

Climate-induced habitat selection predicts future evolutionary strategies of lemmings

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ABSTRACT

Questions: Can we merge theories of habitat selection with changes in habitat and habitat use to predict future strategies of habitat selection? If so, do changes in the frequency of upland and meadow habitats exploited by two species of lemmings confirm that their strategies of habitat selection have also changed?

Field methods: We measured habitat at 300 permanent stations on 12 study plots in 1996 and in 2010. We classified habitat into upland versus meadow categories and estimated population abundances of the two lemming species in both habitats in eight different years.

Statistical and conceptual methods: Logistic regression, path analysis, isodars, invader strategy landscapes.

Assumptions: Lemmings are ideal density-dependent habitat selectors. Habitat selection strategies vary with density and depend on the frequency of alternative strategies.

Results: Meadow habitat became more frequent while the proportion of upland habitat declined. Habitat selection strategies shifted with changes in habitat even though lemming abundance was lower in warm years than in cool years. Shallow selection gradients, which yield a small fitness advantage for the optimum strategy at low density, become increasingly steep at high densities.

Conclusion: Analysis of altered patterns of habitat selection can forecast future strategies of habitat use with changing climate. But reductions in lemming abundance with global warming portend an increasing role for stochasticity in their future habitat selection.

Keywords: Arctic, climate change, competition, *Dicrostonyx*, evolutionarily stable strategies, isodar, *Lemmus*, path analysis, tundra.

INTRODUCTION

The future of Earth's biodiversity will depend, in large part, on three pressing challenges. The first deals with the ability of species to adapt to rapid environmental change. The second depends on the ability of evolutionary ecologists to predict the future ecological and

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evolutionary dynamics associated with those changes. The third is linked to our collective human interest in applying that knowledge to conservation. Here, we focus on the second of those challenges. We demonstrate how to use theories of habitat selection to forecast species' future evolutionary strategies of spatial distribution under a changing climate.

We apply the models to lemmings because the consequences of global warming are most pronounced at the northern latitudes where these species live (IPCC, 2007). Experiments with arctic plants, for example, reveal rapid increases in growth, as well as changes in species composition, with only a 1–3°C increase in summer temperature (Klady *et al.*, 2011). Meanwhile, the legendary 3–4 year population cycles of lemmings [albeit with prolonged periods of low density linked to climate (Angerbjörn *et al.*, 2001)] appear susceptible to disruption by the timing of snow melt, freeze–thaw cycles, and characteristics of the snow pack (Kausrud *et al.*, 2008; Post *et al.*, 2009). Although we are now aware that climate change might alter the temporal dynamics of lemming populations and their dependent communities, we are generally ignorant about the longer-term effects that climate change may have on their habitat and habitat selection strategies (Krebs, 1964; Rodgers and Lewis, 1986; Pitelka and Batzli, 1993; Morris *et al.*, 2000).

Direct effects of climate on lemming dynamics are questionable, however, because voles continued to cycle in several sites in eastern Finnmark during the recent collapse of lemming cycles (Ims *et al.*, 2011). Questions about climate's influence also arise because lemming cycles appear to have returned in the same areas (Ims *et al.*, 2011), and vole cycles have also returned in southern Finland despite an increasingly milder climate (Brommer *et al.*, 2010). It is thus crucial that we determine whether the direct effects of climate on lemming abundances are modified by indirect pathways linking habitat change with density-dependent habitat preference and spatial distribution. As we do so, we must also begin to develop and test models that evaluate the evolutionary stability of current patterns by predicting the fitness of alternative strategies of habitat selection.

The fitness of most strategies of habitat selection depends not only on the density of competitors, but also on the frequency of alternative strategies (Brown, 1998; Vincent and Brown, 2005). The relative advantages of different strategies can often best be revealed by graphing the adaptive landscape of habitat selection (Morris, 2003a, 2011; Morris *et al.*, 2011). The evolutionary stability of a strategy can then be illustrated by constructing the neighbourhood invasion strategy (NIS) landscape, which graphs the fitness of an individual following a rare strategy as a function of neighbouring resident (common) strategies (Apaloo *et al.*, 2009). When the habitat selection strategy consists of the proportional use (p) of only two alternatives, it is possible to assess a single strategy against all other $0 \leq p \leq 1$ possibilities. More compelling still, if one assumes that a population of habitat selecting individuals can achieve evolutionary stability, it is then possible to draw the NIS landscape from current patterns of habitat selection (Morris, 2011). Tracking those patterns either through time, or with changes in habitat such as those associated with global warming, opens the door for predicting future spatio-temporal dynamics. The predictions will be most reliable when abundant species yield steep fitness gradients. Predictions will be least reliable at low abundance when relaxation of density-dependent competition allows stochastic effects to exert their greatest influence.

