Forecasting ecological and evolutionary strategies to global change: an example from habitat selection by lemmings

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Abstract

Ecologists and evolutionary biologists must develop theories that can predict the consequences of global warming and other impacts on Earth's biota. Theories of adaptive habitat selection are particularly promising because they link distribution and density with fitness. The evolutionarily stable strategy that emerges from adaptive habitat choice is given by the system's habitat isodar, the graph of densities in pairs of habitats such that the expectation of fitness is the same in each. We illustrate how isodars can be converted into adaptive landscapes of habitat selection that display the density- and frequency-dependent fitness of competing strategies of habitat use. The adaptive landscape varies with the abundance of habitats and can thus be used to predict future adaptive distributions of individuals under competing scenarios of habitat change. Application of the theory to three species of Arctic rodents living on Herschel Island in the Beaufort Sea predicts changes in selection gradients as xeric upland increases in frequency with global warming. Selection gradients will become more shallow for brown lemming (*Lemmus trimucronatus*) and tundra vole (*Microtus oeconomus*) strategies that preferentially exploit mesic habitat. Climate change will cause selection gradients for the alternative strategy of using mostly xeric habitat to become much steeper. Meanwhile, the adaptive landscape for collared lemmings (*Dicrostonyx groenlandicus*), which specialize on xeric *Dryas*-covered upland, will become increasingly convex. Changes in the adaptive landscapes thus predict expanding niches for *Lemmus* and *Microtus*, and a narrower niche for *Dicrostonyx*. The ability to draw adaptive landscapes from current patterns of distribution represents one of the few methods available to forecast the consequences of climate change on the future distribution and evolution of affected species.

Keywords: arctic, climate change, conservation, evolution, habitat, habitat selection, isodar, lemmings

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Introduction

Climate warming is changing the distribution and quality of habitats on an unprecedented global scale (e.g., IPCC, 2007). Although the effects of global warming are most noticeable at northern latitudes (e.g., IPCC, 2007), other anthropogenic disturbances are also changing the distribution and quality of habitats, and represent major extinction risks to Earth's biota (Thomas *et al.*, 2004). It is thus paramount that ecologists and evolutionary biologists develop theories to forecast ecological and evolutionary dynamics associated with global change, and demonstrate their application in the field.

Theories of habitat selection offer special promise because all organisms require space in which to live,

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habitat loss and habitat change are dominant causes of global extinctions (Owens & Bennett, 2000; Jablonski, 2008), and the theory's predictions have been confirmed in numerous taxa (Morris, 1988, 2003, 2006). Theories of habitat selection are helping us to better understand evolution (Rosenzweig, 1987; Brown & Pavlovic, 1992; Ravigné *et al.*, 2009), disentangle the effects of interacting species (Morris *et al.*, 2000), appreciate the importance of stochastic dynamics (Jonzén *et al.*, 2004) and source–sink regulation (Holt & Barfield, 2008; Morris, 2010), and improve the management and conservation of wildlife (e.g., Aldridge & Boyce, 2008; McLoughlin *et al.*, 2010).

Encouraged by recent convergence in modelling habitat selection (Fortin *et al.*, 2008), we explore how changes in habitat composition alter strategies of density-dependent habitat choice and their associated fitness landscapes. Our primary intent is to develop the theory and concepts necessary to predict ecological and

evolutionary consequences of habitat change. We nevertheless demonstrate the utility of our approach to habitat selection by arctic rodents for whom the ecological effects of global warming are particularly noticeable. Changes in snow characteristics, cover, depth, and the length of the snow-free period alter the distribution and temporal availability of winter habitats occupied by lemmings and specialized predators. Changing snow regimes appear to cause lemming and vole population cycles to collapse (Ims *et al.*, 2008; Kausrud *et al.*, 2008; Post *et al.*, 2009), and portend local extinctions of predators (Gilg *et al.*, 2009). The return of multiannual vole cycles in southern Finland suggests that climate's influence varies with context and species composition of the vole community (Brommer *et al.*, 2010). There can be little doubt, however, that increasing temperatures and changes in precipitation create similar changes in the distribution and quality of habitats (as demonstrated by dramatic differences in arctic plant communities caused by experimental warming, Walker *et al.*, 2006), such as the frequency of mesic and xeric habitats exploited by lemmings and voles throughout northern Canada (Batzli *et al.*, 1983; Rodgers & Lewis, 1986; Morris *et al.*, 2000; Gruyer *et al.*, 2010).

We begin by developing the requisite theory necessary to build adaptive landscapes of habitat selection. We apply the theory to the current and expected future distributions of habitats exploited by three-species of arctic rodents living on a small island in the Beaufort Sea. We conclude by discussing the implications of the theory, and its application, to our understanding of ecological and evolutionary dynamics.

Materials and methods

Theory

Imagine a habitat-selecting species occupying two adjacent habitats of equal area that produce equal fitness at low density, but possess different carrying capacities (Fig. 1a). Assuming that each additional individual has an equal and negative influence on the fitness it can accrue from a habitat, the population density in habitat i at time $t+1$ is given by the Ricker (1954) equation:

$$N_{i(t+1)} = N_{i(t)} e^{r\left(1 - \frac{N_{i(t)}}{K_i}\right)}, \qquad (1)$$

where N also equals population size in the equal sized habitats, r is the maximum instantaneous rate of population growth at low density, and K is the habitat's carrying capacity. Thus,

$$\ln\left(N_{i(t+1)}\right) - \ln\left(N_{i(t)}\right) = r_i - \frac{r_i}{K_i} N_i, \qquad (2)$$

