We acknowledge that any difference between analyses on adults versus juveniles would hint at interaction, but single isodar analyses with small samples are on a slippery enough statistical slope without compounding the problem with additional multiple passes through the data.

The population of each species was clearly heterogeneous and was divided easily into adult and juvenile classes (Fig. 4). Our field ageing criteria included pelage and reproductive characters that resulted in a small overlap in the body sizes of adult and juvenile *Dicrostonyx* (14 adults belonged to the largest 'juvenile' body-mass class of 45 g because we classified small reproductive animals as adults). These few individuals have no influence on our analysis of demographic differences in habitat use. There was no overlap between ageing and body-mass classes for *Lemmus*.

Lemmus preferred wet habitat, whereas *Dicrostonyx* preferred dry habitat (Table 4; hierarchical log-linear analysis; Norušis, 1992b: habitat \times species interaction, partial $\chi^2_1 = 97.37$, $P < 0.0001$). The proportional occupation of wet meadow versus hummock habitats by adult and juvenile lemmings varied between species (habitat \times species \times age interaction, likelihood ratio $\chi^2_1 = 8.02$, $P = 0.005$). The habitat distribution of juveniles tended to be more extreme than that of adults. The relative abundance of *Lemmus* juveniles was much greater in wet than in hummock habitat. The relative abundance of juvenile *Dicrostonyx* was greater in hummock than in wet habitat.

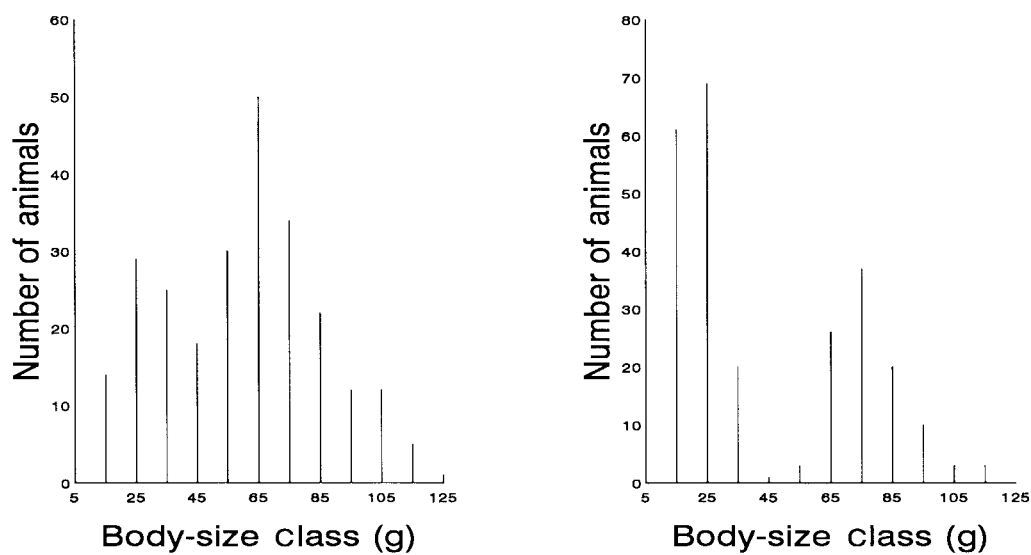


Fig. 4. The distributions of body-size (mass) classes clearly distinguished two demographic modes for *Dicrostonyx* (left) and *Lemmus* (right).

Table 4. Captures of adult and juvenile lemmings in wet-meadow and hummock habitats in a tundra mosaic in northern Canada

Species	Age	Habitat	
		Hummock	Wet meadow
<i>Dicrostonyx</i>	Juvenile	57	12
	Adult	145	47
<i>Lemmus</i>	Juvenile	37	118
	Adult	45	64

Did juveniles occupy stations with similar habitat characteristics to those of adults? We chose to analyse this question within habitats to avoid complicating the choice of wet-meadow versus hummock habitat with that of the selection of stations within a habitat. We tested for differences in each habitat and for each species with stepwise discriminant function analyses on the principal component (PC) scores weighted by the number of captures of each age class. Components were entered into the analysis if significant at the 0.05 level; they were deleted if $P > 0.1$.

Dicrostonyx juveniles occupied significantly different types of stations than adults in both habitats (Table 5). In the preferred hummock habitat, juvenile collared lemmings preferentially occupied stations with higher mean scores on PC2 (0.78 *vs* 0.56; sites with many *Dryas*-covered hummocks) and lower mean scores on PC3 (-0.48 *vs* -0.08; sites with few tall shrubs) than adults. These characteristics correspond to the 'driest' hummocks occupied by either species. In wet habitat, juvenile *Dicrostonyx* also occupied different types of stations than adults; again, they were captured at sites with more *Dryas* than those used by adults – stations with lower mean scores on PC1 (-1.14 *vs* -0.23; 'flat' wet areas covered by a mixture of graminoids and *Dryas*) and higher mean scores on PC2 (0.07 *vs* -0.42; areas with relatively fewer graminoids than those used by adults). The differential habitat occupation of juvenile *Dicrostonyx* from that of adults in both habitats is consistent with interference from *Lemmus* that should have a greater effect on juvenile *Dicrostonyx* than on adults.

