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Patch use and vigilance by sympatric lemmings in predator and competitor-driven landscapes of fear

Angélique Dupuch · Douglas W. Morris ·
William D. Halliday

Abstract Prey living in risky environments can adopt a variety of behavioral tactics to reduce predation risk. In systems where predators regulate prey abundance, it is reasonable to assume that differential patterns of habitat use by prey species represent adaptive responses to spatial variation in predation. However, patterns of habitat use also reflect interspecific competition over habitat. Collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus trimucronatus*) lemmings represent such a system and possess distinct upland tundra versus mesic meadow habitat preferences consistent with interspecific competition. Yet, we do not know whether this habitat preference might also reflect differences in predation risk or whether the two species differ in their behavioral tactics used to avoid predation. We performed experiments where we manipulated putative predation risk perceived by lemmings by increasing protective cover in upland and meadow habitats while we recorded lemming activity and behavior. Both lemming species preferentially used cover more than open patches, but *Dicrostonyx* was more vigilant than *Lemmus*. Both species also constrained their activity to protective patches in upland and meadow habitats, but during different periods of the day. Use of cover and vigilance were independent of habitat,

suggesting that both species live in a fearsome but flattened landscape of fear at Walker Bay (Nunavut, Canada), and that their habitat preference is a consequence of competition rather than predation risk. Future studies aiming to map the contours of fear in multi-prey–predator systems should consider how predation and competition interact to modify prey species' habitat preference, patch use, and vigilance.

A. Dupuch
Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, Ripon, QC J0V 1V0, Canada

A. Dupuch · D. W. Morris (✉)
Department of Biology, Lakehead University, Thunder Bay, ON P7B 5E1, Canada
e-mail: Douglas.Morris@lakeheadu.ca

W. D. Halliday
Department of Biology, University of Ottawa, Ottawa, ON K1N 6N5, Canada

Introduction

Prey living in risky environments can draw on a retinue of adaptive behaviors in order to balance the conflicting demands of securing resources while evading predators. Individual responses typically include a combination of tactics ranging from time allocation, habitat preference, apprehension (including vigilance), and foraging tenacity (Brown and Kotler 2004). Prey individuals should, ceteris paribus, avoid times, habitats, and patches when and where predation risk is highest. Predation risk depends on the spatial distribution of foraging patches and how well those patches correspond with the abundance, lethality, movement, and activity of predators. For instance, if patches are small relative to the movements of predators, then fine-grained use of those patches by predators might equalize risk across space. If so, any reduction in risk to prey will need to occur through reduced foraging, increasing vigilance, or foraging at times when predators are least effective, rather than through differential patch use. Changes in prey vigilance and time allocation will cascade onto the predator's use of individual patches (Brown et al. 1999; Brown and Kotler 2007), but not necessarily onto its use of different patch types.

Risk also depends on the state of foragers. Desert gerbils, for example, prefer safe foraging patches over risky ones

(Kotler et al. 1991, 1992; Kotler 1997). Moreover, foraging behavior over the lunar cycle determines the energetic state of gerbils that is at its lowest ebb during the full moon. Consequently, gerbils forage with more apprehension in order to rebuild their energetic state (Kotler et al. 2010). Similarly sophisticated behavioral responses to predators and predator distribution are widespread among taxa and ecosystems (e.g., Werner et al. 1983; Grand and Dill 1997; Morris 2005a, b; Hammond et al. 2007; Heithaus et al. 2007; Dupuch et al. 2009).

Risk management through patch use and habitat selection is so pervasive that it is often reasonable to assume that differential patterns of habitat use by prey species represent adaptive responses to spatial variation in predation and particularly so in systems where predation is thought to regulate prey abundance. The distribution and abundance of prey in such fearful systems correlate with the spatial map of their underlying landscape of fear (Brown et al. 1999; Laundré et al. 2001, 2010) where they trade-off food for safety (Brown and Kotler 2004; van der Merwe and Brown 2008). Estimates of time allocation, vigilance, and harvest rates can be integrated to measure the peaks and valleys in prey species' landscapes of fear (Laundré et al. 2001, 2010). Such maps are likely to be complicated, however, whenever space use also reflects density-dependent interspecific competition for habitat. Increased prey density can alter trade-offs between food and safety in a variety of ways. Resource depletion, for example, can be expected to increase the marginal fitness value of food and in turn to alter vigilance level and harvest rates (Brown 1999). An assessment of predation risk via vigilance and harvest rates will thus include the competitive effect.