yields a habitat's per capita population growth rate for the species at different densities. Using per capita growth rate as
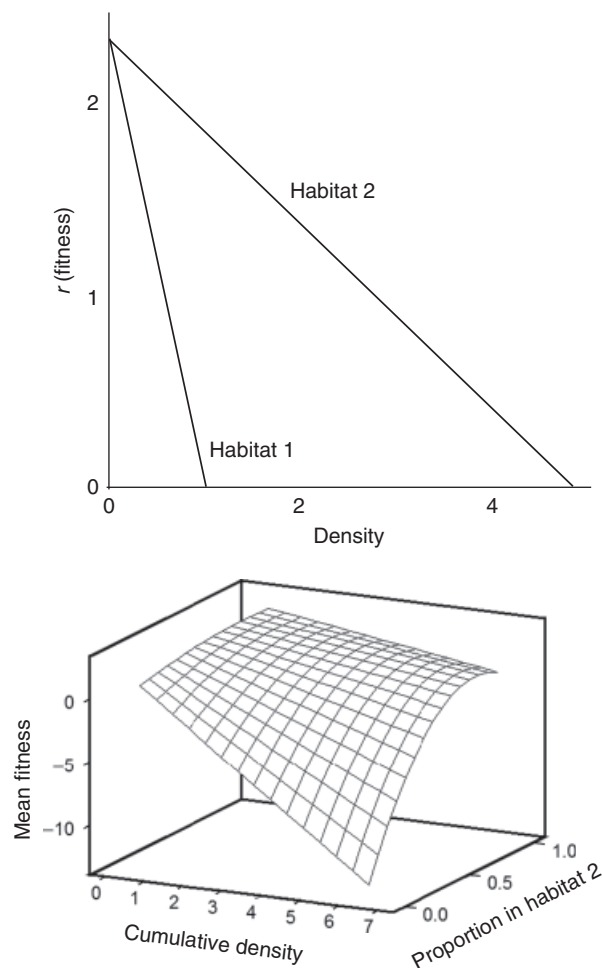

Fig. 1 (a) An illustration of diverging fitness-density functions in two adjacent habitats occupied by a density-dependent habitat selector. (b) The adaptive landscape of habitat selection for distributions of individuals between the two habitats at different cumulative densities [cumulative density ranges from $0.01(K_1 + K_2)$ to $1.1(K_1 + K_2)$. The landscape sinks, and its selection gradients become steeper, with increasing population density. Parameter values correspond to those of *Lemmus* living on Herschel Island if dry and wet habitats were equally abundant ($r_1 = r_2 = 2.3026$, $K_1 = 1$, $K_2 = 4.88$, $p = q = 0.5$).

our estimate of fitness (W), we note that the fitness functions diverge from one another (Fig. 1a). Consider a suite of possible strategies ($u \equiv [0,1]$) of habitat selection (e.g., Vincent & Brown, 2005) that allocate different proportions of individuals to each habitat. Mean fitness of the jth strategy is given by

$$\overline{W}_j = \frac{\left(r_1 - \frac{r_1}{K_1} N_1\right) N_1 + \left(r_2 - \frac{r_2}{K_2} N_2\right) N_2}{TotN}, \qquad (3)$$

for all possible values of cumulative population density ($TotN = N_1 + N_2$). Plotting mean fitness of each strategy against cumulative density generates the adaptive landscape of density- and frequency-dependent habitat selection (Morris, 2003, 2010; Morris *et al.*, 2009). The landscape sinks, and its slopes

become steeper (stronger selection gradients), with each increase in population size (Fig. 1b). The strength of selection for adaptive habitat use is much stronger at high population sizes than it is when population densities are low.

If we aspire only to predict the future distribution of individuals, then we need only to apply the isodar (derived below) to the anticipated future frequency of habitats. An appreciation of the height, shape, and contortions of the adaptive landscape is necessary, however, for those who wish to gain deeper insights into how adaptive habitat selection and niche evolution proceed with changes in density and habitat distribution.

We use the adaptive landscape to answer two questions. (1) What is the optimum strategy of habitat selection? (2) How does the adaptive landscape change with differences in habitat composition?

Assuming that individuals are free to occupy whichever habitat they choose (Fretwell & Lucas, 1969), the optimum strategy of habitat selection maximizing an individual's fitness occurs when the densities of individuals fall on the system's habitat isodar

$$N_2 = \frac{r_2 - r_1}{r_2} K_2 + \frac{r_1}{r_2} \frac{K_2}{K_1} N_1, \tag{4}$$

(the set of densities in a pair of habitats such that an individual's expected fitness in one habitat is equal to that in the other, Morris, 1988) which, in the case of diverging fitness functions with equal r, reduces to $N_2 = \frac{K_2}{K_1} N_1$. The optimum strategy of habitat selection, in this instance, is constant for all population densities (the adaptive landscape is maximized at the same proportional use of habitat for all population sizes, Fig. 1b).

In order to calculate changes in the adaptive landscape with changes in the proportions of the two habitats we generalize our estimate of mean fitness as

$$\overline{W}_{jk} = \frac{\left(r_1 - \frac{r_1}{K_1} N_1\right) p_k N_1 + \left(r_2 - \frac{r_2}{K_2} N_2\right) q_k N_2}{(p_k N_1) + (q_k N_2)}, \tag{5}$$

where $(p_k + q_k = 1)$ represent the proportions of habitats 1 and 2 respectively that are available for occupation by population k. The adaptive landscape changes, as does the best strategy of density-dependent habitat selection (but not the requirement that individuals move until their expectation of fitness in each habitat is equalized).

There may be few natural systems for which we can obtain the accurate estimates of population growth rates and carrying capacity in different habitats that we need to draw the adaptive landscape of habitat selection. We can, however, expect natural selection to hone adaptive strategies of habitat use. Accordingly, we should be able to use a system's isodar to infer how the adaptive landscape changes with differences in the abundance of habitats.

Fortunately, if we know a system's isodar, we need only to estimate growth rate and carrying capacity in one habitat to draw the fitness landscape. In order to appreciate this point, assume that we have estimated densities in a pair of habitats and used regression to generate the general empirical isodar, $N_2 = C + bN_1$. We can use our understanding of natural history

to estimate r_2 (we demonstrate how to use rodent litter sizes and reproductive intervals to estimate maximum population growth rate in preferred habitats; see 'Results'), and our knowledge of density-dependent population growth to estimate the habitat's carrying capacity (accurate measurements of carrying capacity can be obtained from experiments assessing optimal density-dependent foraging behaviour, Morris & Mukherjee, 2007). Substituting these values into the theoretical isodar [Eqn (4)] allows us to calculate the two remaining parameter values (use the intercept to calculate $r_1 = r_2 - \frac{Cr_2}{K_2}$; knowing r_1, use the slope to calculate $K_1 = \frac{r_1}{r_2} \frac{K_2}{b}$).