Lemmus juveniles also used stations in wet habitat that differed from those of adults (Table 5). The mean value on PC3 was less than that of adults (-0.34 *vs* -0.02; stations with few tall shrubs). The characteristics of stations used by juvenile brown lemmings in hummock habitat did not differ from those of adults. The differential use of only

Table 5. Summary of significant stepwise discriminant function analyses evaluating age differences in the use of habitat by two lemming species occupying a tundra mosaic in northern Canada

Species	Habitat	d.f.	χ^2	P	Significant PCs
<i>Dicrostonyx</i>	Hummock	2	10.84	0.004	PC2, PC3
<i>Dicrostonyx</i>	Wet meadow	2	19.87	<0.0001	PC1, PC2
<i>Lemmus</i>	Wet meadow	1	9.49	0.002	PC3

wet-meadow habitat by juvenile and adult brown lemmings reinforces our interpretation that brown lemming habitat use responds to the density of *Lemmus*, with no obvious effect from *Dicrostonyx*. The absence of density-dependent and age-specific effects in hummock habitat suggests that it may be generally unsuitable for brown lemmings.

Regardless, juvenile lemmings tended to occupy more extreme stations than adults. One cannot ignore the role of demography when evaluating habitat preferences of either lemming species.

DISCUSSION

Habitat preference

The density of each lemming species in its preferred habitat was affected adversely by either the density of the second species or by the covariance in joint density in the wet-meadow habitat. Each species occupied both habitats, and their relative abundance in each habitat was influenced by density-dependent habitat selection. In both species, competition appeared to be caused by interference from other individuals. At least two models can account for the pattern, both of which assume that dominant individuals exclude subordinates.

In one scenario, dominants distinguish between wet and hummock habitat and value all sites within each habitat more or less equally (an ideal despotic distribution; Fretwell and Lucas, 1970). Mean fitness should be higher in the high-quality habitat than in the low-quality one. For *Dicrostonyx*, fitness would be higher in the hummocks than in the meadow; the opposite would be the case for *Lemmus*. As long as the mean quality of habitats is more or less constant, the intensity of interference would be similar between habitats, regardless of local variation in habitat quality.

Alternatively, dominant individuals may preferentially occupy the best available sites regardless of the habitat in which they occur (an ideal pre-emptive distribution; Pulliam, 1988; Pulliam and Danielson, 1991). Increased density of the competitor will reduce the number of high-quality breeding sites. The resulting distribution of individuals between habitats will depend on the underlying distribution of site quality.

Our tests of habitat use by juvenile lemmings can help us distinguish between the two models. In both cases, the relative density of juveniles (subordinates) in wet and hummock habitats should be different from that of adults. If dominant adult individuals distinguish only between wet and hummock habitats, however, there should be no difference in the kind of station occupied by the two age classes. If, on the other hand, dominant individuals preferentially occupy the highest quality sites within a habitat, juveniles should occupy significantly different types of sites than adults.

Our data support the pre-emptive hypothesis. Juvenile *Dicrostonyx* occupied different kinds of sites than adults within both wet-meadow and hummock habitats. Juvenile *Lemmus* occupied sites with fewer tall shrubs than those used by adults, but only in the wet-meadow habitat, which was disproportionately 'preferred' by juvenile brown lemmings. Two types of additional data will be required to test, definitively, for pre-emptive habitat selection: further comparative data on population densities in the same census grids to evaluate relative habitat preferences at moderate densities (and to search for curved or non-linear isodars), and experimental data to demonstrate that lemmings preferentially occupy sites of the highest quality.

Competitive co-existence

The demographic differences in habitat use make it all the more remarkable that we were able to document that competition for habitat is asymmetrically biased in favour of *Lemmus*. Despite a high proportion of juveniles, increased density of brown lemmings was correlated with reduced density of *Dicrostonyx* in its preferred hummock habitat. Collared lemmings had no direct effect on *Lemmus* in either habitat.

The interactive effect of the two species in wet meadows is more difficult to interpret. Recall that the interaction term has large values when both species are rare. It will have its lowest values (negative) when one species is abundant and the other is rare. When *Lemmus* was most abundant in its preferred wet-meadow habitat, the interaction with *Dicrostonyx* was low (Fig. 5; *Dicrostonyx* density in wet meadow was necessarily low). But low *Lemmus* densities in the wet habitat were also associated with low densities of its putative competitor. Any competitive effect depends on their joint densities, but only in wet meadows.

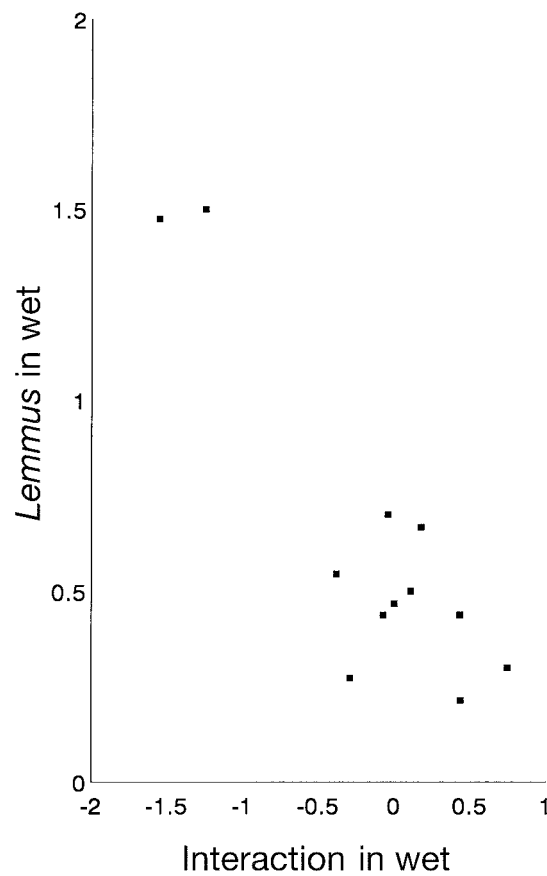


Fig. 5. The density of *Lemmus trimucronatus* in wet-meadow habitat is a negative function of the covariance in density of two lemming species in wet meadows.