Risk can be increased if more prey attract predators or if competing prey species themselves pose a risk (Morris 2009). Risk can also be diluted at higher prey densities through a variety of mechanisms including an increase in the probability of predator detection (Pulliam 1973), dilution of risk amongst more individuals (e.g., Roberts 1996), or the likelihood that sated predators kill a smaller proportion of prey (Krause and Ruxton 2002). Assessments of such risks are likely to be confounded when prey interfere with one another. In this scenario, the risk of injury and the costs of defense against such injuries are directly attributable to the competing species and not to predators. It may thus be necessary to control for competitive effects while assessing risk management, or when mapping the landscape of fear in a predator–prey system where two or more sympatric prey species compete for habitat, and particularly so when one species is dominant over another. Collared (*Dicrostonyx groenlandicus*) and brown (*Lemmus trimucronatus*) lemmings appear to represent such a system.

Lemmings are notorious for their multi-annual cycles that appear tied to, if not driven by, density-dependent predation by both specialized and generalist predators (e.g., Wilson et al.

1999; Gilg et al. 2003; Gauthier et al. 2004, 2009; Krebs 2011; Legagneux et al. 2012; it is not clear, however, whether predators regulate lemming populations (e.g., Oksanen 1983, 2008, 2009). Collared and brown lemmings are similarly well known for their distinct upland tundra versus mesic meadow habitat preferences (Watson 1956; Krebs 1964; Batzli et al. 1983; Rodgers and Lewis 1986; Batzli 1993; Pitelka and Batzli 1993) that nevertheless deteriorate with increasing density (Morris et al. 2012) and are determined in part by interspecific interference competition (Morris et al. 2000). But we do not know whether the habitat preferences might also reflect differences in predation risk (the landscape of fear), whether the two species differ in their ability to reduce risk, or whether they differ in the relative importance of different behavioral tactics used to avoid predation.

Thus, we describe experiments where we manipulated putative predation risk perceived by lemmings by increasing protective cover in upland and meadow habitats while we recorded lemming activity and behavior. We begin by describing our study system in the Canadian Arctic, how we altered cover, and how we recorded lemming behavior. We analyze for differences in time allocation and vigilance between the lemming species and between habitats. We conclude by discussing the possible effects of habitat and prey behavior on the dynamics of these keystone (Krebs 2011) arctic herbivores and, more generally, what lessons they reveal about prey living in fearful landscapes.

Material and methods

Study area

We conducted experiments at Walker Bay, located on the Kent Peninsula, Nunavut, Canada (68°21′N; 108°05′W), during two annual field trips (June–July 2010 and 2011). The relatively flat landscape at Walker Bay is characterized by a mosaic of xeric upland hummocks dominated by *Dryas integrifolia* and *Salix arctica*, to mesic sedge-covered (*Carex* spp.) meadows. *Dicrostonyx* and *Lemmus* abundances were relatively high in both habitats in 2010 and peaked in 2011 (Table 1; see Morris and Dupuch (2012) for details on estimating lemming abundance).

Experimental design

We randomly allocated pairs of experimental patches (distance between patches in each pair=2 m) within 5 m of each of 16 live trap stations (two patches at each of eight stations each year) with signs of rodent activity (active burrows and runways, fresh latrines, and lemming sightings/ captures). We used quiet digital trail cameras equipped with

Table 1 Relative abundance (number of different individuals captured·station^{-1}) of *Dicrostonyx* and *Lemmus* in upland and meadow habitats evaluated by live trapping in 12 control plots at Walker Bay (Nunavut, Canada) in 2010 and 2011

Year	Relative abundance			
	Dicrostonyx		*Lemmus*	
	Upland	Meadow	Upland	Meadow
2010	0.25	0.14	0.38	0.22
2011	0.92	0.62	0.40	0.21

infrared motion detectors (model PC90, Reconyx, Holmen, Wisconsin) to evaluate vigilance and patch use by *Dicrostonyx* and *Lemmus*. Patch size corresponded to the 40° field of view exposed by two cameras located approximately 1 m apart and set at right angles to record a sequence of photographs (three in 2010 and two in 2011). We placed the cameras in the field 20–22 h before the beginning of the experiment so that lemmings could acclimate to their presence. We studied time allocation in both lemming species by calculating diel activity and the intensity of patch use (the mean number of image sequences per camera during which *Lemmus* or *Dicrostonyx* was clearly identified in at least one photograph). We estimated vigilance by counting the number of sequences where individuals were in an upright or head-up alert posture (Electronic supplementary resource 1). The vast majority of images revealed no awareness of the camera or its operation.