Although this approach portrays the general features of the adaptive landscape, in order to be useful, errors in estimating parameter values (r and K) must cause much less 'distortion' in the adaptive landscape than do changes in the relative abundances of habitats. We address this concern by simulating adaptive landscapes obeying the hypothetical isodar, $N_2 = 2N_1$ (Fig. 2). We assume that the true parameter values are given by $r_1 = r_2 = 1$, $K_1 = 4$, $K_2 = 8$, that the initial proportions of habitats 1 and 2 are $p = q = 0.5$ respectively, and that climate change increases the frequency of habitat 2 by 50% ($p = 0.25$, $q = 0.75$). Inspection of Eqn (3) reveals, for this example, that an inflated value of r will increase the mean fitness for each strategy equal to the inflation factor, and for all values of N. The slope of the adaptive function, for a given population size, becomes steeper (the range of fitness increases) but the general shape and position of the adaptive landscape remains constant (compare Fig. 2a with c). Our estimate of the 'strength of selection' will be biased because the speed of adaptation depends directly on the slope of the selection gradient (e.g., Bell, 2008), but our ability to define the best strategy, and relative values of competing strategies, is unchanged. Fitness, in this model, is maximized for all values of r when two thirds of the individuals live in habitat 2. Errors in estimating K change the slope of the landscape, but do not alter its shape (compare Fig. 2c with d, please note the differences in scale).

Altering the proportions of habitat available for individuals to occupy, however, alters the shape of the adaptive landscape (e.g., compare Fig. 2a with b). In the examples illustrated in Fig. 2a and b, the landscape is more convex when the frequency of habitat 2 is high (Fig. 2b), than it is when the frequency of the two habitats is equal (Fig. 2a). More importantly, fitness in Fig. 2b is maximized at a higher occupation of habitat 2 (a greater proportion of individuals use habitat 2).

Thus, for populations with adaptive habitat selection, and which consequently possess a linear isodar passing through the origin, errors in estimating population growth rates will modify our interpretations about the speed of adaptation, but will reliably reveal the best strategy of habitat use. This strategy will change if the proportions of habitats available to the population changes. It is thereby possible to use patterns of current adaptive habitat use to predict future strategies of habitat selection associated with changes in the frequency of habitats.

One would also like to know how changes in a habitat's quality alter adaptive landscapes. We addressed this problem with additional simulations that increased r in only one of the two habitats [the isodar no longer passes through the origin, Eqn (4)] and found similar patterns (in this instance we
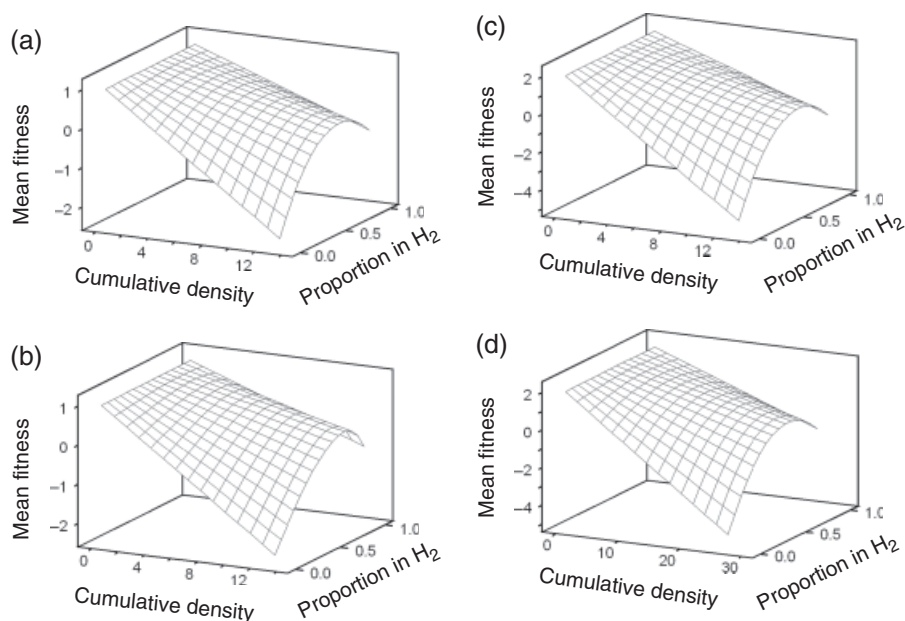
Fig. 2 Examples of the effect of different estimates of r and K on the shape of adaptive landscapes in comparison with changes in the frequency of habitats used by a population of a habitat-selecting species. (a) The correct estimates of $r_1 = r_2 = 1$, $K_1 = 4$, $K_2 = 8$, $p = q = 0.5$. (b) The correct values of r and K, but with $p = 0.25$, $q = 0.5$. (c) Inflated values of r ($r_1 = r_2 = 2$, $K_1 = 4$, $K_2 = 8$, $p = q = 0.5$). (d) Inflated values of both r and K ($r_1 = r_2 = 2$, $K_1 = 8$, $K_2 = 16$, $p = q = 0.5$). Please note that steeper slopes of the adaptive landscapes in (c) and (d) are obscured by differences in scale along the ordinate (fitness). Maximum mean fitness and its variance are twice as great in (c) and (d) as they are in (a), as is the value of r.

estimated both r_1 and r_2, used the intercept of Eqn (4) to calculate K_2 and substituted all values into the term for the isodar slope to calculate K_1. Adaptive slopes become steeper in landscapes with higher rs, but best strategies are invariant to estimates of r and K for a fixed isodar. The adaptive landscape shifts its shape with changes in the proportional representation of habitats (displayed for converging fitness functions in Fig. 3; Appendix S1 in Supporting Information provides an initial theoretical treatment of this effect).

To briefly summarize: If one knows a system's habitat isodar it is possible to infer underlying fitness functions by estimating two of the isodar's four 'unknown' growth rate and carrying capacity parameters, and thus graph the adaptive landscape of habitat selection. The slope of the landscape, and hence the pace of adaptation, varies directly with the magnitude of the fitness estimates. The shape of the landscape, however, and the ranking of alternative habitat-selection strategies (distributions of individuals between habitats) is robust to errors in fitness parameters. New strategies can emerge if the relative abundances of the habitats change (Appendix S1, Supporting Information).

