Habitat change and the scale of habitat selection: shifting gradients used by coexisting Arctic rodents

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The conservation and understanding of biodiversity requires development and testing of models that illustrate how climate change and other anthropogenic effects alter habitat and its selection at different spatial scales. Models of fitness along a habitat gradient illustrate the connection between fine-scale variation in fitness and the selection of habitat as discontinuous patches in the landscape. According to these models, climate change can increase fitness values of static habitats, shift the fitness value of habitat patches along underlying gradients of habitat quality, or alter both fitness and habitat quality. It should be possible to differentiate amongst these scenarios by associating differences in the abundance and distribution of species with metrics of habitat that document the gradient while controlling for changes in density at larger scales of analysis. Comparisons of habitat selection by two species of lemmings, over an interval of 15 years, are consistent with the theory. The pattern of habitat selection at the scale of wet versus dry tundra habitats changed through time. The change in habitat selection was reflected by different, but nevertheless density-dependent, patterns of association with the structure and composition of habitat. Abundant collared lemmings abandoned stations where altered habitat characteristics caused a shift to new locations along the wet-to-dry gradient. The confirmation of scale-dependent theory provides new insights into how one might begin to forecast future habitat selection under different scenarios of climate and habitat change.

Direct and indirect anthropogenic effects are changing habitat at unprecedented rates. In addition to major assaults from deforestation, desertification, transportation and energy corridors, agricultural expansion, and urban sprawl, terrestrial habitats and the species that use them face additional challenges caused by long-range pollutants and global warming. Similar problems challenge aquatic ecosystems. One can make a rather convincing case that habitat loss and change thus represent the most pressing issue for the conservation of biodiversity, as well as a challenging intellectual hurdle to be overcome by theoretical and empirical ecologists. Although significant progress has been made at describing resource selection (McLoughlin et al. 2010), advancing and assessing theories of habitat selection (Holt 2003, Morris 2003, Holt et al. 2004, Stamps et al. 2009a, b), and applying a joint eco-evolutionary understanding to the evolution of habitat preference (Brown 1998, Vincent and Brown 2005, Kimbrell and Holt 2007, Cressman and Krivan 2010, Gomulkiewicz et al. 2010), we lack a general conceptual model demonstrating how the scale of habitat influences density-dependent habitat selection.

Empirical studies describing habitat and resource selection typically assume that organisms either make active choices at different, usually hierarchical, scales or that resource selection depends on the scale of observation (Johnson 1980,

Morris 1987a, Orians and Wittenberger 1991, Ciarniello et al. 2007, Aldridge and Boyce 2008). Theories incorporating spatial scale into habitat selection are much less frequent and tend to emphasize how movement and landscape heterogeneity influence distribution and abundance (Morris 1987b, 1992, Brown and Pavlovic 1992, Holt and Gaines 1992, Kawecki and Holt 2002, Holt 2003, Ale et al. 2011, and Cohen 2006 provide intriguing insights into how habitat heterogeneity influences ecological dynamics and subsequent evolution). There has been even less formal treatment of the correspondence between fitness achieved at small scales, and distribution at larger scales (see Emlen et al. 2006 for one interesting approach). We attempt to fill this void with a simple heuristic model clarifying the relationship between fitness obtained along a habitat gradient and patterns of abundance in different habitats. We then evaluate whether long-term data on selection of temporally varying habitats along a mesic-xeric gradient exploited by two species of arctic lemmings are consistent with the model's assumptions.

Habitat gradients, habitat change and fitness

We imagine (as in Ale et al. 2011) that the relevant characteristics of habitat influencing fitness can be aligned along

a single composite habitat gradient (such as the mesic-xeric cline exploited by lemmings). We also assume that the expectation of fitness is a continuous function along the gradient (neither assumption is vital to our general model) such as might be expected if individuals were capable of establishing a home range occupying only one portion of the gradient (Fig. 1). We further assume that the distribution of
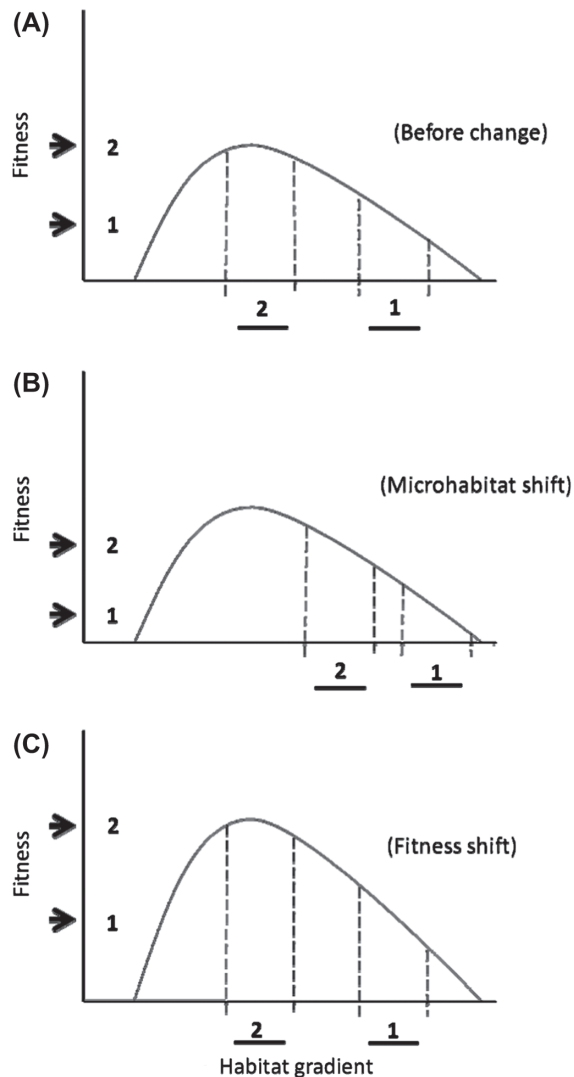