Cover supplied by upright willows, such as *Salix lanata* and *Salix richardsonii*, is an important habitat characteristic determining *Dicrostonyx* and *Lemmus* microhabitat use (supposedly because it reduces predation risk, Predavec and Krebs 2000; Morris and Dupuch 2012). We therefore manipulated the putative predation risk perceived by lemmings by creating a cover treatment. We placed a 0.5-m-high hexagonally shaped tent (six 1-m-long sides) covered with shade cloth over one of the two sets of cameras at each sampling station. The tent had no effect on the resolution, field of view, or operation of the cameras. We placed the tent over one of the two adjacent patches for 48 h and then switched it to the opposing patch for the following 48 h (including the acclimation period, cameras were thus located at each sampling station for a total of 5 days). This reversal of the cover treatment between the adjacent patches allowed us to control for any underlying differences in cover or patch use by the lemmings.

We defined pairs of patches in each sampling station as upland (*n* =7 in 2010; *n* =4 in 2011) or meadow (*n* =1 in 2010; *n* =4 in 2011) habitat based on its classification from vegetation data estimated in 2010 (see Morris and Dupuch (2012) for further details about the classification of stations). We reasoned that if the two habitats differ in predation risk, lemmings should increase foraging in covered patches in the habitat with greater risk (Brown 1988; Brown et al. 1992). This pattern is most typically revealed by the amount of food remaining in artificial food trays (the giving-up density (GUD); Brown 1988; Brown et al. 1992; Brown and Kotler 2004). GUDs reflect the time allocated to, and efficiency of, foraging. In this way, camera images of lemming presence (an estimate of patch residence time) and vigilance (an estimate of reduced efficiency at other fitness-enhancing activities including foraging) are analogous to GUDs. Thus, if one or the other habitat exposes lemmings to greater predation risk, then there should be a significant interaction between habitat and the relative number of camera images taken under cover. We therefore used the images to compare the difference in covered and open patch use between the two habitats and expected a significantly lower difference in the safest habitat.

We did not investigate the habitat effect in 2010 because patch use by lemmings was estimated at only one station in wet habitat (compared to seven stations in dry habitat). Most photos in 2010 were of *Lemmus*, so we also did not investigate the patch use of *Dicrostonyx* that year.

Statistical analysis

Dicrostonyx were about four times more abundant in 2011 than in 2010, whereas *Lemmus* abundance was similar in both years (Table 1). We therefore expected patch use and vigilance to be more affected by competition in 2011 than in 2010 and analyzed data from each year separately. We used linear mixed models (patch nested within sampling station was treated as a random effect) to investigate whether patch use by lemmings depended on the habitat (meadows versus upland) and cover treatment (presence versus absence) in 2011. We included the interaction between these explanatory variables in the analysis, as well as the interaction between the cover treatment and species identity (*Lemmus* versus *Dicrostonyx*), to determine whether the effects of cover were similar in meadow versus upland habitats and between the two species. We also included the presence versus absence of the competing species within a patch as an additional variable to control the effect of interference between the species, which is known to affect habitat use at high densities (Morris et al. 2000). In order to accurately estimate the cover treatment effect, we removed data from a species with zero records within a patch (*N* =7 over 32 stations × patches × species combinations in 2011). We used log-transformed patch use (calculated as the mean number of image sequences showing *Lemmus* or *Dicrostonyx* within a patch) to meet the assumption of normality. The degrees of freedom for the three-way interaction among habitat, cover treatment, and species, which would be necessary to test whether *Lemmus* and *Dicrostonyx* had similar perception of upland and meadows in terms of predation risk, were too small to test this

effect. So, we used a second set of linear mixed effect models (with station treated as a random effect) to investigate whether the difference between covered and open patch use (Δ = number of sequences in the presence of cover minus those in the absence of cover) depended on habitat and species identity. We used the interaction between these two variables to test whether perception of upland and meadows was similar between the two species.