Dicrostonyx density in the hummock habitat showed a similar interaction. Collared lemming density in hummocks was high when the interaction with *Lemmus* in the wet habitat was low, but as we have seen, this occurred when brown lemming density in the wet habitat was high. Thus, when brown lemmings are moderately abundant, they appear to inflate the density of collared lemmings in hummock habitat.

We tentatively interpret the interaction term to include two effects: one reflects the spatial dynamics of lemmings in tundra mosaics (low density in preferred habitats when both species are relatively rare); the other represents a multiplicative effect on the intensity of competition that manifests itself in wet meadows. When brown lemmings are very abundant in their preferred wet habitat, they may inhibit the occupation of wet meadows by *Dicrostonyx*, resulting in high collared lemming densities in hummock habitat. The hypothesis depends critically on two census grids with high *Lemmus* density (Figs 3 and 5).

Interference competition should often be associated with shared habitat preference or centrifugally organized communities (Rosenzweig, 1981, 1991; Pimm and Rosenzweig, 1981; Rosenzweig and Abramsky, 1986; Morris, 1988) where competitors share a preference for the richest habitat, but have distinct secondary choices. According to theory, shared preferences should most readily evolve when habitats differ from one another quantitatively (Rosenzweig, 1979, 1981, 1991; Morris, 1988), whereas distinct preferences emerge when habitats vary qualitatively, and when consumers differ in exploitation efficiency. Previous studies have suggested that the centrifugal model may apply to lemmings sharing a preference for 'moist' habitats, with a secondary preference towards dry habitats by *Dicrostonyx* and one towards wet meadows by *Lemmus* (e.g. Rodgers and Lewis, 1986b). Our data from Walker Bay suggest a somewhat different interpretation where *Lemmus* density, and by inference its habitat preference, is biased towards wet meadows. When both species are abundant and competition from *Lemmus* is high, *Dicrostonyx* appears to be more restricted to dry hummocks than when lemming densities are low. Consistent with this view, our data from 1997 suggest that *Dicrostonyx* preference shifts down the moisture gradient towards moist sites when *Lemmus* is absent.

Dramatic differences in plant communities between hummock and meadow habitats, and equally dramatic differences in diets (e.g. Rodgers and Lewis, 1986a), support the 1996 isodar interpretation that the two species prefer qualitatively different habitats, at least at high densities at the Walker Bay site. If so, and if the mechanism of interspecific competition is indeed interference by *Lemmus*, we may need to revisit predictions that differential exploitation should be the prevalent mechanism of competition among interacting species that occupy qualitatively different habitats. But qualitative differences do not exclude the possibility that the two habitats also differ in productivity, which would undoubtedly play a role in species co-existence, and in mechanisms of competition.

Isolegs

What can we infer about the isolegs and their effects on competitive co-existence? Recall that, when drawing the absolute isolegs, they represent the respective isodar intercepts for differing densities of the two species. In the case of *Lemmus*, the isodar intercept is uninfluenced by the density of *Dicrostonyx* alone, but is increased slightly when one or the other species is rare in the wet habitat (the interaction term is negative). The isodar intercept is at a minimum when both species are about equally abundant in the wet habitat. Thus, the near-vertical *Lemmus* isoleg is slightly curved to the right (Fig. 6).

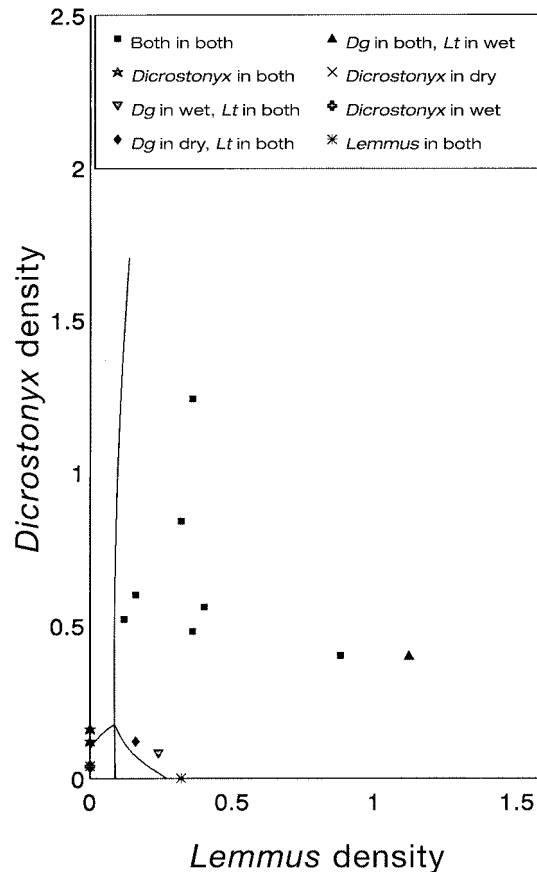


Fig. 6. The approximate absolute isolegs for two species of lemmings that co-exist in Canada's Arctic. To the left of the curved 'vertical' isoleg, *Lemmus* exists only in its preferred wet habitat; to the right, it occupies both. *Dicrostonyx* occupies only its preferred dry habitat 'within' its convex/concave isoleg, but occupies both habitats above the isoleg. The ghost of competition occurs within the irregular polygon bounded by the positively sloped *Dicrostonyx* isoleg and the vertical *Lemmus* isoleg. The isolegs represent caricatures based on each species' isodar. All data collected in 1997 lie on the ordinate (*Lemmus* was absent from all sample grids). *Dg* = *Dicrostonyx groenlandicus*, *Lt* = *Lemmus trimucronatus*.