Lemmings and habitat change

We demonstrate how to apply the theory with a three-species rodent community living in rolling tundra 180 m above sea level on Canada's Herschel Island, Yukon Territory (69°36′N; 139°04′W). Although collared lemmings (*Dicrostonyx groenlan-*

dicus) have the most northerly distribution of the three species, their southern geographic range overlaps that of brown lemmings (*Lemmus trimucronatus*) across the Canadian-US Arctic, and both species overlap with tundra voles (*Microtus oeconomus*) along the Arctic coastline in western North America (e.g., Banfield, 1974; Krebs *et al.*, 2002). Our detailed assessment of habitat and habitat use by these species is being reported elsewhere (S. B. Ale, D. W. Morris, A. Dupuch & D. E. Moore, unpublished results). Nevertheless, we must first understand density-dependence in habitat use in order to draw adaptive landscapes of habitat selection, so we summarize the methods and relevant results here.

We live-trapped collared lemmings, brown lemmings, and tundra voles in eight 60 m square trapping grids. We placed four grids encompassing mesic vs. xeric habitats along each of two adjacent valleys (distance between grids > 100 m). Wet meadows in the valley floor were dominated by sedges (*Eriophorum* spp. and *Carex* spp.) and grasses (e.g., *Arctagrostis latifolia*) with a few small shrubs (*Salix* spp.), whereas dry upland habitat on the slopes was composed mainly of *Dryas integrifolia* hummocks dotted with forbs (e.g., *Saxifraga* sp., *Lupinus arcticus*), and mixed lichens.

We trapped rodents during three periods in each of 2 years (biweekly during July and August 2007; 3-week intervals during June–August 2008). We placed a single Longworth live-trap, containing cotton and one or more pieces of apple, at each of the 25 stations (15 m spacing) on each grid following 2 days of prebaiting with open locked traps. We protected each trap from direct sunshine and precipitation by covering it with
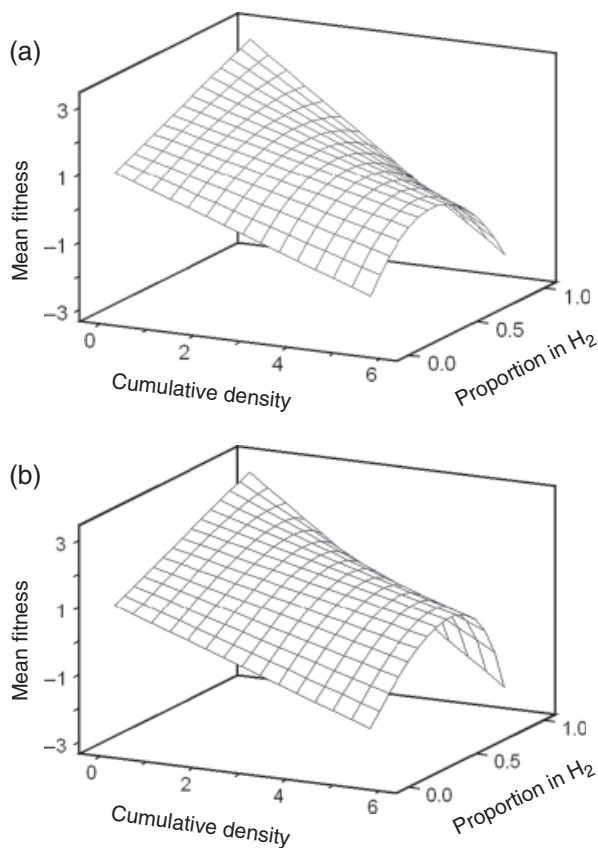
Fig. 3 Examples of the effect of changes in adaptive landscapes of habitat selection caused by changes in the frequency of habitats when fitness functions converge. (a) The 'control' adaptive landscape ($r_1 = 1$, $r_2 = 3$, $K_1 = 2$, $K_2 = 3$, $p = q = 0.5$). (b) The adaptive landscape where the frequency of habitat 2 is 0.75 ($r_1 = 1$, $r_2 = 3$, $K_1 = 2$, $K_2 = 3$, $p = 0.25$, $q = 0.75$).

a small wooden board. We unlocked traps in the morning for 3 consecutive days and checked them 5 and 10 h later before locking them open until the following morning (total of six trapping 'sessions' during each 3-day period). We identified each captured animal to species, marked it with a unique ear-tag, and recorded its age (juvenile or adult), mass, body-length, and sex before releasing it at the point of capture.

We estimated the number of animals of each species using a habitat on a grid as the number of different individuals captured in the habitat divided by the number of stations in the grid that occurred in that habitat (number of animals station^{-1} period^{-1}). Animals using both habitats contributed equally to each density estimate. Enumeration is appropriate for our density estimates because all comparisons depend on relative rather than absolute densities, the majority of animals were captured during a single trapping period, and 91% of all rodents known alive in two or more periods were recaptured during each of those periods.

We quantified the underlying habitat gradient by measuring 16 habitat variables at each station in 2007 in order to 'ordinate'

habitat along the dominant mesic to xeric cline in our study plots. All variables represented those previously identified as significant predictors of the two tundra habitats (Morris *et al.*, 2000, Table S1 in Supporting Information provides a full list and description). Variables included 'cover' by habitat classes (collected at points separated by 1 m along a randomly oriented 10 m transect centred on each station), maximum height of shrubs (in each of 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 also included an estimate of variation in shrub and hummock heights (absolute difference between the two maxima) as well as variation in the number of hummocks along the two segments of the 10 m transect. We completed the habitat assessment by estimating the proportions of area within a 5 m radius of each station belonging to dry and wet habitat.

Analysis

We used principal components (PC) analysis (FACTOR routine, SPPS-16) to extract composite summary variables describing habitat variation on our grids. We eliminated all variables represented in fewer than 5% of the 200 samples (eight grids, 25 stations in each grid), as well as those that were unrelated to any other variable (Table S1, Supporting Information). Three PCs accounting for nearly 60% of the common variation amongst variables summarized different microhabitat gradients along the predominant xeric–mesic cline (Fig. S1, Supporting Information). We entered the PC scores into a discriminant function (DF) Analysis in order to classify stations into two separate classes along the xeric–mesic axis represented by the PCs. Our purpose was to organize the habitat data with methods analogous to polar ordination (Bray & Curtis, 1957) that would categorize two habitats needed for the isodar analysis. We selected only those stations that we classified in the field as pure xeric (*Dryas*) habitat (56) or pure mesic (grass-sedge) habitat (40) to represent two polar reference classes for the DF analysis. The analysis correctly classified 92 of the 96 stations. We used the DF scores of the remaining 104 'ungrouped' stations to classify each as either xeric or mesic. Our approach thus created distinct habitat classes presenting clear options of habitat choice for small mammals (although the PCA/DFA protocol is well suited to isodar analyses of small mammal habitats in tundra ecosystems, the ends of the gradient were based on natural history and thus included variation associated with a single observer's (D. E. M.) ability to distinguish the two classes; we do not advocate its use for descriptive ordinations of vegetation or plant communities).