We analyzed the differences in vigilance between species and habitat (as well as the interaction term) with mixed effect logistic regressions, using the presence versus absence of vigilance behavior within a patch used by *Lemmus* or *Dicrostonyx* (patch nested within station was treated as a random effect). Competition can increase vigilance in order to avoid aggression and interference (Slotow and Coumi 2000; Treves 2000; Beauchamp 2008), so we also included the presence of the competing species within the patch as an explanatory variable. Similarly, we included the interaction term between species and the presence versus absence of the competing species within the patch to determine whether competition-induced vigilance was similar between *Lemmus* and *Dicrostonyx*. Vigilance level is also known to be influenced by visual obstruction of the surroundings (Devereux et al. 2006; Embar et al. 2011). We therefore also added the presence versus absence of cover in models to control for its effect on lemming vigilance behavior.

We used bias-corrected Akaike's information criteria (AICc; Burnham and Anderson 2002) to select the best model from each set of analyses. We selected the model with the lowest AICc score, except when one or more additional models were within two points of the lowest scoring model, in which case we selected the more parsimonious model (i.e., with the smallest number of parameters). We performed all analyses in R (R Development Core Team 2011) with the functions "lme" (linear mixed models) and "lmer" (logistic mixed models) in the "nlme" (Pinheiro et al. 2012) and "lme4" (Bates et al. 2011) packages, respectively.

For each species in each habitat, we compared diel patterns of patch use in the presence versus absence of cover at a patch with a permuted Kolmogorov–Smirnov test (999 permutations; N_{tot}=24 because the diel period was divided in 12 periods of two consecutive hours). Any difference would indicate that predation risk perceived by the species in a given habitat was different over the diel period. The two species may also resolve competition by using habitats at different periods of the day. We thus used a second Kolmogorov–Smirnov test to contrast diel patterns between species in each habitat (presence and absence of cover combined). Analyses were performed in R with the function "ks.boot" in the package "Matching" (Sekhon 2011). We adjusted p values for multiple comparisons with a Holm's sequential Bonferroni correction.

The small data set from 2010 allowed us to only investigate the effect of cover treatment on *Lemmus* patch use with a Wilcoxon signed-rank test. Similarly, we observed vigilance in *Lemmus* and *Dicrostonyx* at only two and three patches, respectively, in 2010, which prevented us from investigating variation of vigilance behavior by lemming species during that year.

Results

Lemmus and *Dicrostonyx* preferentially used patches offering cover

Lemmus used significantly more cover than open patches in 2010 (N=10, Z=2.67, p=0.008; Fig. 1a). Results from 2011 confirmed *Lemmus'* preference for cover and showed a similar preference in *Dicrostonyx* (Fig. 1b). The best model included only the cover effect (Table 2) and showed that this preference was independent of species and habitat (Tables 2 and 3 and Fig. 1), suggesting that perceived predation risk did not differ between habitats. The difference in patch use between cover and open patches was similar in both habitats, regardless of the lemming species (Table 2 and Fig. 2).

Dicrostonyx was more vigilant than *Lemmus*

In 2010, 27 of the 151 sequences containing *Dicrostonyx* showed an individual in an upright observant posture, a behavior never observed in *Lemmus* (*Lemmus* used only a "head-up" alert pose when vigilant; 2 of the 594 sequences in 2010). Results from 2011 confirmed the higher vigilance in *Dicrostonyx* (39 of the 277 sequences) than in *Lemmus* (11 of the 366 sequences) (Table 3 and Fig. 3) and showed that vigilance behavior was not related to habitat or cover treatment regardless of the lemming species (Table 2 and Fig. 3a). Both *Lemmus* and *Dicrostonyx* were significantly more vigilant in a patch when the other species also used that patch (Table 3 and Fig. 3b).