Figure 1. An illustration demonstrating how fitness can differ between habitats arrayed along a continuous gradient. The humped curves represent the distribution of fitness expectations that would be obtained if individuals occupied all locations along the gradient. Solid bars labelled 1 and 2 indicate two habitats that correspond to either a discontinuity in the gradient, or are arbitrarily identified at different points along the gradient by the investigator. Arrows on the ordinate identify expected fitness differences between individuals sampled from each habitat. (A) The fitness expectations of the two habitats before climate or other environmental changes. (B) An example of a microhabitat shift where the fitness expectations have been reduced for both habitats because their characteristics have changed their position along the gradient. The shift need not be equal for both habitats. (C) An illustration of how a change in the fitness distribution can change mean fitness of the two habitats even though their position on the gradient has remained constant (an increase in the height of the fitness function increases mean habitat quality).

sites along the gradient is either discontinuous in space, as occurs at sharp habitat boundaries such as those in the Arctic's patterned ground, or that the investigator has identified 'distinct' habitats for the study of habitat selection. Under these conditions, an individual's mean fitness expectation will often be greater in one habitat than in the other, as will the density of habitat selecting animals (Fretwell and Lucas 1969, Rosenzweig 1981, Morris 1988, Fig. 1; it is also possible of course that habitats located above and below the median of a 'Gaussian' (or more complicated non-linear) gradient could yield similar fitness and density).

An environmental change, such as global warming, can alter the characteristics of each habitat and thereby shift their position (and associated fitness values) along the gradient. Figure 1B illustrates only one of the many possibilities where the shift yields different fitness expectations in the two habitats than occurred prior to the environmentally induced change. Many other scenarios that might alter fitness and density include different shifts in each habitat, shifts in the entire gradient (neither illustrated), or a change in the fitness associated with each otherwise 'stable' habitat (Fig. 1C). Fitness functions could change, for example, through genetic evolution, phenotypic plasticity and adaptive behaviours (such as increased vigilance toward predators).

We illustrate how this view of scale-dependence can influence density and habitat selection in Fig. 2A. The shaded bands represent arbitrary density-dependent relationships between fitness and density in the two habitats (Fig. 1 is silent on how fitness and density covary). If we assume that individuals select habitat according to an ideal-free distribution (Fretwell and Lucas 1969) such that fitness at any given density is equal in both habitats, then Fig. 2 also represents the expected pattern of abundance in the two habitats. Quadrangles represent the potential ranges of fitness and density if the variation in population size is small, such as might occur in a well-regulated population, or in a census taken only when the spatial variation in population size is small.

The consequences of large variation in underlying habitat quality, and rather small variation in population density, are illustrated in Fig. 3 where we plot the respective densities in the two habitats against one another (the habitat isodar, Morris 1988). If the range of densities is high, and if local variation in quality is moderate (the signal from density dependence is high relative to the noise from local heterogeneity), the regression will faithfully represent the differences between the habitats in their respective fitness–density functions (the diagonal shaded bar). If the range of densities is low, however, then the variation in fitness expectations of individuals within habitats could approach that among them and mask differences between habitats (the five-sided figures corresponding to the scenarios depicted in Fig. 2A (solid line) and Fig. 2B (bold dashed lines) respectively; density-vague habitat selection (Oatway and Morris 2007)). Resource-selection coefficients based on the use of occupied versus unoccupied sites by such a population might also detect no preference for one habitat over the other because individuals occupy both habitats across the (narrow) range of sampled densities (Fortin et al. 2008, McLoughlin et al. 2010).