Accumulating evidence documents that stochastic influences on population dynamics, such as those caused by climatic variation, act on populations through both direct and delayed density-dependent processes (e.g. Wang *et al.*, 2011). Climatic variability that lowers a habitat's carrying capacity magnifies the effects of density dependence on population dynamics (Wang *et al.*, 2006). Correlations between demography and climatic variation might

also appear simply because unstable systems lack direct density-dependent feedback in response to environmental stochasticity (Wang *et al.*, 2011). Less appreciated, perhaps, are the differential effects that climate-induced environmental stochasticity can evoke on habitat quality and habitat selection (Morris, 2003b, 2004; Schreiber, 2012). If changing climate alters the quality and distribution of habitats, then one can safely assume that the dynamics of species depending on those habitats will be affected, as will their evolutionary trajectories of habitat use. The interaction between abundance and habitat change may be amplified in open populations where individuals disperse among habitat patches varying in density and fitness prospects.

The important point is that the effects of climate change transcend direct impacts on population dynamics and habitat. Thus, we must first differentiate the relative magnitudes of direct climate-mediated influences on a species' dynamics from those caused by habitat change and its associated indirect effects on habitat selection and species interactions. We use data collected over a 16-year interval to evaluate each possibility.

We begin by demonstrating how to reveal global invasion strategy landscapes for habitat choice by ideal habitat selectors. We then use our 16-year data set to demonstrate how one can apply the theory to predicting the future evolutionary strategies of habitat selection by lemmings. We partition our empirical work into six steps (for a description of each step in detail, see the online Appendix at evolutionary-ecology.com/data/2786Appendix.pdf):

1. Summarize covariation in climate variables near our study site.
2. Use the summary to investigate which components of climate are changing through time.
3. Determine whether lemming abundance and the composition and classification of habitat also varied predictably through time.
4. Document habitat change on each of our study plots by contrasting habitat measurements made in 1996 with an otherwise identical set measured in 2010.
5. Evaluate whether patterns and processes of density-dependent habitat selection by the two lemming species changed between 1996 (Morris *et al.*, 2000) and 2010–2011.
6. Assess the relative contributions of climate, habitat change, and competition to the changing habitat preferences of lemmings.

We then evaluate the evolutionary implications of changes in habitat selection on lemming dynamics, as well as the short- and long-term consequences of climate change to arctic ecosystems. We conclude by identifying some of the crucial gaps in knowledge that require further research.

CONSTRUCTING GLOBAL-INVADER LANDSCAPES FOR DENSITY-DEPENDENT HABITAT SELECTION

We imagine that an individual can freely establish itself in a single habitat i , and that population growth obeys Ricker's (1954) equation:

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

where N represents the density of individuals in habitat i at times t and $t + 1$ respectively, r is the maximum instantaneous rate of population growth, and K is the habitat's

carrying capacity. This equation yields the per capita population growth rate (our estimate of fitness)

$$\ln(N_{i(t+1)}) - \ln(N_{i(t)}) = r_i - \frac{r_i}{K_i} N_i.$$

Under ideal habitat selection, the growth rates in two occupied habitats are equal, thus

$$N_2 = \frac{r_2 - r_1}{r_2} K_2 + \frac{r_1 K_2}{r_2 K_1} N_1 \quad (2)$$

represents the system's isodar (Morris, 1988, 2003a), the set of densities in the two habitats which equalizes fitness between them at any population size. We use our understanding of natural history to estimate r_2 and K_2 [the technique is robust to errors in parameter estimates (Morris *et al.*, 2011)]. Recalling that the isodar is the solution to ideal habitat selection and fits the general model of a linear equation, $N_2 = C - bN_1$, we use the intercept to calculate $r_1 = r_2 - \frac{Cr_2}{K_2}$, then, knowing r_1 , we use the isodar slope to calculate $K_1 = \frac{r_1 K_2}{r_2 b}$. With all parameters estimated, we can now calculate the expected fitness of an individual using any possible strategy of habitat selection across a range of population sizes, determine the fitness expected by an individual following the alternative IFD strategy, and plot the resulting data as a three-dimensional invader strategy landscape (Apaloo *et al.*, 2009) (see, for example, Fig. 5).

MATERIALS AND METHODS

We live-trapped two species of lemmings (*Dicrostonyx groenlandicus* and *Lemmus trimucronatus*) in twelve 60 m × 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 eight different years (1996, 1997, 1999, 2004, 2007, 2009, 2010, and 2011). We oriented grids to represent the local availability of sedge-dominated (*Carex* spp.) meadows and upland hummock habitat (covered with *Dryas integrifolia* and *Salix arctica*) that characterize tundra in the Walker Bay landscape. We estimated each species' abundance separately for each grid, habitat, 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 per station).

We documented climate change with eight climatic variables from the Cambridge Bay airport (operating from 1950 until present and located approximately 150 km northeast of Walker Bay; http://climate.weatheroffice.gc.ca/climateData/canada_e.html). We summarized the common variation among variables with principal components analysis (PCA), and rotated the components (varimax) to obtain the most parsimonious interpretation of underlying climatic variation.