The densities of all rodents were low in both years. Densities were lower in 2008 than in 2007 (S. B. Ale, D. W. Morris, A. Dupuch & D. E. Moore, unpublished results), were lower still in 2009 (C. J. Krebs, unpublished results), and selection of mesic vs. xeric habitats by each species was independent of the other two. Knowing this, we calculated each species' habitat isodar by geometric mean regression (Morris *et al.*, 2000). We then estimated each species' maximum population growth rate (based on reproductive rates) and relative carrying capacities of each habitat so that we could convert the isodar to its corresponding adaptive landscape. Weather records near

Herschel Island document increased temperature and reduced precipitation, a drying pattern that is also revealed in the colonization of stabilized frost boils by polargrass (*Arctagrostis latifolia*) and Arctic lupine (*Lupinus arcticus*, Kennedy *et al.*, 2001). These changes in climate, vegetation, and soil moisture suggest, in future, that wetlands within the Island's small valleys will contract and increase the proportion of 'dry habitat'. Accordingly, we forecast adaptive landscapes of habitat selection by the island's rodents assuming that dry habitat increases by approximately 25%.

Two species (*Dicrostonyx* and *Microtus*) did not possess a valid isodar. We assumed that densities of these species would remain near their 2007–2008 levels, then modelled their adaptive landscape of habitat selection across a range of different compositions of the xeric hummock and mesic meadow habitats.

Results

Lemmus is a density-dependent habitat selector

Lemmus occupied both habitats in each year. On average, *Lemmus* were nearly five times as abundant in meadows as they were in xeric upland [*Lemmus* isodar; density in meadow $= -0.03 + 4.88$ density in upland, geometric mean regression (95% confidence intervals for the slope $= 3.42$ and 6.96, and for the intercept $= -0.11$ and 0.02; $F_{1,11} = 25.71$, $P < 0.001$, $R^2 = 0.73$, Fig. 4)].

Dicrostonyx and Microtus specialized on different habitats

Microtus preferentially occupied mesic habitat (captured in xeric habitat in only one grid in 2007 and in four grids during 2008). *Dicrostonyx* was mostly restricted to xeric
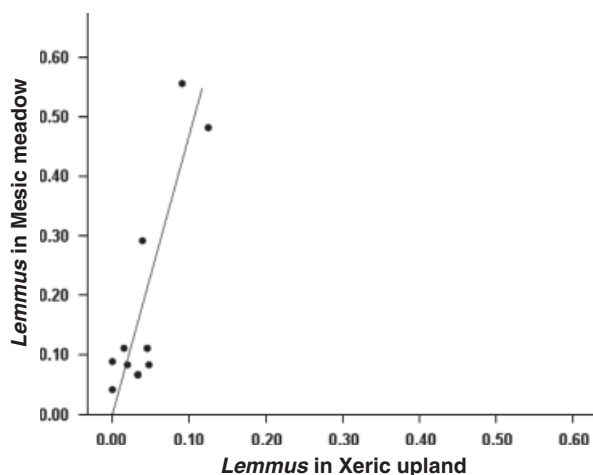

Fig. 4 The isodar for *Lemmus trimucronatus* (number of animals station^{-1} period^{-1}) occupying mesic meadow and xeric upland habitats on Herschel Island, Yukon Territory, Canada (after S. B. Ale, D. W. Morris, A. Dupuch & D. E. Moore, unpublished results).

habitat (captured in mesic habitat in four grids during 2007 and in only one grid in 2008, S. B. Ale, D. W. Morris, A. Dupuch & D. E. Moore, unpublished results). Neither *Dicrostonyx* nor *Microtus* had a statistically significant isodar. At the scale of xeric and mesic habitats on our Herschel Island study plots, neither species is a density-dependent habitat selector. Yet it is clear that each has a distinct preference for the opposite end of the moisture gradient (mean *Microtus* density in wet $= 0.14$, in dry $= 0.01$, paired $t = 3.31$, $P = 0.001$; mean *Dicrostonyx* density in dry $= 0.09$, in wet $= 0.04$, paired $t = 2.25$, $P = 0.04$, $N = 16$).

Models predict, in future, that Lemmus will reduce specialization on mesic habitat

We modelled rodent adaptive landscapes by assuming that females produce, on average, two litters each reproductive season, and that mean litter sizes varied from four for *Dicrostonyx* to six for *Microtus* [*Lemmus* was intermediate (five), our reproductive estimates for all species are somewhat conservative (e.g., Banfield, 1974), but will not influence the 'shape' of the adaptive landscape]. We assumed that maximum fitness for *Lemmus* was equal in both habitats at low density (diverging fitness functions as illustrated by the *Lemmus* isodar), and arbitrarily set the *Lemmus* carrying capacity in dry habitat $= 1$ (the actual values of K do not influence the shape of the landscape, Fig. 2).

Based on the proportions of xeric and mesic habitats in our study grids (73% mesic), selection on *Lemmus* is slightly stabilizing (maximum fitness is attained when approximately 77% of the population occupies wet habitat, Fig. 5a). Although the adaptive landscapes appear similar when the frequency of dry habitat is increased to 90% of the total area (Fig. 5b), fitness is maximized when a much smaller proportion of individuals occupy wet habitat (50%). Despite identical maximum and minimum fitness values for the two scenarios, the slopes of selection gradients for intermediate strategies are much shallower on a dryer Herschel Island. Fitness drops off dramatically at high densities, however, when a small proportion of individuals occupy the wet end of the habitat gradient. Regardless, the reduced variation in fitness across a moderate range of 'preferences' for wet habitat reduces the penalty for suboptimal distributions and suggests that future isodars on Herschel Island will have more residual variance about the regression than does the current one.