Whether the range of sampled densities is small relative to underlying habitat variation, and whether fitness is
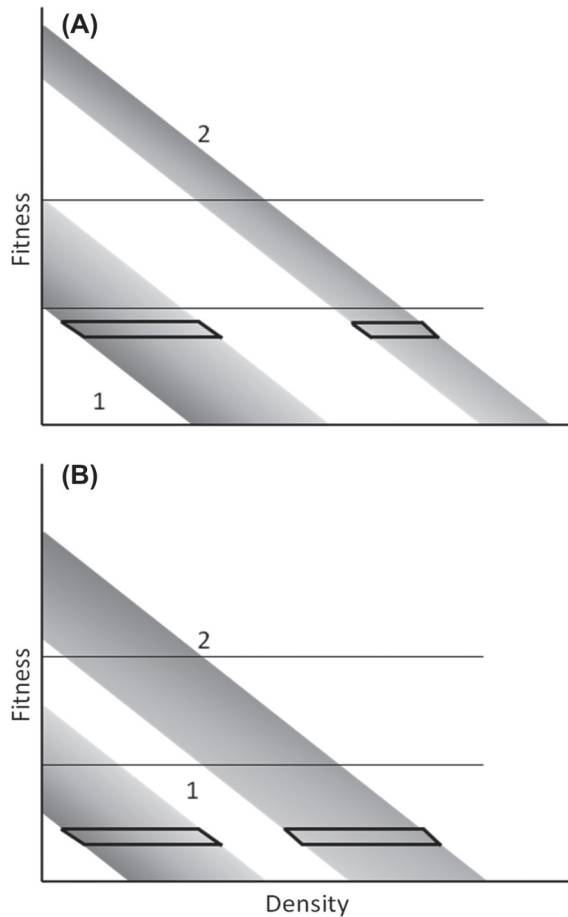
Figure 2. An illustration of potential relationships between fitness and density emerging from the two habitats depicted in Fig. 1A and 1B when the variation in density is small. Diagonal shaded bars represent frequency distributions of fitness associated with 'microhabitat' quality along the portion of the habitat gradient represented by each habitat. The bar for habitat 2 in (A) is narrower than that of habitat 1 because habitat 2 encompasses a smaller range of fitness values in Fig. 1A than does habitat 1. Long horizontal lines represent the solutions expected from an ideal-free distribution (equal fitness) at two different densities. The bold quadrangles correspond with the respective ranges of fitness and densities that could emerge from a study of an ideal-free habitat selector with low variance in density (such as could occur if the population is tightly regulated). Panel (A) corresponds to the fitness distribution in Fig. 1A, panel (B) corresponds to that represented by Fig. 1B (a microhabitat shift).

reduced or increased by a microhabitat shift, depends on several assumptions including the relationship between fitness and the habitat gradient, the position of the habitats along the gradient, constancy of density dependence, and the density and frequency of interacting species. It is also possible, of course, that climate or other changes simultaneously alter a population's fitness function at the same time that the habitats are being repositioned along the underlying gradient. Our main point here is to note, regardless of the mechanics, that it may often be difficult to detect the consequences of climate and other changes influencing habitat selection at large scales unless there is also large variation in population size. This general problem will emerge whenever within-habitat variance in fitness exceeds variation in density.
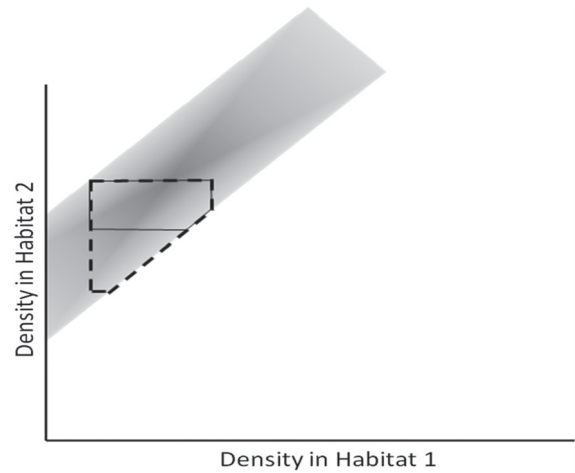

Figure 3. The resulting 'vague' ideal-free relationship between the densities expected in both habitats (the habitat isodar). The diagonally shaded bar represents the expected frequency of paired densities that could emerge if the samples were drawn from the entire range of possible densities where both habitats were occupied. The solid five-sided figure represents the range of expected densities in the two habitats associated with the small range of densities illustrated in Fig. 2A (corresponding with the fitness values before change in Fig. 1A). The larger bold dashed figure represents the range of densities depicted in Fig. 2B (a small range of densities following a microhabitat shift). The dashed figure is larger than the solid one because the range of densities in habitat 2 is greater in Fig. 2B than it is in Fig. 2A. Analyses at this scale may be incapable of detecting density-dependent habitat selection even though the pattern is a subset of that expected from density-dependent habitat choice.

Less often recognized is the converse problem that analyses of data with only fine-scale resolution can yield patterns of 'spurious microhabitat association' that misrepresent large differences between habitats, or the preferences of organisms perceiving habitat at larger scales of resolution (Morris 1987a, Jorgensen 2004). It will thus often be advisable to analyze for changes in habitat selection associated with temporal variation in habitat at both large and small scales (Ale et al. 2011) as has been recommended frequently for all studies of habitat selection (Johnson 1980, Kotliar and Wiens 1990, Schaefer and Messier 1995, Mayor et al. 2007, Bellier et al. 2010).

We propose that an effective analysis assessing temporal changes in habitat gradients could thereby proceed in three-stages. First, compare the values of paired estimates of small-scale habitat metrics measured at the two (or more) different times. This analysis will demonstrate whether or not measurements of habitat (position along the habitat gradient) changed from one period to another, but it will not necessarily reveal changes in habitat preference or selection by the target species. Second, summarize the changes in habitat measurements at a larger scale of spatial resolution corresponding to that where one can obtain estimates of population density necessary to detect a temporal change in density-dependent habitat selection. Third, use the summary to control for the effects of large-scale (and density-dependent) change while searching for significant differences from one time until another in the use of the microhabitat

metrics at fixed sampling points that would indicate a shift along the gradient.