To assess whether habitat changed through time, we compared the habitat variation that we measured at all 300 permanent sampling stations during June 2010 with the same 13 variables used by Morris *et al.* (2000) to classify habitat in 1996 (Table A1 in the online Appendix provides a full list of variables and their description). We used the comparison to calculate a 'habitat-change index' [HCI, the number of meadow stations on a grid in 2010 minus the number in 1996 (Morris and Dupuch, 2012)]. A value of zero on the habitat-change index

corresponds to no change (the same number of meadow versus upland stations, but not necessarily identical meadow and upland stations), whereas a positive value indicates that a grid comprised more meadow stations in 2010 than in 1996; negative values represent grids that included more upland.

We assessed whether the pattern and density dependence of habitat selection changed between the beginning (1996) and end of our study (2010 and 2011 combined) by contrasting the 1996 habitat isodar generated for lemming abundances by Morris *et al.* (2000) with a new one based on the 2010 habitat classification and 2010–2011 abundances. We assessed whether changes in lemming habitat occupation depended directly on climate, or were better explained by climate's impact on changes in habitat or total lemming abundance. We used these patterns to inform hypotheses on the potential set of cause-and-effect relationships responsible for lemming habitat selection. We identified the most parsimonious of these alternatives with structural equation modelling (path analysis). We reasoned that if climate change impacted lemming habitat selection directly, then there should be a strong association between climatic variables and the abundance of lemmings in their preferred habitat and, at best, weak 'residual' associations with habitat change and variation in the total number of lemmings. If so, then future strategies of habitat selection would depend only on climate change. Indirect effects, however, would be revealed by significant relationships between relative habitat occupancy and both habitat change and the total number of lemmings. These indirect effects would implicate density-dependent habitat selection and thereby validate our use of isodars to forecast the fitness of alternative habitat selection strategies.

RESULTS

Most of the variation (84%) in climatic variables was summarized by four principal components (PCs; Table 1). PC2 and PC3 increased significantly over the past 56 years (see online Appendix), as did mean annual temperature (Fig. 1). Coincident with the changes in climate, a quarter of our 300 permanent sampling stations ($n = 76$) were classified differently by a discriminant function analysis in 2010 than in 1996 (the classification of 51 stations changed from upland to meadow; 25 changed from meadow to upland; 7 of the 12 study grids included more meadow habitat; see online Appendix, Fig. A1). The tundra at

Table 1. Varimax rotated principal component (PC) coefficients of eight climate variables collected at Cambridge Bay (northern Canada) from 1956 to 2011

Variables	PC1	PC2	PC3	PC4
Onset of winter	-0.94	-0.08	-0.21	0.03
Duration of winter	0.87	0.35	0.13	-0.01
Total snowfall (cm)	0.56	0.23	-0.42	0.09
Snow depth at the end of May (cm)	0.11	0.96	-0.03	0.05
Mean snow depth (cm)	0.46	0.80	0.09	-0.03
Summer temperature (°C)	0.28	-0.06	0.85	-0.09
Annual temperature (°C)	-0.05	0.14	0.84	0.19
Total rainfall (mm)	0.01	0.01	0.06	0.99

Note: The four PCs explain 28%, 22%, 21%, and 13% (a total of 84%), respectively, of the common variation in climate. Values in **bold** type signify the major variables contributing to each PC.

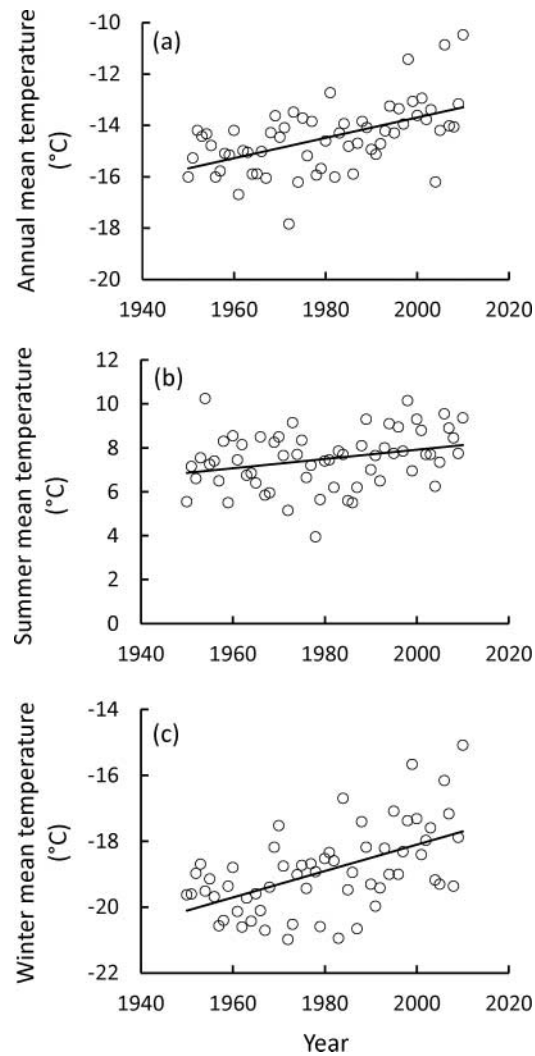


Fig. 1. Annual (a), summer (b), and winter (c) mean temperature from 1950 to 2011 at Cambridge Bay, Nunavut. Annual temperature: Pearson correlation = 0.55, $P < 0.001$, $n = 62$. Summer temperature: Pearson correlation = 0.33, $P = 0.09$, $n = 62$. Winter temperature: Pearson correlation = 0.58, $P < 0.001$, $n = 62$.