The collared lemming isoleg is more complicated because *Dicrostonyx* habitat selection is influenced by the density of *Lemmus* in the hummock habitat, by the interaction between the two species in the wet-sedge habitat, and by its own density in meadows. Note that the competitive effect of *Lemmus* in the drier habitat reduces the isodar intercept, and recall that *Lemmus* density in hummock habitat increases with total density (Table 3). The isoleg, at least to the right of that for *Lemmus* where brown lemmings occupy hummocks, has a negative slope. The slope is modified by the interaction term in the wet habitat that acts to increase the isodar intercept when either species is rare. When *Lemmus* is relatively

common and *Dicrostonyx* is rare (lower right), the interaction term is negative (increased density of *Dicrostonyx* in the hummock habitat; the rate of decline in the isodar intercept is reduced). As one moves northwest along the isoleg, the density of *Lemmus* declines and the standardized density becomes negative (the interaction term is positive; reduced density of *Dicrostonyx* in hummocks). The collared lemming isoleg, to the right of the brown lemming isoleg, is concave away from the origin (Fig. 6).

The point where the isolegs cross corresponds to a stunning discontinuity in habitat selection by collared lemmings. To the left of the near-vertical *Lemmus* isoleg, the main competitive effect by brown lemmings evaporates because they occupy the wet habitat only (competition with *Lemmus* in hummocks is zero). But the interaction term increases as the densities of each species decline (the standardized densities for both species are negative). Thus, left of the *Lemmus* isoleg, the intercept of the *Dicrostonyx* isodar increases with increasing *Lemmus* density. The value of the interaction changes with the product of the joint densities; the positive part of the collared lemming isoleg will be bowed outward (the isodar intercept changes most rapidly when the standardized densities are near the origin; Fig. 6).

We have drawn the caricatures of the isolegs in Fig. 6 to be 'less than' any single 1996 data point. We did this because it is very difficult to draw the actual isolegs in this system (note, for example, that the isodar for *Dicrostonyx* includes the density of *Lemmus* in hummocks, but the isodar for *Lemmus* does not), and each species occupied both habitats at all but three sample grids where both species were present (collared lemmings were absent from the wet habitat on one grid and absent from the dry habitat on another; brown lemmings were absent from the dry habitat on one grid; no collared lemmings were captured on a fourth grid).

Nevertheless, we were able to anchor the ordinate of the *Dicrostonyx* isoleg. We first calculated the intercept from the isodar equation. Recall that the interaction term is based on standardized values and that it is zero only when each species is at its mean density in the wet habitat. We noted that *Lemmus* cannot occupy the hummock habitat to the left of its isoleg, then assumed that the density of both species in the wet habitat was zero. We converted the resulting isodar intercept (density of *Dicrostonyx* in hummock) to its isoleg using geometric regression (density of *Dicrostonyx* on the entire grid = $0.047 + 0.53$ *Dicrostonyx* density in hummock habitat; Table 3).

The data from 1997 appear to confirm our predicted non-linearity in the *Dicrostonyx* isoleg. Collared lemmings occupied both hummock and wet habitats on two grids (8 and 13 captures respectively), and both lie above the calculated isoleg intercept. Single captures on three other grids revealed *Dicrostonyx* present in hummock habitat on two grids, and present in the wet habitat on the other (Fig. 6, below the isoleg intercept). These results demonstrate that the apparent preference of *Dicrostonyx* for dry hummocks is diluted in the absence of *Lemmus* and that the *Dicrostonyx* isoleg has a region of positive slope that reduces the ghost region (Fig. 6). But it is also evident that habitat preferences of the two lemmings may be manifested through the ghost of competition, because each species is likely to occupy a separate habitat when densities are low.

Thus, when brown lemmings occupy only their preferred habitat, any increase in *Lemmus* density reduces the wet habitat's suitability for *Dicrostonyx* and reinforces the collared lemming's preference for hummocks. Further increases in the number of brown lemmings causes their density to exceed the *Lemmus* isoleg and they begin to invade hummocks where their competitive effect on collared lemmings is most intense. Every additional

increase in brown lemming density reduces the difference in habitat suitabilities for *Dicrostonyx*.

The competitor-dependent habitat preference of *Dicrostonyx* is consistent with several studies that have documented its increased preference for moist habitats when *Lemmus* is relatively rare (reviewed in Rodgers and Lewis, 1986b). Our interpretation is also consistent with the more recent results of Krebs *et al.* (1995) for Pearce Point, where brown lemming densities were very low; collared lemmings occupied both wet and dry habitats.

The isodars (and isolegs) may vary with the accumulation of more data, especially so if they turn out to be non-linear, as implied by the differences in habitat use by juveniles and adults. But even if the isodars do change with more data, there is no reason to necessarily assume that our estimates of competitive interaction will vary dramatically and, if they do not, the isolegs won't change either. In any case, it is the relative shapes and positions of the isolegs that intrigue us, not their absolute locations.

Isoclines

Figure 7 illustrates our interpretation of the two lemming isoclines during summer. The figure, like any other phase plane for two species, could illustrate numerous isoclines corresponding to different rates of population growth. Stable 'textbook' zero-growth isoclines will occur only if population growth for both interacting species is asymptotic towards a stable density, and if the intensity of intraspecific competition exceeds that between species. For species with unstable fluctuating dynamics, however, zero-growth isoclines and their ephemeral points of 'stable' co-existence will be associated only with the respective maxima and minima of their respective densities. Keeping these distinctions in mind, the *Lemmus* isoclines are vertical because the significant negative interaction with *Dicrostonyx* in wet meadows is best explained by the pattern in *Lemmus* density (see above). When brown lemmings are abundant in wet meadows, collared lemming density in the wet habitat is low, as is the interaction term (Fig. 5). When brown lemming density is low in the wet habitat, so too is the density of *Dicrostonyx* (the standardized interaction is large). The negative correlation between the joint densities of both species and *Lemmus* density in wet meadows is caused by the density-dependent habitat selection of *Lemmus*, not by a multiplicative competitive interaction.