A test with Arctic lemmings

The scenario we outline above is similar to climate-induced habitat change for lemmings existing in the Canadian Arctic (Morris et al. 2011). The 2.1°C increase in mean annual temperature near our Walker Bay research site since 1950 (data from Cambridge Bay, 69°6′N, 105°3′W, approximately 150 km NE; < http://climate.weatheroffice.gc.ca/climateData/canada_e.html >) mirrors the 1–2°C increase reported for much of the arctic over the past few decades (Anisimov et al. 2007), and the consistent decadal increase in mean temperature observed since 1970 (Chylek et al. 2009). Associated tundra responses to increasing temperatures include changes in plant-community composition (Klady et al. 2011) and expanding shrub cover (Sturm et al. 2001). The normalized difference vegetation index (NDVI), a measure of vegetation productivity linked to shrub cover and growth, has increased throughout the arctic (Tape et al. 2006) and particularly so in the region including our study area at Walker Bay (Bhatt et al. 2010). It should thus be possible to jointly assess changes in habitat, and lemming habitat selection, across the 15-year time-span of our Walker Bay research.

The tundra landscape at Walker Bay is shared by dominant brown lemmings *Lemmus trimucronatus* that typically prefer wetter habitats than the subordinate but typically more abundant collared lemming *Dicrostonyx groenlandicus* (Morris et al. 2000). We document that the relative abundances of the two species, and their apparent habitat preferences, have varied through time. We seek to evaluate whether variation in lemming habitat selection is consistent with our general model of scale-dependent change along a habitat gradient.

Methods

Species and study area

We live-trapped both lemming species in twelve 60×60 m census grids at Walker Bay on the Kent Peninsula of Canada's Nunavut Territory (68°21′N, 108°05′W) in June or July during seven different years (1996, 1997, 1999, 2004, 2007, 2009 and 2010; we restrict our analyses to comparisons between 2010 and 1996 in order to maximize our ability to detect climate-induced habitat change). We oriented plots to represent the local availability of each habitat, arranged them to minimize small-mammal movement from one plot to another (plots were at least 100 m apart and largely separated by ridges, ponds or mud flats) and live-trapped lemmings for three consecutive days (Morris et al. 2000, 2011). Each 25-station plot (15 m spacing) included a mosaic of mesic sedge-dominated tundra (*Carex* spp., wet habitat) and xeric hummocks (dry habitat) covered with *Dryas integrifolia* and *Salix arctica*. Patches of taller (~0.5 m) *Salix richarsonii* occur throughout the relatively flat landscape at Walker Bay.

We estimated each species' abundance separately for each grid, habitat (wet vs dry), and year by calculating the number of different individuals captured in a habitat divided by the number of stations on the grid occurring in that habitat (number of individuals·station^{-1}). Simple enumeration is an appropriate density estimate because we recaptured virtually all lemmings known alive (Morris et al. 2000, 2011).

Habitat change

In June 2010, we re-measured the same 13 variables first measured by Morris et al. (2000) in 1996 to classify habitat on the permanent stations and plots (Table 1). We summarized 12 of those variables with a principal components analysis (PCA; SPSS-18) to describe habitat variation in 2010. We excluded the proportion of dry habitat (the 13th variable) estimated at a station because this measure could vary with the evaluator's perception that may have changed since 1996. We were nevertheless concerned that excluding a variable would yield somewhat different PCA scores and habitat classifications (below), so we repeated our analyses with all 13 variables and obtained redundant results. Each analysis extracted four principal components with nearly identical associations of variables (Table 1, only 'difference in shrub height' was associated with different variables in 2010 than it was in 1996).

We classified the stations into the xeric versus mesic habitats used by lemmings with a discriminant function analysis on the PC scores (DFA; SPSS-18). We created the polar reference groups required by the DFA by selecting stations that we classified in the field as pure dry or pure wet habitat in both 1996 and 2010. We reasoned that reference

Table 1. Varimax rotated principal component coefficients of 12 habitat variables collected in 12 grids occupied by two lemming species at Walker Bay (Nunavut, Canada) in 2010. Values in bold represent the variables yielding the greatest contributions to each PC. Superscripts denote the variables associated with each of the four PCs from data collected in 1996 (Table 1 in Morris et al. 2000).

Variables	PC1	PC2	PC3	PC4
Number of hummocks	**0.80**[1]	0.35	0.07	0.00
Proportion cover by low-shrubs ≤ 25 cm tall	**0.75**[1]	−0.17	0.17	0.16
Proportion cover by mud or water	**−0.71**[1]	−0.22	0.53	0.20
Maximum height of hummocks (cm)	**0.69**[1]	0.48	0.21	0.13
Maximum height of shrubs (cm)	0.37	**0.83**[3]	0.13	−0.03
Proportion cover by shrubs > 25 cm tall	−0.04	**0.79**[3]	0.06	−0.14
Absolute difference in shrub height (cm)	0.11	**0.67**[1]	0.08	0.14
Proportion cover by grasses or sedges	−0.04	−0.12	**−0.95**[2]	−0.07
Proportion cover by *Dryas*	0.28	0.27	**0.44**[2]	−0.30
Proportion cover by lichens	0.11	0.13	**0.17**[2]	−0.17
Absolute difference in hummock height (cm)	−0.06	0.15	0.08	**0.84**[4]
Absolute difference in number of hummocks	0.27	−0.06	−0.06	**0.67**[4]