Walker Bay in 2010 was composed of significantly more meadow habitat than it was only 14 years earlier (see online Appendix, Fig. A2).

Lemming abundances varied dramatically from year to year with high numbers in 1996 and 2011 (Table 2). Despite the 50-fold variation in abundance through time, approximately 50% of the observed spatial variance was accounted for by density-dependent habitat selection (Table 3, Fig. 2). Isodars for both species in 2010–2011 included only intra-specific competition, whereas inter-specific interactions dominated those calculated from the 1996 data (Morris *et al.*, 2000) (Fig. 2).

Table 2. Total number of different individuals captured and relative abundance (number of individuals per station) of two lemming species (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) living in hummock and meadow habitats in 12 grids at Walker Bay (Nunavut, Canada) in early summer during eight years between 1996 and 2011

Years	Number of different individuals caught						Relative abundance					
	<i>Dicrostonyx</i>			<i>Lemmus</i>			<i>Dicrostonyx</i>			<i>Lemmus</i>		
	Hummock	Meadow		Hummock	Meadow		Hummock	Meadow		Hummock	Meadow	
1996	114	36		48	95		0.80	0.27		0.31	0.63	
1997	8	5		0	0		0.05	0.04		0.00	0.00	
1999	54	32		7	9		0.33	0.23		0.05	0.06	
2004	49	50		14	35		0.47	0.28		0.16	0.17	
2007	14	13		7	4		0.15	0.08		0.05	0.02	
2009	3	2		1	2		0.02	0.02		0.04	0.01	
2010	32	17		45	40		0.25	0.14		0.38	0.22	
2011	110	94		43	36		0.92	0.62		0.40	0.21	

Table 3. Summaries of habitat isodars evaluating density-dependent habitat selection of meadow and upland habitats by *Dicrostonyx groenlandicus* and *Lemmus trimucronatus* occupying a tundra mosaic at Walker Bay in northern Canada during 2010–2011

Species	95% confidence interval		R^2 adj.	F	P
	Intercept	Slope			
<i>Dicrostonyx</i> ($n = 21$)					
Du = 0.19 + 0.94 Dm	0.05 to 0.29	0.69 to 1.29	0.54	25.01	<0.001
<i>Lemmus</i> ($n = 22$)					
Lm = 0.02 + 0.52 Lu	-0.06 to 0.07	0.37 to 0.73	0.42	16.07	<0.001

Note: Du = *Dicrostonyx* abundance in upland, Dm = *Dicrostonyx* abundance in meadow, Lu = *Lemmus* abundance in upland, Lm = *Lemmus* abundance in meadow [analysis by geometric mean regression; Package 'lmodel2' (Legendre, 2008)].