Diel patterns of activity differed between open and cover patches

Lemmus and *Dicrostonyx* were active throughout the day in both upland and meadow habitats (Fig. 4), and their diel patterns of patch use were similar in both habitats (Kolmogorov–Smirnov permutation tests; meadow, 163.5 sequences·camera^{-1}·24 h, p=0.760; upland, 158 sequences·camera^{-1}·24 h, p=0.130). Both species used open patches differently from cover patches through the diel period in upland habitat (Kolmogorov–Smirnov permutation tests; *Dicrostonyx*, 57.5 sequences·camera^{-1}·24 h, p=0.017; *Lemmus*, 100.5 sequences·camera^{-1}·24 h, p=0.007). These differences were mainly explained by the inactivity of *Dicrostonyx* in open patches from 8 to 14 h and inactivity from 14 to 20 h by
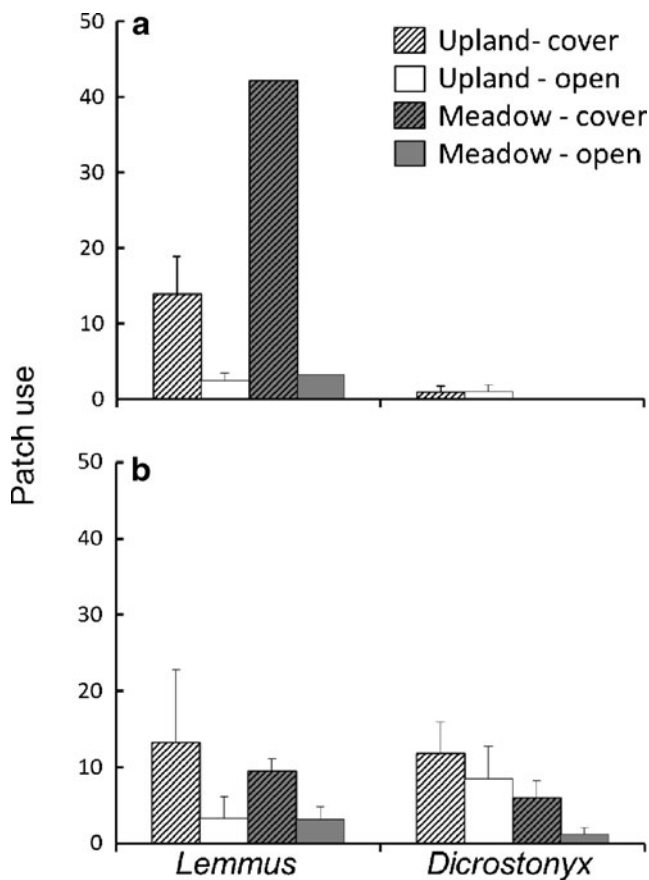
Fig. 1 Patch use (mean number of sequences·camera^{-1} ± S.E.) by *Lemmus* and *Dicrostonyx* in 2010 (**a**) and 2011 (**b**) in upland and meadow habitats when artificial cover was present versus absent in patches at Walker Bay (Nunavut, Canada). *Error bars* were not calculated in meadow habitat in 2010 because only one station was sampled in this habitat

Lemmus (Fig. 4a, c). A similar pattern of inactivity in open patches was observed by *Lemmus* in meadow habitat (Fig. 4d; significant difference in diel pattern between open and cover patch use in meadow [Kolmogorov–Smirnov permutation tests; 82.5 sequences·camera^{-1}·24 h, $p = 0.014$]). Contrary to *Lemmus*, *Dicrostonyx* used cover and open patches similarly through the diel period in meadow habitat (Kolmogorov–Smirnov permutation tests; 81 sequences·camera^{-1}·24 h, $p = 0.150$; Fig. 4b).

Discussion

Lemmings may use either habitat selection, differential patch use, or both, to reduce predation risk (Predavec and Krebs 2000). At the scale of habitats, lemmings should increase foraging in covered patches in the habitat with greater risk (Brown 1988; Brown et al. 1992). We, however, detected no difference between habitats in the preference of the two species for increased cover.

Table 2 Assessment of models best representing the patch use (estimated as the mean number of sequences·camera^{-1}), the difference in patch use between covered and open patches, and vigilance (estimated as the presence of vigilance behavior at a patch) by *Lemmus* and *Dicrostonyx* at Walker Bay (Nunavut, Canada) in 2011 (only the five best models are shown)

Models	K	AICc	ΔAICc
Intensity of patch use			
Patch use = cover + competitor	5	155.62	0
Patch use = cover	**4**	**156.23**	**0.61**
Patch use = habitat + cover + competitor	6	157.40	1.78
Patch use = habitat × cover[a] + competitor	7	158.32	2.70
Patch use = competitor + cover + species identity	6	158.42	2.80
Difference of patch use between covered and open patches			
No selected model[b]			
Vigilance			
Vigilance = competitor + species identity	**5**	**50.13**	**0**
Vigilance = habitat + competitor	5	52.70	2.57
Vigilance = competitor	4	53.48	3.35
Vigilance = species identity	4	54.90	4.77
Vigilance = species identity + habitat	5	56.10	5.97