groups assigned through this collective understanding of arctic natural history would most clearly correspond with the similarly documented xeric versus mesic habitat preferences of the two lemming species (Krebs 1964, Rodgers and Lewis 1986, Pitelka and Batzli 1993), and also ensure that comparisons between years used similar reference points on the gradient. We used the classification probabilities from the DFA to then separate all 300 stations into either dry (probability > 0.5) or wet habitat (all others), and compared this classification with that produced by the same procedure at the same stations in 1996 (Morris et al. 2000). These analyses allowed us to assess temporal changes in small-scale (station to station) variation, as well as its role in determining shifts in each species' habitat use.

We controlled for changes in habitat at the larger scale of individual study plots by calculating a 'habitat-change index' (number of wet stations on a plot in 2010 minus the number in 1996). A value of zero indicated that the index was identical between the two years (the same number of wet versus dry stations, but not necessarily the same wet and dry stations), positive values indicated that a plot was more mesic in 2010 than in 1996, and negative values documented plots that had become drier.

Analysis

We used a rather broad set of analyses to assess whether habitat change and shifts in lemming habitat selection were consistent with our model's interpretation of habitat scale. We describe each 'step' so that readers can evaluate every test on its merits, as well as our ability to control potentially confounding variables. We then provide a brief non-technical summary that we hope will help to lead readers through our results without the burden of memorizing the details of each analysis.

Our working hypothesis was that global warming shifted the classification of xeric versus mesic habitats recognized by the two lemming species. Thus, we used mixed-effects logistic regression (Package 'lme4', Bates et al. 2011) to test whether the presence versus absence of *Lemmus* and *Dicrostonyx* at a station (n = 300) was related to the 12 habitat variables for each species × year combination (1996 and 2010; four analyses). We included the presence versus absence of the other species in the model because competition can influence habitat use by these lemmings at Walker Bay (Morris et al. 2000).

The distributions of habitat variables other than cover by grasses and sedges were either bimodal or zero-inflated. We transformed these variables into binary indicators representing 1, their presence versus absence, or 2, whether their value was less than or greater than the median score. We used a stepwise Akaike's information criterion (AIC) method for variable selection, then calculated the odds ratios of the selected variables to help interpret the final model (an odds ratio greater than unity indicates preference for that variable whereas a ratio less than one indicates avoidance).

We then investigated whether the selected model for each species in 1996 was different from that in 2010 (a change in microhabitat preference). If microhabitat selection by each species was more or less constant through time, then models calculated separately in 1996 and 2010 should share similar habitat variables. In order to confirm this assumption, we fitted the 1996 model to the 2010 data and compared its AIC with that of the original 2010 model. We concluded that a species' habitat selection changed through time only if the difference in AIC exceeded two units, and if the list of significant habitat variables was different between the fitted and original 2010 model.

A temporal shift in habitat selection could arise because the characteristics of the stations used by a species changed (same stations with different microhabitat values), or because the species shifted its use of stations to those with different characteristics (leading to abandonment of some stations and occupation of different ones). We reasoned that we could differentiate these alternatives with two pairs of logistic regressions (function 'glm' in R). The first pair evaluated the probability that each species abandoned use of stations in 2010 that it had occupied previously in 1996 (analysis A, Table 2). The second pair analysed the probability that each species chose to occupy stations in 2010 that it had not occupied in 1996 (analysis B, Table 2). Each analysis included independent variables representing species interactions and habitat change at two spatial scales. We used the 'habitat-change index' to represent directional changes among study plots, then created a new variable to represent habitat change at the scale of trapping stations within sampling plots (stations with the same wet or dry classification in both 1996 and 2010 were coded as 0 (no microhabitat change), and those with different wet-to-dry or dry-to-wet classifications in 1996 and 2010 were coded as 1 (different microhabitat, sample sizes precluded our ability to also include the direction of change)).

We accounted for the possibility that inter- and intraspecific competition for habitat also changed at the scale of plots by creating two variables representing the difference in abundance on a plot between 2010 and 1996. One variable represented the change in the target species' density, the second that of its competitor.

In order to account for differences in the use of stations in a plot caused by competition for space with the other lemming species, we created a binary variable indicating whether the target species preferentially abandoned stations that only it occupied in 1996 and that were subsequently occupied by the competitor (coded 1; Table 2) versus abandoning stations that the competitor either occupied or did not use in both 1996 and 2010 (coded 0; Table 2). We used the log ratios from the significant variables (analysis A) to

Table 2. Summary of the different binary combinations of species occurrence used as dependent or independent variables in the analyses of station abandonment (analysis A) and occupation of 'new' stations (analysis B). 'X' indicates combinations that were not used in either analysis.