When *Lemmus* is absent or very rare, and *Dicrostonyx* is moderately abundant, collared lemmings occupy both habitats. The *Dicrostonyx* isoclines in this zone will have a negative, but shallow, slope because the significant interaction term in *Dicrostonyx*'s isodar suggests that there may be some competition from *Lemmus* in wet meadows. Competition with *Lemmus* will decline towards the ghost region as *Dicrostonyx* shifts its habitat occupation towards dry hummocks.

When both species occupy their preferred habitat only (the ghost of competition), both sets of isoclines must pass through the ghost region. Moreover, we know that there can be no direct competitive effects, that the isoclines are perpendicular to one another, and must, therefore, cross. But we also know that the points where the isoclines cross cannot represent stable equilibria because the zero-growth isoclines are ephemeral, and other isoclines in this region take on positive and negative values as each species' density increases and declines respectively. If both species occupy both habitats, other isoclines must occur above the isoleg for *Dicrostonyx* and to the right of that for *Lemmus*. We know that *Lemmus* is a superior competitor to *Dicrostonyx* in this zone, and that *Lemmus* could, if the carrying

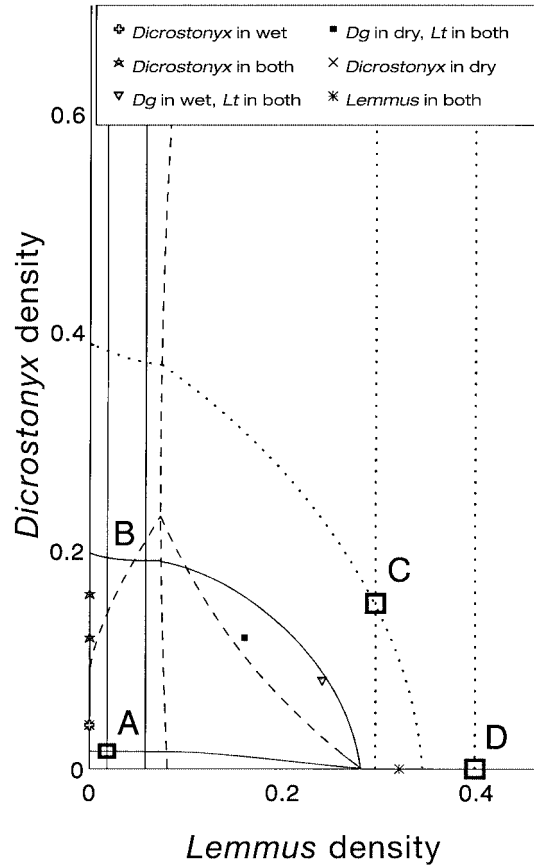


Fig. 7. Examples of the competitive isoclines superimposed on the isogons (dashed curves) for two species of co-existing lemmings. Example A (solid curves) represents the ephemeral zero-growth isoclines when both species are sparse and their respective carrying capacities are low (a population minimum). Example B (also solid curves) represents transitional isoclines as populations increase to, or decline from, high carrying capacities. Dotted curves represent ephemeral zero-growth isoclines for two examples when carrying capacities are high (population maxima, C, D). Large squares indicate points of possible short-term ‘equilibria’ (equal population growth rates or exclusion of *Dicrostonyx*). The range of low- to high-density zero-growth isoclines will depend on local fluctuations in the mean population densities across both habitats. *Dg* = *Dicrostonyx groenlandicus*, *Lt* = *Lemmus trimucronatus*.

capacities of each species were similar and stable, thereby exclude by competition collared lemmings at equilibrium (Fig. 7).

The collared lemming isoclines at high density are similar to those at low density. In the zone above the *Dicrostonyx* isogon, and to the left of the *Lemmus* isogon, the two species jointly occupy the wet habitat and the isoclines will have a shallow slope. To the right of the *Lemmus* isogon, both species occupy both habitats and *Dicrostonyx* faces much more competition from *Lemmus*. The slope of the *Dicrostonyx* isoclines will increase (the isoclines will be concave downward; Fig. 7).

Our purpose has been to draw the general shapes of lemming isoclines as populations vary through time. The dynamics themselves are rooted, presumably, in time lags associated with predator–prey interactions. The shapes of the isoclines will remain the same whether the dominant interactions are those associated with lemmings as prey (e.g. Hanski *et al.*, 1993; Hanski and Henttonen, 1996), or with lemmings as the ‘predator’ on their food resources (Oksanen, 1990; Oksanen and Oksanen, 1992). Yet we must interpret our isoclines with caution because they represent average effects of species interaction. Thus, in landscapes composed of mostly dry habitat, average *Lemmus* density (and maximum carrying capacity) might never become high enough to have a major influence on *Dicrostonyx* populations (all combinations of density lie on the left side of Fig. 7).

The role of isolegs in non-stable dynamics

Regardless of which interpretation of exploiter dynamics one chooses, and regardless of the small state-space that the ghost occupies, the isolegs would appear to play a major role in the non-stable population dynamics of lemmings. The dynamics of each species will, in turn, have dramatic effects on the other. Moreover, the non-linear isoclines suggest that the dynamics of each species will depend on initial conditions. We illustrate examples of these effects in Fig. 8.