Dicrostonyx and Microtus strategies also reflect anticipated climate change

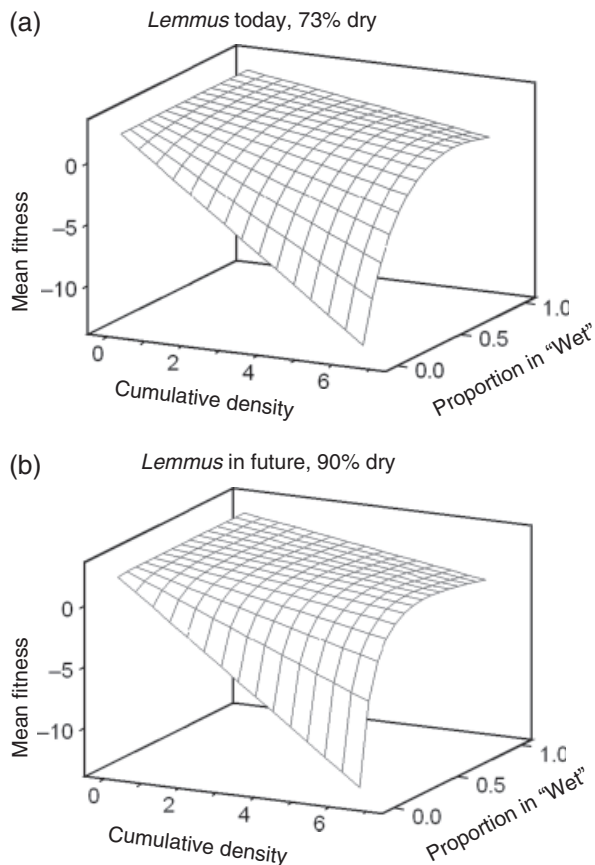We were unable to use the same procedure for *Dicrostonyx* and *Microtus* because neither possessed a

(a)
Lemmus today, 73% dry

(b)
Lemmus in future, 90% dry

Fig. 5 *Lemmus* adaptive landscapes inferred from its isodar of habitat selection in wet meadow vs. dry upland habitats on Herschel Island, Yukon Territory, Canada. (a) The current adaptive landscape (73% xeric habitat). (b) The future adaptive landscape assuming that xeric habitat increases to 90%. Cumulative densities range from $(K_{dry} + K_{wet})/2$ to $(K_{dry} + K_{wet})$. Parameter values correspond to $(r_{dry} = r_{wet} = 2.3026, K_{dry} = 1, K_{wet} = 4.88)$.

statistically significant isodar. We suspect that the absence of a habitat isodar for these species is linked to their relatively low densities on Herschel Island [the maximum density observed for both species was $<50\%$ the maximum density observed for *Lemmus* (S. B. Ale, D. W. Morris, A. Dupuch & D. E. Moore, unpublished results)]. Our suspicion is bolstered by the observation that *Dicrostonyx* is a density-dependent habitat selector of xeric vs. mesic habitats elsewhere in its range where population densities can be more than an order of magnitude greater than those we observed on Herschel Island (Morris *et al.*, 2000). We arbitrarily set the growth rate in the secondary habitat of each species at one half the value calculated in the preferred habitat. We assumed that the slope of the fitness function for the best habitat $=-1$, and that of the secondary habitat $=-2$ (simulations using other values, including equal growth rates in both habitats, yielded outcomes similar to those

we present here). Lacking evidence for density-dependent habitat use, we assumed that densities of *Dicrostonyx* and *Microtus* are 'stable' at one half the cumulative carrying capacity of both habitats (these values also have little effect on the landscape's shape), and estimated fitness in each habitat with Eqn (2).

The adaptive landscape for *Dicrostonyx* reveals an intriguing pattern, shifting from a shallow landscape with weak stabilizing selection when dry habitat is sparse, to a convex landscape with much stronger stabilizing selection when dry habitat is abundant (Fig. 6a). Mean fitness increases gradually, and selection gradients on either side of the optimum strategy become steeper, as xeric hummocks become more abundant. Although the pattern of habitat occupation varies with the frequency of habitats, the percentage use of habitat becomes more stable as the preferred dry habitat increases in abundance.

The adaptive landscape for *Microtus* is similar, but in the opposite direction (more stabilizing as wet habitat increases in abundance), and with somewhat shallower stabilizing selection (Fig. 6b). If Herschel Island 'dries out' as predicted, then a greater proportion of *Microtus* can be expected to occupy hummock habitat. But the selection gradient favouring the optimum choice is so shallow, when dry habitat is abundant, that a wide variety of strategies preferring greater proportional occupation of wet habitat are likely to coexist.

Discussion

Our models and data illustrate how habitat-selection theory and its emergent isodars can forecast changes in the proportional occupation of two different habitats if one or the other becomes more abundant. The models assume, for each population size, an evolutionarily stable strategy of habitat selection (e.g., Fretwell & Lucas, 1969; Morris *et al.*, 2001; Vincent & Brown, 2005; Cressman & Křivan, 2006; Křivan *et al.*, 2008) that equalizes linear per capita population growth rates in each habitat (each individual entering a habitat has an equal and negative effect). A remarkable result, under these restrictive assumptions, is that one does not require an estimate of fitness in order to predict adaptive evolution to changing habitats. Any reasonable estimate of population growth rate and carrying capacity, in only one of the two habitats, will produce a reliable caricature of evolutionary responses to variation in habitat composition.