	Analysis A		Analysis B	
	Present in 1996	Absent in 1996	Present in 1996	Absent in 1996
Variables				
Dependent				
Present in 2010	0	X	X	1
Absent in 2010	1	X	X	0
Independent				
Present in 2010	0	1	0	0
Absent in 2010	0	0	1	0

979

assess the relative roles of scale and competition on a species' choice to abandon stations in 2010 that it had occupied 14 years earlier (1996). We created a similar binary variable for a second pair of logistic regressions (analysis B) indicating whether the target species used stations occupied by only the second lemming species in 1996 and that were subsequently abandoned by that species in 2010 (coded 1; Table 2), versus stations that the second species either occupied or did not use in both 1996 and 2010 (coded 0; Table 2). We used the log ratios from this analysis to assess the roles of scale and competition on each species' choice to occupy sites that had been abandoned by the competitor.

We were concerned that any shifts in habitat use by lemmings from 1996 to 2010 might be influenced by the relative availability of wet and dry habitats in each plot. We controlled for this effect by including the proportion of wet stations in each plot in 2010.

In summary, we were able to incorporate changes in habitat at individual stations while controlling for changes among plots (habitat-change index), frequencies of wet versus dry habitat within plots, intraspecific density, and the effects of interspecific competition for space on the occupation of new stations in 2010 (analysis B), or their abandonment from 1996 (analysis A). We entered all variables into the appropriate analysis, then selected the most parsimonious model using AIC.

Results

Classification of wet versus dry stations changed through time

More stations were classified as wet in 2010 (173, discriminant function analysis, $\chi^2 = 109.71$, $p < 0.001$, n = 300)

than in 1996 (147). One quarter of the stations (76) had a different classification in 2010 than in 1996 (51 stations and seven of the 12 study plots became wetter, 25 stations were drier). These changes reflect the consistent increase in mean annual temperature observed at nearby Cambridge Bay, as well as increases in NDVI observed in the central Canadian arctic (Bhatt et al. 2010). Lemmings at Walker Bay thus represent an appropriate model for assessing scales of temporal change in habitat.

Microhabitat preference reflected interspecific competition

The microhabitat preferences of *Dicrostonyx* and *Lemmus* depended on the presence of the putatively competing species in both 1996 and 2010. Each species preferred to use microhabitat not containing the other species (Table 3).

Lemmings avoided stations occupied by the other species and their microhabitat preference changed through time

In 1996, *Dicrostonyx* was four times as likely to avoid stations where *Lemmus* was present than where *Lemmus* was absent (odds ratio = 0.25). *Dicrostonyx* in 1996 also avoided stations with mud or water as well as those covered by grass and sedges (odds ratios < 1, Table 3) while selecting stations with heterogeneous hummocks and those with extensive cover by low-lying shrubs (odds ratios > 1, Table 3). *Dicrostonyx*'s habitat selection changed in 2010 when they still avoided stations used by *Lemmus*, but selected stations where shrubs were tallest. The large difference in AIC between *Dicrostonyx*'s habitat selection in 2010, and the 1996 model fitted to the 2010 data (Table 3), confirmed the hypothesis that their habitat use changed through time.

Table 3. Mixed logistic regression summaries evaluating microhabitat preference by *Dicrostonyx* and *Lemmus* occupying a tundra mosaic at Walker Bay (northern Canada, Nunavut) in 1996 and 2010. Akaike's information criterion (AIC) for each model, as well as the odds ratio and the 95% confidence intervals of selected variables, are shown. [b]indicates binary variables coded as low (equal or below the median) or high (above the median).

Model	AIC	Odds ratio	95% CI
Dicrostonyx 1996	306.3		
Intercept		0.33	0.20–0.54
Proportion cover by low shrubs[b]		1.84	1.16–2.92
Proportion cover by grasses and sedges		0.68	0.52–0.88
Presence of mud and water		0.31	0.11–0.90
Absolute difference in hummock height[b]		1.71	1.12–2.62
Presence of *Lemmus*		0.25	0.13–0.45
Dicrostonyx 2010	254.6		
Intercept		0.11	0.06–0.20
Mean maximum height of shrubs (cm)[b]		3.53	1.83–6.80
Presence of *Lemmus*		0.39	0.19–0.79
Dicrostonyx 2010 using the model from 1996	261.7		
Lemmus 1996	345		
Intercept		0.55	0.40–0.76
Proportion cover by grasses and sedges		1.46	1.16–1.83
Presence of *Dicrostonyx*		0.27	0.15–0.50
Lemmus 2010	362.2		
Intercept		0.27	0.17–0.42
Presence of tall shrubs		2.30	1.37–3.87
Number of hummocks[b]		2.11	1.36–3.28
Presence of *Dicrostonyx*		0.69	0.49–0.97
Lemmus 2010 using the model from 1996	380.4		

Lemmus' habitat selection complemented that by *Dicrostonyx*. In 1996 *Lemmus* avoided stations occupied by *Dicrostonyx* (odds ratio = 0.27) while selecting stations covered by grasses and sedges (odds ratio = 1.46; Table 3). *Lemmus'* habitat selection also changed in 2010 when they still avoided *Dicrostonyx* while they were more than twice as likely to select stations with many hummocks and tall shrubs than those with less (odds ratios = 2.11 and 2.3 respectively). *Lemmus'* habitat use, as was the case for *Dicrostonyx*, also changed location between 1996 and 2010 (the 1996 *Lemmus* model yielded a poor fit to *Lemmus'* selection of habitat in 2010 (Table 3)).