Imagine that the densities of the two species are low and lie just inside the boundary of the ghost region. If *Dicrostonyx* density increases more rapidly than that of *Lemmus*, as may occur if *Dicrostonyx* is locally more abundant than *Lemmus*, the joint dynamics are likely to break out to the left of the *Lemmus* isoleg. *Dicrostonyx* may encounter some competition in the wet habitat, but will not be affected greatly by *Lemmus* until increasing *Lemmus* density drives the two species into co-existence within the hummock habitat. Even though competition from *Lemmus* is intense in hummocks, *Dicrostonyx*, capitalizing on its numerical advantage, will experience low average competition until *Lemmus* becomes relatively abundant. The increasing competition with *Lemmus*, and the increased density of *Dicrostonyx*, will slow population growth and the densities of both species will rotate clockwise in the northwest portion of the density space. Variation in *Dicrostonyx* density will be pronounced with high amplitude.

But if *Lemmus* is locally more abundant, and increases more rapidly at first with a resulting breakout into the jointly occupied habitat region of the isoleg space, *Dicrostonyx* will be in intense competition with *Lemmus* in the region immediately to the right of the *Lemmus* isoleg, where *Dicrostonyx* is restricted to hummock habitat. Lacking the numerical dominance that occurs when it is the breakout species, *Dicrostonyx* population growth, and potential population size, will be inhibited. As *Lemmus* density increases, more and more individuals will inhabit the hummock habitat, which must necessarily represent a sink for *Lemmus* (otherwise they would simply drive collared lemmings to extinction). Expansion into sink habitat should reduce the population growth rate of brown lemmings, and thereby hasten their population decline. Simultaneously, high densities of brown lemmings will have a direct negative impact on the density of collared lemmings in their preferred hummock habitat, and could thereby speed the decline of collared lemmings as well. The densities of both species will vary with a counter-clockwise rotation, but *Dicrostonyx* abundance will be much lower than when it breaks out first. Note that *Lemmus* will also be most abundant if both species break out together (the joint dynamics will cross the *Lemmus* isoleg while

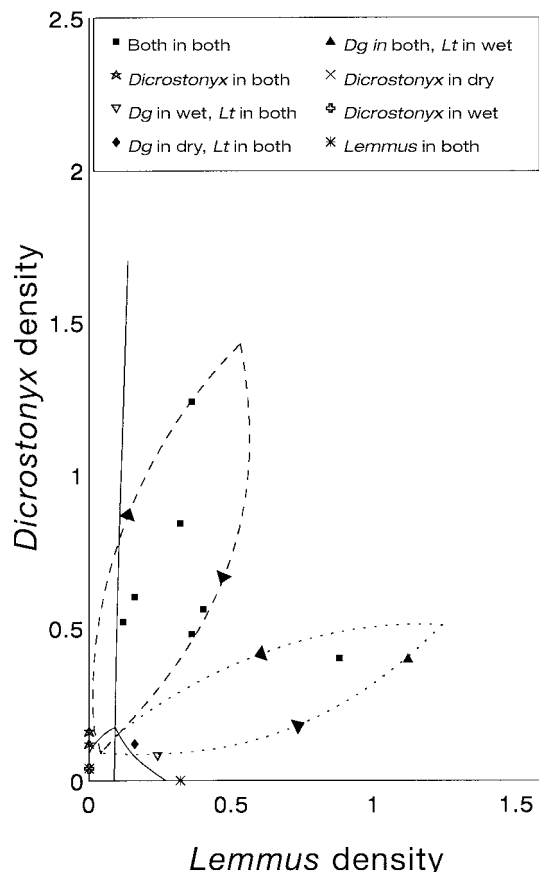


Fig. 8. The phase graph that represents habitat and competitive effects on lemming abundance. The dashed ellipse corresponds to an example of the dynamics that may occur when *Dicrostonyx* 'breaks out' from low density before *Lemmus*. The dotted ellipse represents an example of the dynamics that may occur if *Lemmus* density increases most rapidly. Solid lines are the species' absolute isolegs; arrows represent the direction of the joint population dynamics. *Dg* = *Dicrostonyx groenlandicus*, *Lt* = *Lemmus trimucronatus*.

Dicrostonyx density is still relatively low). Perhaps the tantalizing 'bunny-eared' dichotomy (we prefer the term 'lagomorphed dynamics') in relative densities illustrated in Fig. 8, in a landscape with more or less equal proportions of wet and dry habitats, is more than coincidence.

Asymmetries in population density are likely to be even more pronounced in landscapes biased to one or the other habitat. Lemming dynamics correspond with the prediction. At Barrow, in a landscape dominated by wet habitat, brown lemmings fluctuate dramatically, while collared lemmings, virtually absent at Barrow, are more abundant in drier inland landscapes (Pitelka and Batzli, 1993). At Pearce Point, brown lemmings are nearly absent, whereas collared-lemming dynamics vary between study areas differing in habitat composition (Krebs *et al.*, 1995).

Competition or apparent competition?

Our data are insufficient to differentiate clearly between a competitively mediated ghost and an alternative predator-mediated ghost of apparent competition. Note that our analysis is uncertain only about the underlying mechanism causing interspecific density and habitat interactions between lemmings, not about any patterns in the data, or about our interpretations of interspecific effects. We can, at least, provide predictions that would differentiate between the competition and apparent-competition hypotheses: (1) If lemming isodars are the result of predation, an experiment that excludes predators should yield isodars significantly different from those we report here. (2) A predator-mediated ghost of apparent competition between collared and brown lemmings requires that the predominant predator(s) is either a prey or a prey-habitat specialist. (3) If the predator is a *Lemmus* specialist, the predatory risk for *Dicrostonyx* must be positively correlated with the density of *Lemmus* (to yield the significant negative effect of brown lemmings on collared lemming density in hummock habitat). (4) If the predator is a *Dicrostonyx* specialist, there should be no substantial risk on *Lemmus* (because reduced density of *Dicrostonyx* in hummock habitat was associated with increased density of *Lemmus* in that habitat). (5) Predatory risk in wet habitats should be large when the densities of both species are low in that habitat as well as when they are high (caused by the significant interaction in wet meadows).