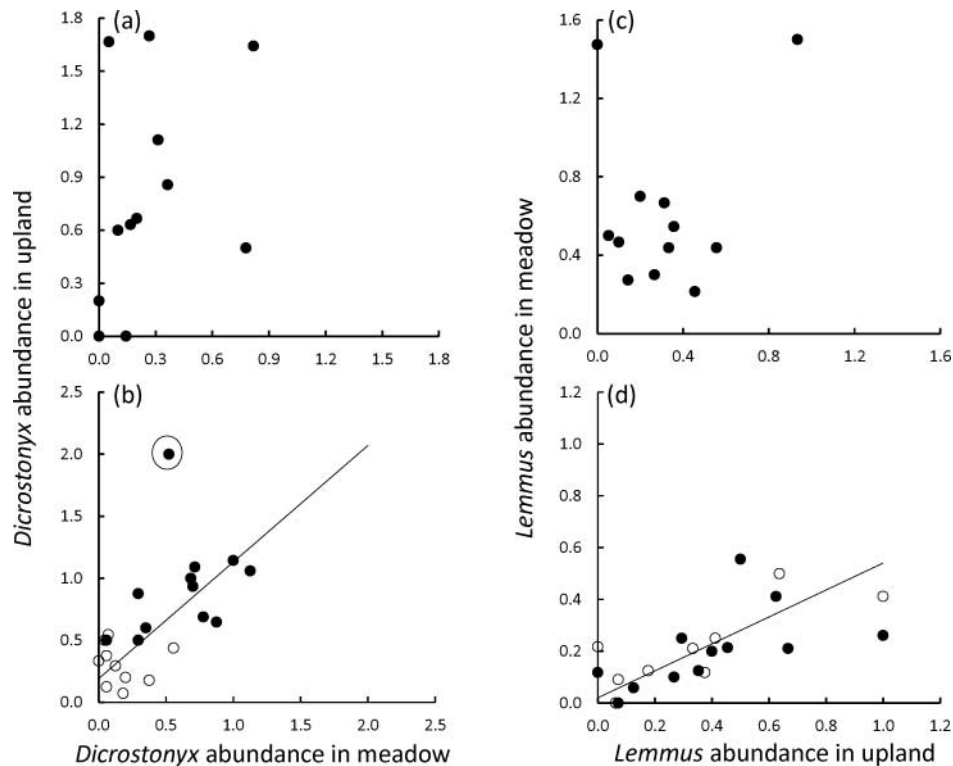


Fig. 2. The *Dicrostonyx* (a, b) and *Lemmus* (c, d) isodars comparing abundances in preferred versus secondary habitats in 12 tundra grids at Walker Bay in the central Canadian Arctic in 1996 (a and c) and 2010–2011 (b and d). In (b) and (d), open circles represent the 2010 data and closed circles the 2011 data. The circled point in (b) represents an outlier not included in the 95% confidence interval of the model. The lack of fit in the 1996 isodars occurred because habitat selection was caused by inter-specific, rather than intra-specific, competition (Morris *et al.*, 2000).

Table 4. Results of the most parsimonious models [lowest AIC_c (Burnham and Anderson, 2002)] evaluating the effects of climate change (PC scores), habitat change (habitat change index; HCI), and competition on the presence/absence (logistic regression) and abundance (multiple linear regression) of *Dicrostonyx groenlandicus* and *Lemmus trimucronatus* in their preferred habitat at Walker Bay (northern Canada, Nunavut) in 1996, 1997, 1999, 2004, 2007, and 2009–2011

	<i>n</i>		Estimate (± s.e.)	<i>Z</i>	<i>P</i>
<i>Presence/absence of Dicrostonyx in upland</i>					
Model	96				
Dm			1.12 (0.45)	2.51	0.012
<i>N</i>			1.22 (0.46)	2.64	0.008
<i>Presence/absence of Lemmus in meadow</i>					
Model	96				
Dm			−3.74 (1.05)	−3.55	<0.001
PC1			2.09 (0.73)	2.88	0.004
<i>N</i>			7.32 (1.74)	4.21	<0.001
	<i>n</i>	<i>R</i> ² adj.	Estimate (± s.e.)	<i>F</i>	<i>P</i>
<i>Dicrostonyx abundance in upland</i>					
Model	51	0.74		49.22	<0.001
Lm			−0.26 (0.05)	24.40	<0.001
HCI			0.09 (0.04)	5.90	0.019
<i>N</i>			0.56 (0.05)	111.93	<0.001
<i>Lemmus abundance in meadow</i>					
Model	51	0.55		31.88	<0.001
PC1			0.08 (0.03)	5.38	0.024
<i>N</i>			0.18 (0.03)	30.69	<0.001

Note: Dm = *Dicrostonyx* abundance in meadow, Du = *Dicrostonyx* abundance in upland, Lm = *Lemmus* abundance in meadow, *N* = total lemming abundance.

Our analyses of the effects of climate change on lemming distribution and abundance differed between species. The presence and abundance of *Dicrostonyx* in its preferred upland habitat varied with the total number of lemmings, and its abundance also depended on habitat change (Table 4). The presence and abundance of *Lemmus* in its preferred meadow, however, depended on the total number of lemmings and climate rather than on habitat change (Table 4).

The impact of climate occurred mainly through its strong effect on the total number of lemmings sharing sample grids (Table 5). Climate alone, despite inherently stochastic variation, accounted for 37% of the observed variance in the total number of lemmings on a census grid. Total lemming numbers increased in years following severe winters (PC1) with high accumulations of snow (PC2). Total lemming numbers were less in warm than in cold years (PC3).

The pattern of potential effects yielded a rather complicated set of potential pathways leading from climate change to changes in the proportional occupation of upland habitat by *Dicrostonyx* (Fig. 3). Our path analysis revealed a much simpler structure that accounted

Table 5. Summary of the effects of climate change (PC scores) and habitat change (habitat change index; HCI) on the total number of two species of lemmings sharing a sample grid at Walker Bay, Nunavut, Canada (analysis by multiple linear regression)

Variables	Estimate (\pm s.e.)	R^2 adj.	d.f.	F	P
Model		0.37	5,45	6.95	<0.001
HCI	0.05 (0.04)			1.74	n.s.
PC1	0.26 (0.05)			21.71	<0.001
PC2	0.21 (0.07)			8.70	0.005
PC3	-0.11 (0.05)			5.85	0.019
PC4	-0.10 (0.07)			2.07	n.s.

for 79% of the difference in *Dicrostonyx* abundance in its preferred upland habitat between the two high-density years (Fig. 4). We did not construct pathways for *Lemmus* because habitat change had no effect on its distribution or abundance.