Although we have developed theory here only for linear density-dependent ideal-free habitat selection, isodar theory applies to all forms of ideal habitat choice including so-called despotic (Fretwell & Lucas, 1969) and pre-emptive (Pulliam, 1988; Pulliam & Danielson, 1991) habitat selection often associated with source–sink dy-
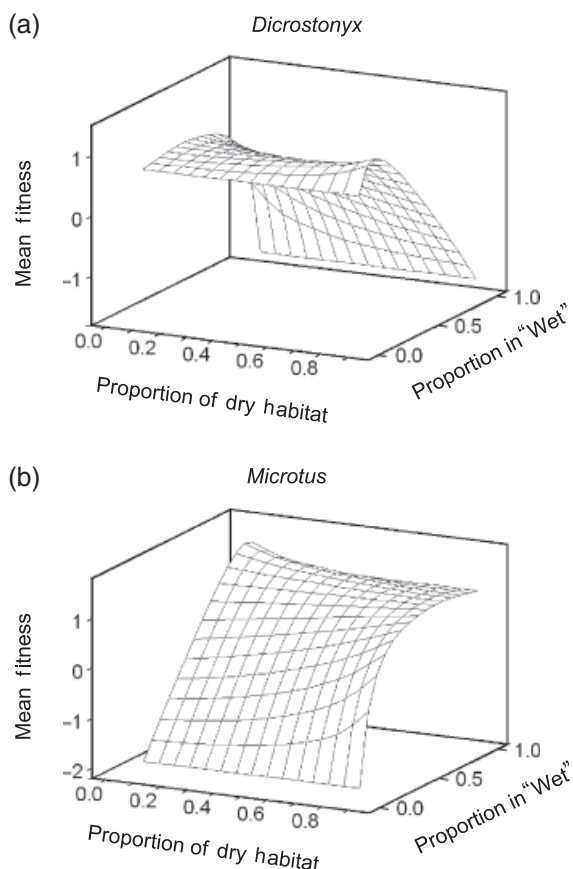
(a)

Dicrostonyx

(b)

Microtus

Fig. 6 Adaptive landscapes for *Dicrostonyx* (a) and *Microtus* (b) preferentially occupying dry and wet habitats respectively on Herschel Island, Yukon Territory, Canada. Each landscape assumes that fitness is twice as great in the primary habitat as it is in the secondary one, and that fitness declines linearly with slope −1 in the primary habitat, and with a slope of −2 in the secondary habitat. Parameter values for *Dicrostonyx* correspond to (r_{dry} = 2.08, r_{wet} = 1.04, K_{dry} = 2.08, K_{wet} = 0.52). Parameters for *Microtus* equal (r_{dry} = 1.2425, r_{wet} = 2.485, K_{dry} = 0.6212, K_{wet} = 2.485).

namics. Nonlinear fitness functions typical of despotic or pre-emptive distributions tend to produce curved or nonlinear isodars (Morris, 1994; Knight *et al.*, 2008). Such isodars often require more parameter values than do linear ones, but there is no conceptual reason why they cannot also be converted to adaptive landscapes that are then used to predict strategies of habitat occupation.

Another apparent limitation is that variation in population size may be too small to detect density-dependent habitat selection. Yet, even in these instances, as we demonstrate for *Dicrostonyx* and *Microtus* living on Herschel Island, one may be able to infer likely adaptive changes in distribution.

Isodars, and the accuracy of their forecasts, are prone to measurement and statistical 'errors'. Measurement

errors arise through biased estimates of population density, whereas statistical errors are represented by the confidence intervals about the isodar regression. Both types of errors can be minimized by increasing the number of samples and the precision and accuracy of population estimates. Although we were limited in our ability to expand sample size for the rodent isodars on Herschel Island, we remain confident in our interpretations of habitat use because we used the same procedures on all sampling plots, our population estimates were based on species with consistently high recapture rates, and all density estimates are relative rather than absolute.

In order to assess whether our confidence is justified, we recalculated the *Lemmus* isodar using only data from the third capture period in each year (there were too few lemmings in other sessions to analyse each one separately). We reasoned that we could discount bias if this isodar fell within the confidence intervals of the original. The new isodar was nearly identical to the original [*Lemmus* density in meadow = −0.09 + 4.96 density in upland, geometric mean regression (95% confidence intervals for the slope = 3.06 and 8.03, and for the intercept = −0.44 and 0.12); $F_{1,7}$ = 15.19, P = 0.005, R^2 = 0.68].

Regardless, one would still like to know the expected limits of the future forecasts for habitat use. Perhaps the simplest way to do this is to calculate separate adaptive landscapes for the upper and lower confidence intervals associated with the empirical isodar (or about the density estimates for nonhabitat selecting species such as *Microtus* and *Dicrostonyx* on Herschel Island). This practice has two desirable outcomes. (1) It will set reasonable bounds on predicted habitat use. (2) The boundaries of those future forecasts are tied directly to the accuracy of current patterns of habitat selection. If the boundaries are deemed too large, additional sampling can be undertaken to reduce error in the isodar and thereby reduce the 'confidence intervals' around competing forecasts of future habitat use.

The adaptive landscapes that we display sink with density and shift shapes with changes in habitat composition. Although such density- and frequency-dependent evolution is apparent from models that merge ecological and evolutionary dynamics (e.g., Metz *et al.*, 1996; Geritz *et al.*, 1997; Vincent & Brown, 2005), our theory and results are the first to demonstrate clearly that sinking and shifting adaptive landscapes also depend on the geographical landscape in which they are embedded.

Our models predict, if the increasingly drier climate of Herschel Island (Kennedy *et al.*, 2001) increases the relative abundance of upland xeric tundra, that a greater proportion of the *Lemmus* population will occupy the

dry end of the habitat gradient. The same prediction emerges for the extreme mesic specialist, *Microtus*. Each species, however, can exploit a wide range of habitat-selection strategies biased towards mesic habitat with relatively minor fitness consequences. The same is not true for the xeric specialist, *Dicrostonyx*. On a drying Herschel Island, strategies that depart in either direction from *Dicrostonyx's* increasing, and increasingly narrow, optimal preference for xeric habitat yield demonstrably lower fitness.

An increasing proportion of xeric upland tundra will thus shift the niches of each species towards the dry end of the habitat gradient. But while *Dicrostonyx's* niche narrows, those of both *Lemmus* and *Microtus* will expand (shallow landscapes with weak selection). We can interpret the community consequences from these niche shifts by superimposing each adaptive landscape onto the others. The adaptive landscapes of the two broad-niched mesic specialists become more similar with increased abundance of xeric habitat. We thus anticipate that these species will compete more in future than at present. *Dicrostonyx's* maximum fitness corresponds with rapidly declining fitness by *Lemmus*. Heightened competition between these species is thus unlikely. The adaptive landscape of *Microtus*, on the other hand, bulges outward with each increase in the proportion of dry habitat. Fitness differences between *Dicrostonyx* and *Microtus* strategies will still be substantial on a dry island, but less than those under current conditions.