Changes in habitat use were associated with changes in station occupation. *Dicrostonyx* used 99 of the 300 stations in 1996, and reused only 20 of them while selecting 33 new stations in 2010. Similarly, *Lemmus* occupied 106 stations in 1996, and reused only 32 of them in 2010 while occupying 72 new stations.

Habitat change and interspecific interactions altered *Dicrostonyx's* habitat preference

The shift in habitat use by *Dicrostonyx* was caused mainly by habitat change and competition from *Lemmus* (Table 4). *Dicrostonyx* was more than twice as likely to abandon a station if the station had been 'invaded' by *Lemmus* (*Lemmus* absent in 1996 but present in 2010) than it was if the station had been occupied or unused by *Lemmus* in both years (Table 4). *Dicrostonyx* was also more than twice as likely to abandon a station when the classification changed between the two years, than when it did not, and was more likely to abandon a station if its abundance on the plot was much lower in 2010 than in 1996 (odds ratio = 1.64, Table 4). Although *Lemmus* abandoned a similar number of stations as did *Dicrostonyx* (74 vs 79), no variable in the accompanying logistic regression was statistically significant (Table 4).

Both of these patterns were retained when we classified habitat in 2010 based on 13 (rather than 12) variables. The 'best' model for *Dicrostonyx* was identical to that we describe above, but a competing model including only *Dicrostonyx* abundance and invasion by *Lemmus* was more parsimonious (ΔAIC = 0.88). The significance of habitat change in the best model, however, was marginally significant (p = 0.08; 95% CI of the odds ratio = 0.91–3.46). The strong similarity among models suggests that our original interpretation is correct and that the change in a station's classification was partially responsible for its abandonment by *Dicrostonyx*.

The reverse pattern occurred for the selection of new stations. *Dicrostonyx* appeared to occupy new stations independent of changes in habitat and differences in density (Table 5). *Lemmus*, on the other hand, was more than three times as likely to use a new station on those plots where its abundance in 2010 was highest in comparison with 1996 (odds ratio = 0.32), and 1.45 times as likely to select a new station if it had been abandoned by *Dicrostonyx* (Table 5). Analyses using 13 habitat variables yielded identical results.

Discussion

Our heuristic model illustrates how differences in mean fitness between large-scale habitats can emerge from continuous gradients in habitat quality. The model also illustrates how climate and other environmental changes can shift the locations of pre-defined habitats along the underlying gradient. Depending on the shape of the fitness function, such shifts may or may not translate into differences in mean fitness, and subsequently into differences in density. The fitness function can also change, and particularly so if phenotypic responses are associated with environmental change (Réale et al. 2003, Pelletier et al. 2009). It is thus rather important to develop techniques that can document clearly 1, whether habitat has shifted along a gradient, 2, whether or not a species' habitat use has shifted similarly, 3, the scale at which such shifts are most easily observed and 4, provide insight into the underlying mechanisms.

Analyses of habitat change and habitat use at different spatial scales appear to answer the bell. Although similar combinations of variables consistently define the mesic and xeric habitats typically occupied by lemmings at Walker Bay, stations that were representative of one habitat in 1996 often corresponded to a different habitat in 2010. Not surprisingly, lemmings also shifted their habitat use by 1, abandoning stations that others of their species had occupied in 1996 and 2, occupying stations in 2010 that had been unused in 1996. The change toward newly occupied stations is especially interesting for *Dicrostonyx* because population size,

Table 4. Odds ratios that a station occupied by lemmings at Walker Bay in 1996 was abandoned by the same species in 2010 (analysis A). Models represent the most parsimonious solutions from binary logistic regressions (2010 station classification based on 12 variables) coded 1 if a station was occupied in 1996 only, and coded 0 if occupied in both years. Solutions for the model with the 2010 station classification based on 13 variables are included in parentheses.

Model	Odds ratio	95% CI
Dicrostonyx		
Intercept	1.17 (1.25)	0.75–1.79 (0.81–1.89)
Difference in *Dicrostonyx* abundance*	1.64 (1.72)	1.02–2.94 (1.11–3.03)
Station classification different between 1996 and 2010	2.11 (1.77)	1.07–4.27 (0.91–3.46)
Lemmus absent in 1996 but present in 2010	2.16 (2.06)	1.15–4.18 (1.11–3.96)
Lemmus (no significant model)		

*difference calculated as 1996 value minus the 2010 value.

Table 5. Odds ratios that a station unused by lemmings at Walker Bay in 1996 was occupied by the same species in 2010 (analysis B). Models represent the most parsimonious solutions from binary logistic regressions coded 1 if a station was occupied in 2010 only, and coded 0 if occupied in both years.

Model	Odds ratio	95% CI
Dicrostonyx (no significant model)		
Lemmus		
Intercept	0.81	0.56–1.22
Difference in *Lemmus* abundance*	0.32	0.18–0.56
Dicrostonyx present in 1996 but absent in 2010	1.45	1.08–2.07

*difference calculated as 1996 value minus the 2010 value.

and the concomitant demand for space, was far higher in 1996 (99 stations occupied) than it was in 2010 (53 stations occupied).

The differences in micro-spatial distribution were not driven simply by density-dependent habitat choices. Rather, changes in habitat use represented differential responses to the presence of the competing lemming species, as well as changes in roles that small-scale habitat variation played in habitat choice. Each species tended to avoid stations occupied by its putative competitor, and models of habitat selection calculated with abundance and habitat data from 2010 were different from those calculated with data from 1996.