According to the path analysis, increased *Dicrostonyx* abundance in meadow caused a direct increase in *Dicrostonyx* abundance in upland (Fig. 4, vertical arrow from ΔDm to ΔDu). This direct competitive effect was reinforced by an increasingly meadow-dominated tundra landscape (HCI) that appears to reduce the habitat options for *Dicrostonyx* (diagonal arrow from HCI to ΔDu). But the positive influence from habitat change is mostly neutralized by an indirect effect mediated through reduction of *Dicrostonyx* abundance in meadows (diagonal arrow from HCI to ΔDm ; reduced intra-specific competition). Intra-specific competition for habitat increases, however, with the change in total lemming abundance (diagonal arrows from ΔN to ΔDm and ΔDu). The emergent and important consequence is that, although climate change modified habitats, its main effect on *Dicrostonyx* distribution occurred indirectly through density-dependent habitat selection.

The density-dependent fitness consequences of habitat selection are revealed by the global invader landscape at Walker Bay (Fig. 5). Adaptation by either species towards its optimum habitat selection strategy is weak along shallow selection gradients (low valleys) when populations are small, but strengthens with increasing population size (steep gradients and deep fitness valleys). Selection gradients for *Dicrostonyx* warp from pure (but shallow) preference of upland at very low densities to increasing use of meadow habitat at high density [the landscape is tilted imperceptibly towards upland at very low density where the small but positive *Dicrostonyx* isodar intercept (Table 3) reveals a minor fitness advantage in that habitat]. The depth of selection gradients for *Lemmus* also varies with density, but the strategy of habitat selection (proportional occupation of upland) remains constant (isodar intercept not different from zero, slope <1; the valley of low fitness tracks along a single strategy at all population sizes).

DISCUSSION

The future of habitat selection

Shallow fitness gradients at low density, together with the negative relationship between temperature and lemming abundance, suggest an increasing role for stochasticity in future

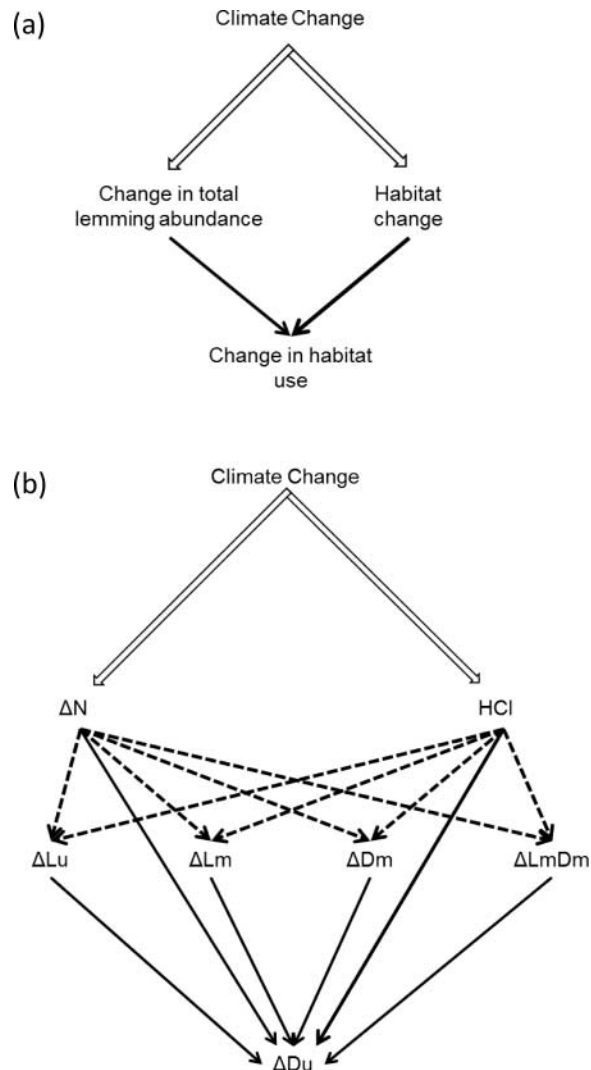


Fig. 3. Hypotheses on the role of climate and habitat change on lemming habitat use. (a) A generic outline of causal paths connecting climate change with habitat change, lemming dynamics, and habitat selection. (b) Diagram of potential direct (solid arrows) and indirect paths (dashed arrows) implicating climate change in the central Canadian Arctic on differences in the abundance of *Dicrostonyx* in its preferred upland habitat between 1996 and 2011. Double arrows represent the direct effects of climate change on habitat change and lemming dynamics, respectively. HCl = habitat change index, Δ = value in 2011 minus the value in 1996, N = total lemming abundance on a grid, Dm = *Dicrostonyx* abundance in meadow, Du = *Dicrostonyx* abundance in upland, Lu = *Lemmus* abundance in upland, Lm = *Lemmus* abundance in meadow, $LmDm$ = standardized interaction between *Lemmus* and *Dicrostonyx* in meadow.