Our models also harbour important lessons for biologists interested in assessing habitat preferences with techniques such as resource–selection functions (e.g., McLoughlin *et al.*, 2010) that rely on use vs. availability data. Changes in availability alter the optimal strategy of habitat selection. A resource–selection function developed in one environment, or at one time, even if it includes the effects of density (e.g., Fortin *et al.*, 2008), is unlikely to be reliable in another.

The maxima of the adaptive landscapes illustrated here represent the best population strategies of habitat occupation, and not necessarily the best individual strategy (Morris, 2010). The mean fitness in our landscapes corresponds to so-called 'MAXN' strategies (Morris, 2010) that weight the fitness of individuals by the number occupying each habitat. Maximum mean fitness is achieved when individuals undermatch their abundance to the best habitat (Kennedy & Gray, 1993, fewer individuals in the best habitat than expected based on its quality) and thereby increase mean fitness in the best habitat more than they reduce it in the poorer one (Morris *et al.*, 2001). Ideal-free habitat selection (Fretwell & Lucas, 1969), where each individual achieves an equal payoff (Křivan *et al.*, 2008), will necessarily yield lower mean population fitness.

Regardless, individuals still move to maximize fitness, and dispersal thus produces an isodar accurately representing the expected fitness that individuals can achieve through habitat selection. The emergent adaptive landscape should represent reliable fitness expectations associated with changes in habitat composition.

Our models are generally insufficient to assess how changes in habitat quality will influence future strategies of habitat selection. If, however, those changes are similar in all habitats such that the relationships among fitness functions remain constant, then the isodar will be unchanged, and our projections should accurately predict future distributions of individuals. Isodars reflect plastic behaviours to density-dependent differences in habitat quality and often respond quickly to habitat enrichment and changes in predation risk (e.g., Lin & Batzli, 2001, 2004). The rapid response suggests two safeguards to their use in predicting future strategies. (1) An isodar calculated from current patterns of habitat occupation should be a reliable indicator of current differences in habitat quality. (2) Potential future isodars can be inferred from experiments that manipulate habitat characteristics such as productivity and physical structure.

Arctic rodents are particularly prone to multiannual population cycles (but perhaps not in much of northwestern North America; Batzli & Jung, 1980; Reid *et al.*, 1995) and one might wonder whether isodars vary with cycle phase. *Dicrostonyx* isodars at Walker Bay in the central Canadian Arctic appear somewhat different at high vs. low density (D. W. Morris and A. Dupuch, unpublished results), but also appear to be associated with changes in climate rather than simply with changes in density. This pattern is, of course, exactly what one should expect if climate change alters the quality of habitats as well as their frequency.

The shape of the adaptive landscape of habitat selection yields additional insights into the types of patterns that we expect in nature. A relatively flat landscape correlates with slow adaptation towards the optimum distribution of individuals between habitats. The fitness consequences of different strategies are minor, so we should expect to find a relatively broad niched population with a poor fit to the system's isodar. Adaptive landscapes tend to be flatter at some densities than at others, and should produce more variation about the isodar at those densities. Rather than criticize a 'poorly fitted' isodar as a weak representation of habitat choice, it may often be more productively used to visualize a relatively flat adaptive landscape. Oatway & Morris (2007) appear to have stumbled onto an example. Manipulations of meadow-vole densities produced significant isodars in only three of four replicated experiments even though other experiments confirmed that the meadow vole is a density-dependent habitat selector (Lin &

Batzli, 2001; Pusenius & Schmidt, 2002). Oatway & Morris (2007) interpreted their result to reflect 'density vague' habitat selection at low density where the fitness consequences of suboptimal habitat distributions were relatively minor. Their interpretation corresponds exactly with our theory's prediction at low population size.

Now that we know how to infer adaptive landscapes from isodars, can we also use them to gain insights into the cyclic population dynamics of northern herbivores, as well as their collapse (and possible recovery) when faced with climate change? Perhaps. Population cycles occur only for species with suitably high rates of population growth (e.g., $r > 2$ in logistic population growth models, May & Oster, 1976). But as we illustrate here, the mean population growth rate depends on density and on the distribution of individuals among habitats. If the maximum growth rate is different between habitats, as we speculate for *Dicrostonyx* and *Microtus* on Herschel Island, then the directional flow of individuals from high to lower-quality habitat will reduce the mean growth rate and dampen any tendency towards cyclical dynamics. Cycles cannot be damped by habitat selection, however, if all occupied habitats yield similarly high fitness at low density. The diverging fitness functions (as we inferred from *Lemmus*' isodar) act to reduce mean K, and hence the amplitude of cycles, but not the cycles themselves. If our interpretations are correct, then *Lemmus* populations on Herschel Island are likely to cycle around relatively low densities dictated by the high abundance of low-preference xeric habitat on the Island.

Regardless of our speculations, it is nevertheless clear that global warming and other anthropogenic actions are changing habitat, and altering the proportional abundances of habitats, at an unprecedented rate. It is also rather obvious that all organisms require habitat in which to live and replace themselves. Isodars offer special promise not only because they are linked to underlying fitness gradients, but also because they apply to organisms as diverse as fleas (Krasnov *et al.*, 2003), cowbirds (Jensen & Cully, 2005), salmonid fishes (Rodríguez, 1995) and kangaroos (Ramp & Coulson, 2002). It is vitally important that we learn how to use current patterns of habitat use to infer possible future scenarios of species distribution and population dynamics. We suspect that isodars, and more generally theories of adaptive habitat selection, will be crucial to achieving that objective.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. A brief theoretical demonstration of how density, area, and carrying capacity influence habitat-selection strategies through the evolution of a mutant habitat-selecting phenotype.

Table S1. A list and description of the 16 vegetation variables measured at each station and used in the Principal Components Analysis to summarize habitat variation in eight small-mammal sampling plots on Herschel Island, Yukon Territory, Canada. Unless stated otherwise, all 'proportion cover' data represent the proportion of point samples (taken at 1 m distance along a randomly oriented 10 m transect centred on each trapping station) where a particular type of vegetation was recorded.

Figure S1. Ordination graphs from the Principal Components Analysis on habitat variables summarizing 'wet' vs. 'dry' habitats on Herschel Island, Yukon Territory, Canada. Variables correspond to those listed in Table S1 (supporting information).

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