The two species, nevertheless, varied dramatically in their patterns of habitat abandonment and in the occupation of 'new' sites. *Dicrostonyx*'s abandonment of stations in 2010 that it had occupied in 1996 was accounted for by 1, reduced density-dependent demand for space, 2, stations with changed wet/dry classifications, and 3, those that were occupied by *Lemmus* in 2010. There was no significant pattern in station abandonment by *Lemmus*. When considering patterns in the occupation of 'new' stations, however, only *Lemmus* displayed a significant response through increased density-dependent demand for space, and a strong tendency to use stations occupied by *Dicrostonyx* in 1996.

We interpret these results as evidence that the characteristics of xeric versus mesic habitats changed at Walker Bay, and that those changes were reflected in each species' habitat use in 2010 compared with 1996. Although we cannot rule out the possibilities that some of these patterns were driven as well by altered fitness functions, our data are nevertheless consistent with the hypothesis that temporal differences in rodent abundance and distribution at Walker Bay reflect changes in the characteristics of habitat at individual sampling stations. Habitat preferences of each species still correspond generally to xeric versus mesic habitats, but the location of each habitat along the larger mesic to xeric gradient has shifted.

Some readers will wonder whether such shifts could be caused by lemmings spilling over from high-quality into lower-quality habitat patches (Holt 1984), and particularly so when lemmings are abundant. Spillovers are often associated with source-sink dynamics (Pulliam 1988, Liu et al. 2011) but are a more general consequence of density-dependent habitat selection. A greater range of habitat patches will be occupied when populations are dense than when they are sparse. Related 'spillovers' could occur when individuals forage amongst neighbouring patches of variable quality in order to garner essential resources. Each of these effects can be instituted, among other possibilities, by changes in density, habitat quality, frequencies of competitors and enemies, and spatial patterning among patches. None of those complications, however, should necessarily change the habitat classification of fixed sampling points through time. It thus appears that habitat patches at Walker Bay have not only shifted in location along the mesic-xeric gradient, but that *Dicrostonyx* has similarly altered its spatial distribution in order to track the ever-shifting habitat mosaic.

The lemmings' response to habitat change is multifaceted and much more than the simple hierarchical scales included in our models. Changes in the classification of individual stations as either wet or dry, as captured by our 'habitat-change index', documented a shift in the habitat gradient. Differences among plots in the sign and value of the index illustrated that the changes in the gradient were not homogeneous throughout the landscape.

Ultimately, any analysis of adaptive habitat selection is based on the premise that fitness is related to habitat variation (Gaillard et al. 2010). The analysis also assumes, at least implicitly, that fitness depends on density (but not necessarily a linear relationship or one that is negative across the entire range of densities). These realities limit the ability of many current applications of resource-selection functions (Manly et al. 2002) and species distribution models (Guisan and Zimmerman 2000, Guisan and Thuiller 2005) to reveal habitat preferences and predict future distribution. One cannot simply measure the characteristics of habitat use relative to their availability (or the presence/absence of species), or map current niche space, and hope to understand the dynamics of habitat selection. This important conclusion is poignantly illustrated by lemmings at Walker Bay where our analyses revealed significant roles for intraspecific and interspecific densities on lemming habitat selection (a general point also made by Fortin et al. 2008 and McLoughlin et al. 2010).

Spatio-temporal variation in habitat selection reveals several difficulties that must be overcome in order to use current patterns to predict future habitat use, distribution and abundance. These difficulties are in addition to recognized problems of mis-matches between the resolution of species' sampling and the availability of environmental data, as well as similar mis-matches between the resolution of habitat models and the spatio-temporal scale of their projections (Guisan and Thuiller 2005). Forecasts based on static or equilibrium assumptions may be unable to track species' responses to changing habitat gradients. We doubt whether ecologists can solve this problem by assessing species' responses over a wider range of environmental variability. Such assessments will often require an increase in the extent of sampling that may not correspond with, or might constrain, local adaptation (Holt and Gaines 1992, Cohen 2006).

If our caricature of scale-dependent habitat selection is correct (Fig. 1), then one should be able to forecast future responses to habitat by first mapping the underlying fitness (or performance, Gaillard et al. 2010) functions along the habitat gradient. Constructing such maps may be possible for species where common-garden experiments can be initiated in a variety of habitats. Performance and fitness, however, depend not just on habitat but on intraspecific density, the densities and density-dependent habitat selection by other species, and the frequencies of alternative habitat-selection strategies (Brown 1998, Vincent and Brown 2005, Morris et al. 2011, Morris 2011). Additional complications can arise if rapid trait evolution (Hairston et al. 2005, Pelletier et al. 2009, Schoener 2011) outpaces our ability to map fitness.

Regardless of these complexities, it is patently clear that climate change is altering arctic habitats, and that keystone species such as lemmings are responding by occupying new sites with different habitat characteristics. Rather than being discouraged by the difficulties in forecasting how these changes might influence future habitat use, distribution, and abundance, we should instead be pleased that we have

the tools and abilities to detect rapid changes in habitat use associated with climate change.

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