habitat selection strategies by lemmings. As the Arctic warms and lemming numbers decline, evolution will occur along the flat sections of the invader landscapes where natural selection has limited strength to guide strategies towards their optimal value. These effects

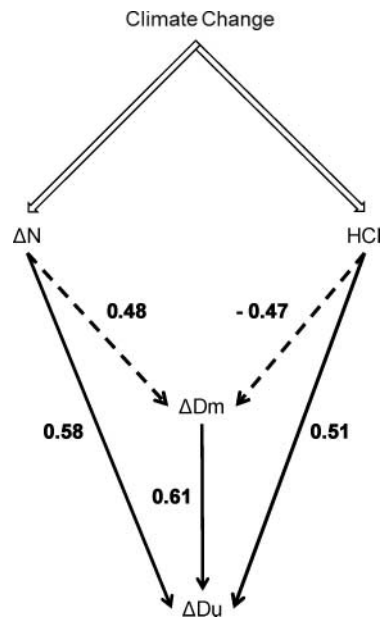


Fig. 4. Indirect effects of climate change on differences in the abundance of *Dicrostonyx* in its preferred upland habitat between 1996 and 2011 revealed by path analysis. Double arrows represent the direct effects of climate change on habitat change and lemming dynamics, respectively. Solid and dashed arrows signify direct versus indirect paths as in Fig. 3. Path coefficients are indicated in **bold**. HCI = habitat change index, Δ = value in 2011 minus the value in 1996, N = total lemming abundance on a grid, Dm = *Dicrostonyx* abundance in meadow, Du = *Dicrostonyx* abundance in upland.

may be tempered by climate-induced reductions in abundance that cause the fitness landscape to sink and thus compress fitness gradients to zones of lower density. Although this process can be expected to retain much of the landscape's original shape, mean fitness and carrying capacity decline as the landscape subsides, and so too does the fitness advantage of individuals obeying the ideal-free strategy (a shorter and thus shallower fitness valley). The net effect is reduced mean population size with increased opportunity for stochastic processes to influence lemmings' niche construction (Odling-Smee *et al.*, 2003). Faced with increased stochasticity, selection may fail to rescue sub-optimal strategies drifting away from evolutionary stability. We can thus conclude that, at least during early summer for lemmings at Walker Bay, continued climate change will have pervasive, quick influences on lemming dynamics and the relative quality of their habitats, as well as short- and long-term effects on lemming distribution.

Indeed, analyses of 61 time series representing 35 different species of northern mammals showed that the high dependence of small-mammal dynamics on environmentally stochastic events, such as climatic variability, is related to both direct and delayed density-dependent regulation (Wang *et al.*, 2011). This conclusion mirrors the results of our path analysis, which suggested that changes in the abundance of *Dicrostonyx* in its preferred upland habitat were caused by both direct effects of habitat change as well as indirect effects mediated through changes in its abundance in meadows.

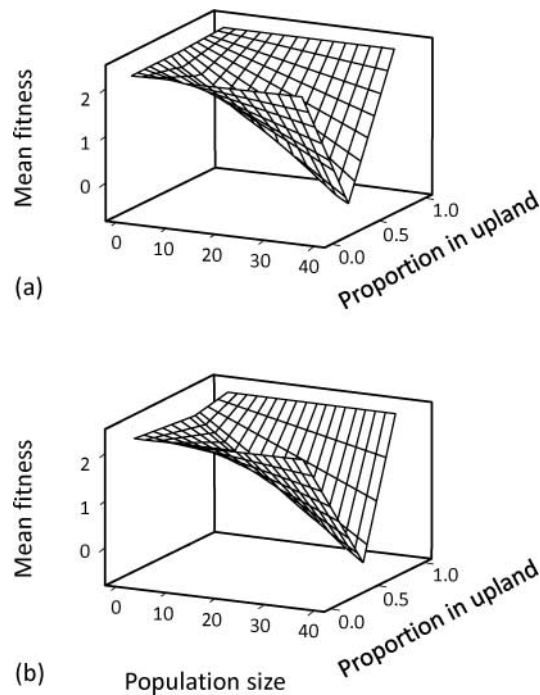


Fig. 5. Global invader landscapes of habitat selection posited for different strategies of habitat occupation by *Dicrostonyx* (a) and *Lemmus* (b) at Walker Bay, Nunavut, Canada. Landscapes are based on habitat isodars calculated from the abundance of each species in upland versus sedge-dominated meadow tundra in 2010–2011 and assume logistic population growth. *Dicrostonyx* females were assumed capable of producing three litters each with four offspring annually at Walker Bay [estimates from Morris *et al.* (2011), assumes overwinter reproduction (Millar, 2001), approximately 12% of all 2011 *Dicrostonyx* captures were juvenile], whereas *Lemmus* was assumed to produce two litters with five offspring (no overwinter reproduction, no juveniles captured in 2011). Carrying capacity for *Lemmus* in meadow was set arbitrarily at 10. The carrying capacities for *Dicrostonyx* were adjusted such that the cumulated carrying capacity in both habitats was equal for both species (ensures that the two landscapes possess similar scales with population size).