It is difficult to reconcile predictions (2) to (5) with the predator community at Walker Bay. Opportunistic ‘marine’ and migratory predators (e.g. pomarine jaegers, *Stercorarius pomarinus*; glaucous gulls, *Larus hyperboreas*; snowy owls, *Nyctea scandiaca*) were abundant during the lemming outbreak in 1996, and the resident predators, many of which responded with high recruitment, also tend to be generalists (e.g. Arctic foxes, *Alopex lagopus*; ermine, *Mustela erminea*; sandhill cranes, *Grus canadensis*). Migratory predators were virtually absent during 1997. Despite a diverse predator assemblage, our data for Walker Bay are most consistent with the competition hypothesis.

We readily acknowledge the speculative nature of our interpretations about habitat use, lemming co-existence and their non-stable population dynamics. We will have achieved our objectives if they cause readers to think about habitat, competition and lemmings in new ways. We caution readers that patterns of wet-meadow versus hummock habitats at Walker Bay do not apply to all co-existing populations of brown and collared lemmings. We believe, however, that these patterns of habitat selection represent a reasonable caricature of lemming habitat use, co-existence and dynamics along a moisture gradient. We do not suggest that the isolegs and their associated ghost of competition, or apparent competition, by themselves, cause the dramatic fluctuations in lemming populations. We do suggest that the habitat preferences – and the coincident density-dependent habitat selection – of *Dicrostonyx* and *Lemmus* have far-reaching consequences for their co-existence and their joint population dynamics. Our inferences are based on the preferences and habitat selection that we observed in the two species and yield testable hypotheses that may, we hope, resolve some of the puzzles of lemming dynamics.

ACKNOWLEDGEMENTS

We thank R. Bromley and the Department of Resources, Wildlife and Economic Development of the Government of the Northwest Territories for use of the Walker Bay Field Station and Reserve. Candid discussions with D. Wilson improved our understanding of lemming co-existence and we thank Deb for both logistic and field support. Detailed and candid reviews by L. Oksanen allowed us

to improve many aspects of the manuscript, including the 'Beddington isodar', and our understanding of habitat-dependent co-existence. We gratefully acknowledge the support of the Northern Scientific Training Program of Canada's Department of Indian Affairs and Northern Development, Lakehead University, the Polar Continental Shelf Project of Canada's Department of Mines, Energy and Resources (this is publication PCS/P/EPCP 01497), and Canada's Natural Sciences and Engineering Research Council support of D.W.M.'s continuing studies in evolutionary ecology and habitat selection.

REFERENCES

- Abramsky, Z., Rosenzweig, M.L. and Pinshow, B. 1991. The shape of a gerbil isocline measured using principles of optimal habitat selection. *Ecology*, **72**: 329–340.
- Abramsky, Z., Rosenzweig, M.L. and Subach, A. 1992. The shape of a gerbil isocline: An experimental field study. *Oikos*, **63**: 193–199.
- Abramsky, Z., Ovadia, O. and Rosenzweig, M.L. 1994. The shape of a *Gerbillus pyramidum* (Rodentia: Gerbillinae) isocline: An experimental field study. *Oikos*, **69**: 318–326.
- Anonymous. 1991. *Minitab Reference Manual PC Version: Release 8*. State College, PA: Minitab Inc.
- Batzli, G.O. 1993. Food selection by lemmings. In *The Biology of Lemmings* (N.C. Stenseth and R.A. Ims, eds), pp. 281–301. New York: Academic Press.
- Batzli, G.O. and Jung, H.G. 1980. Nutritional ecology of microtine rodents: Resource utilization near Atkasook, Alaska. *Arctic and Alpine Research*, **12**: 483–499.
- Batzli, G.O. and Pitelka, F.A. 1983. Nutritional ecology of microtine rodents: Food habits of lemmings near Barrow, Alaska. *J. Mammal.*, **64**: 648–655.
- Batzli, G.O., Pitelka, F.A. and Cameron, G.N. 1983. Habitat use by lemmings near Barrow, Alaska. *Holarctic Ecol.*, **6**: 255–262.
- Beddington, J.R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.*, **44**: 331–340.
- Chitty, D. 1996. *Do Lemmings Commit Suicide?* Oxford: Oxford University Press.
- Efron, B. and Tibshirani, R. 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Stat. Sci.*, **1**: 54–77.
- Elton, C. 1942. *Voles, Mice and Lemmings: Problems in Population Dynamics*. Oxford: Clarendon Press.
- Fretwell, S.D. and Lucas H.L., Jr. 1970. On territorial behavior and other factors influencing habitat distribution. I. Theoretical development. *Acta Biotheor.*, **19**: 16–36.
- Hanski, I. and Henttonen, H. 1996. Predation on competing rodent species: A simple explanation for complex patterns. *J. Anim. Ecol.*, **65**: 220–232.
- Hanski, I., Turchin, P., Korpimäki, E. and Henttonen, H. 1993. Population oscillations of boreal rodents: Regulation by mustelid predators leads to chaos. *Nature*, **364**: 232–235.
- Hassell, M.P. and Varley, G.C. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature*, **223**: 1133–1136.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Ent.*, **91**: 385–398.
- Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. *Theor. Pop. Biol.*, **12**: 197–229.
- Holt, R.D. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *Am. Nat.*, **124**: 377–406.
- Holt, R.D. and Kotler, B.P. 1987. Short-term apparent competition. *Am. Nat.*, **130**: 412–430.
- Holt, R.D. and Lawton, J.H. 1994. The ecological consequences of shared natural enemies. *Ann. Rev. Ecol. Syst.*, **25**: 495–520.
- Holt, R.D., Grover, J. and Tilman, D. 1994. Simple rules for interspecific dominance in systems with exploitative apparent competition. *Am. Nat.*, **144**: 741–771.