Connection to global warming

We suspect that changes in lemming abundance and habitat use are more global than regional responses to climate and habitat change. Our observations of increasing mean annual temperature are consistent with global warming's purported effects on plant growth and vegetation change. Studies of large-scale habitat change document increased 'greening' (Fraser *et al.*, 2011) and productivity (Gauthier *et al.*, 2011) in northern Canada, as well as expanding shrub cover in arctic landscapes (Sturm *et al.*, 2001, 2005). This result is corroborated by recent increases in the normalized difference vegetation index (NDVI), a measure of vegetation productivity often linked to shrub cover and growth (Tape *et al.*, 2006; Bhatt *et al.*, 2010).

The increase in meadow habitat at Walker Bay is also consistent with global patterns. Wet graminoid-dominated vegetation has increased through permafrost thawing in sub-arctic Sweden (Christensen *et al.*, 2004; Malmer *et al.*, 2005). Rising lake levels and increases in the number

and size of ponds during initial phases of warming in permafrost environments (Smith *et al.*, 2003; Walter *et al.*, 2006) are similarly consistent with the perspective that permafrost degradation leads to wet landscapes. Although the responses to permafrost melting tend to be somewhat unpredictable (e.g. Rowland *et al.*, 2010), thawing of near-surface ice increases the moisture content of soil in the active layer above the permafrost (Mackay, 1995; Kokelj and Burn, 2003). Increased moisture content might thereby create more meadow habitat, but perhaps habitat that is too wet for lemmings.

Our analyses also suggest that climate, acting as an exogenous variable, drives the generally synchronous abundance of lemmings (Krebs *et al.*, 2002). Lemming numbers at Walker Bay were highest following severe winters with heavy snowfalls, a pattern that is consistent with their extraordinary ability to reproduce over winter when conditions are favourable (Millar, 2001; Ims *et al.*, 2011). Changing climate has also been inferred to be the ultimate factor associated with fading lemming cycles in southern Norway during the interval from the late 1980s to 2007 (Ims *et al.*, 2008; Kausrud *et al.*, 2008), and during the early to mid 2000s in Greenland (Gilg *et al.*, 2009).

There are insufficient data to speculate on whether general patterns in lemming population dynamics at Walker Bay have been impacted by changing climate. The high densities that we observed in 1996 and 2011, followed by spectacular population crashes in 1997 and 2012 [when only eight lemmings were captured with the same effort as in other years (unpublished data)], nevertheless document highly fluctuating populations consistent with the historical 3–5 year lemming cycles in the Walker Bay area (e.g. Predavec *et al.*, 2001; Krebs *et al.*, 2002). Even if the dynamics are similar to historical trends, the competitive interactions determining habitat use in 2010–2011 were different from those observed during a previous peak in lemming abundance in 1996 by Morris *et al.* (2000).

Implications for arctic ecosystems

The strong connections among climate, lemming dynamics, habitat selection strategies, and competitive interactions are likely to modify the evolution of habitat preference, and thereby vary the feedback from lemmings onto plant communities (Olofsson *et al.*, 2009). The resulting habitat-dependent differences in ecosystem function (Johnson *et al.*, 2011) herald significant changes in arctic ecosystems associated with climate change (Gilg *et al.*, 2009; Gauthier *et al.*, 2011; Krebs, 2011). However, it is too early to speculate on how habitat-dependent differences in the distribution and abundance of lemmings might affect other species in terrestrial arctic food webs. We can anticipate, nevertheless, that lemmings' numerous predators will also vary their use of habitats with changes in lemming habitat selection. Both processes are likely to influence predators' functional responses to prey abundance as they encounter varying numbers of prey in different habitat patches. The potential for such effects to create feedback (Post and Palkovacs, 2009) onto the dynamics of predator–prey interactions suggests two profitable avenues for future research. First, we need to evaluate whether the two lemming species differ in their habitat-dependent responses to predation risk. Second, we need to know whether predator patch use and diet also vary with habitat and climate change.

There is also much pressing work for others whose model systems do not include lemmings. Despite decades of theory on evolutionarily stable strategies, there is a dearth of experimental evidence. Isodars, for example, represent the evolutionarily stable solution to density-dependent habitat selection, but most field studies assume, rather than test, their veracity. When true, we can predict the current selective advantage of ideal habitat selectors

over alternative strategies. Those predictions do not explain why isodars can change so dramatically through time. In the case of lemmings, is it simply because their abundance, or at least that of *Lemmus*, is linked to climate change? Or does habitat selection emerge from more subtle processes that tie habitat preference to less perceptible changes in productivity, resources, habitat physiognomy, and species interactions? Regardless of the answers, there is a clear urgency to find them.

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