- Jarrell, G.H. and Fredga, K. 1993. How many kinds of lemmings? A taxonomic overview. In *The Biology of Lemmings* (N.C. Stenseth and R.A. Ims, eds), pp. 45–57. New York: Academic Press.
- Krebs, C.J. 1964. The lemming cycle at Baker Lake, Northwest Territories, during 1959–1962. *Arctic Inst. North Am. Tech. Paper*, **15**: 1–104.
- Krebs, C.J., Boonstra, R. and Kenney, A.J. 1995. Population dynamics of the collared lemming and the tundra vole at Pearce Point, Northwest Territories, Canada. *Oecologia*, **103**: 481–489.
- McArdle, B.H. 1988. The structural relationship: Regression in biology. *Can. J. Zool.*, **66**: 2329–2339.
- Milinski, M. and Parker, G.A. 1991. Competition for resources. In *Behavioural Ecology: An Evolutionary Approach*, 3rd edn (J.R. Krebs and N.B. Davies, eds), pp. 137–168. Oxford: Blackwell Scientific.
- Montgomery, D.C. and Peck, E.A. 1982. *Introduction to Linear Regression Analysis*. New York: Wiley.
- Morris, D.W. 1988. Habitat-dependent population regulation and community structure. *Evol. Ecol.*, **2**: 253–269.
- Morris, D.W. 1989. Habitat-dependent estimates of competitive interaction. *Oikos*, **55**: 111–120.
- Morris, D.W. 1992. Scales and costs of habitat selection in heterogeneous landscapes. *Evol. Ecol.*, **6**: 412–432.
- Morris, D.W. 1994. Habitat matching rules: Alternatives and implications to populations and communities. *Evol. Ecol.*, **8**: 387–406.
- Morris, D.W. 1996. Coexistence of specialist and generalist rodents via habitat selection. *Ecology*, **77**: 2352–2364.
- Morris, D.W. 1999. Has the ghost of competition passed? *Evol. Ecol. Res.*, **1**: 3–20.
- Norušis, M.J. 1992a. *SPSS SPSS/PC + Professional Statistics, Version 5.0*. Chicago, IL: SPSS Inc.
- Norušis, M.J. 1992b. *SPSS SPSS/PC + Advanced Statistics, Version 5.0*. Chicago, IL: SPSS Inc.
- Oksanen, L. 1990. Exploitation ecosystems in seasonal environments. *Oikos*, **57**: 14–24.
- Oksanen, L. and Oksanen, T. 1992. Long-term microtine dynamics in north Fennoscandian tundra: The vole cycle and the lemming chaos. *Ecography*, **15**: 226–236.
- Oksanen, T., Oksanen, L. and Fretwell, S.D. 1992. Habitat selection and predator–prey dynamics. *Trends Ecol. Evol.*, **7**: 313.
- Ovadia, O. and Abramsky, Z. 1995. Density-dependent habitat selection: Evaluation of the isodar method. *Oikos*, **73**: 86–94.
- Pimm, S.L. and Rosenzweig, M.L. 1981. Competition and habitat use. *Oikos*, **37**: 1–6.
- Pitelka, F.A. and Batzli, G.O. 1993. Distribution, abundance and habitat use by lemmings on the north slope of Alaska. In *The Biology of Lemmings* (N.C. Stenseth and R.A. Ims, eds), pp. 213–236. New York: Academic Press.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *Am. Nat.*, **132**: 652–661.
- Pulliam, H.R. and Danielson, B.J. 1991. Sources, sinks, and habitat selection: A landscape perspective on population dynamics. *Am. Nat.*, **137**: S50–S66.
- Rodgers, A.R. and Lewis, M.C. 1986a. Diet selection in Arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*): Forage availability and natural diets. *Can. J. Zool.*, **64**: 1684–1689.
- Rodgers, A.R. and Lewis, M.C. 1986b. Diet selection in Arctic lemmings (*Lemmus sibiricus* and *Dicrostonyx groenlandicus*): Demography, home range, and habitat use. *Can. J. Zool.*, **64**: 2717–2727.
- Rodríguez, M.A. 1995. Habitat-specific estimates of competition in stream salmonids: A field test of the isodar model of habitat selection. *Evol. Ecol.*, **9**: 169–184.
- Rosenzweig, M.L. 1974. On the evolution of habitat selection. In *Proceedings of the First International Congress of Ecology*, Wageningen, pp. 401–404. The Hague: Centre for Agricultural Publishing and Documentation.
- Rosenzweig, M.L. 1979. Optimal habitat selection in two-species competitive systems. In *Population Ecology* (U. Halbach and J. Jacobs, eds), pp. 283–293. Stuttgart: Gustav Fischer Verlag.

- Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology*, **62**: 327–335.
- Rosenzweig, M.L. 1991. Habitat selection and population interactions: The search for mechanism. *Am. Nat.*, **137**: S5–S28.
- Rosenzweig, M.L. and Abramsky, Z. 1986. Centrifugal community organization. *Oikos*, **46**: 339–348.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science*, **185**: 27–39.
- Stenseth, N.C. and Ims, R.A., eds. 1993. *The Biology of Lemmings*. New York: Academic Press.
- Sutherland, W.J. 1983. Aggregation and the ‘ideal free’ distribution. *J. Anim. Ecol.*, **52**, 821–828.
- Watson, A. 1956. Ecological notes on the lemmings *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* in Baffin Island. *J. Anim. Ecol.*, **25**: 289–301.