The number of parameters, the Akaike Information Criterion corrected for small sample size, and the difference in AICc from the lowest scoring model are shown. Bold text indicates the selected model. Cover: binary variable (0: absence; 1: presence) coding the presence of the cover in a patch. Competitor: binary variable (0: absence; 1: presence) coding the presence of the other species in a patch. Habitat type: binary variable (0: meadow, 1: upland). Species identity: binary variable (*Lemmus* = 0, *Dicrostonyx* = 1)

K number of parameters, *AICc* Akaike Information Criterion corrected for small sample size, *ΔAICc* difference in AICc from the lowest scoring model

[a] Simple terms (habitat type + cover) were also included in the model

[b] The model including only the intercept had the lowest AICc

Reversing Brown's reasoning, similar preferences for cover in meadow and upland tundra habitat imply similar risks in those habitats. Risk, however, can be modified by population density and density-dependent habitat selection in at least two ways: (1) changes in density that motivate movement between habitats can equalize risk (a risk pump [China et al. 2008]; a risk pump can occur when individuals moving from a high density to low density habitat dilute predation risk). An example is found in China et al. (2008) who manipulated the densities of *Gerbillus andersoni allenbyi* and *Gerbillus pyramidum* in large outdoor enclosures composed of stabilized and semistabilized dune habitats. GUDs at low gerbil density were higher in risky stabilized dune than in the safer semistabilized habitat. The GUDs converged at higher densities because directional movement into risky stabilized habitat by food-seeking gerbils caused a reduction in their perceived predation risk.

Risk can also be modified (2) by short-term apparent competition (Holt and Kotler 1987). According to this

Table 3 Summary of the best mixed models (random variable: patch nested within station) evaluating (a) the effect of the cover tent presence on patch use by *Lemmus* and *Dicrostonyx* (linear mixed model) and (b) the effect of competitor presence and species identity on vigilance in *Lemmus* and *Dicrostonyx* (logistic mixed regression) at Walker Bay (Nunavut, Canada) in 2011

Variables	Estimate (S.E.)	Test value[a]	*p* value
Intensity of patch use (N=50)			
Intercept	0.84 (0.25)	11.49	0.002
Cover	0.97 (0.28)	12.11	0.001
Vigilance (N=38)			
Intercept	−2.76 (1.07)	−2.59	0.010
Species identity	1.82 (0.83)	2.19	0.028
Competitor	2.38 (1.02)	2.33	0.020

Cover: binary variable (0: absence; 1: presence) coding the presence of the cover tent in a patch. Competitor: binary variable (0: absence; 1: presence) coding the presence of the other species in a patch. Species identity: *Lemmus* = 0, *Dicrostonyx* = 1

[a] Test value is *F* value for intensity of patch use and *Z* value for vigilance

mechanism, increased abundance of one or the other species in a habitat could attract higher numbers of, or concentrate the foraging activities by, predators. Increased predation in that habitat is harmful to both prey species (apparent competition; Holt 1977). Risk could be reduced for the second species, however, if it responds to the negative apparently competitive effect by avoiding patches or habitats with high densities of the first species.

Considering the first mechanism, a risk pump could have occurred at Walker Bay if the much higher densities of *Dicrostonyx* in 2011 diluted predation risk for both species. Alternatively, short-term apparent competition could have occurred if increased abundance of *Dicrostonyx* in its preferred upland tundra caused predators to concentrate their foraging in that habitat. Either effect would change perceived predation risk by *Lemmus* and be revealed if the ratio of
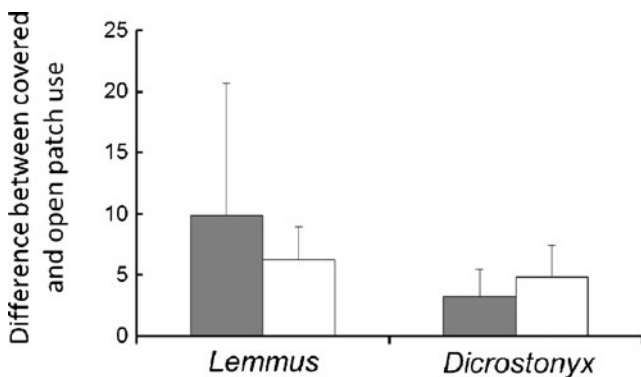

Fig. 2 Difference (mean ± S.E.) between covered and open patch use (Δ=number of sequences in the presence of cover minus in the absence of cover) by *Lemmus* and *Dicrostonyx* between meadow (*gray bar*) and upland habitats (*white bar*) at Walker Bay (Nunavut, Canada) in 2011
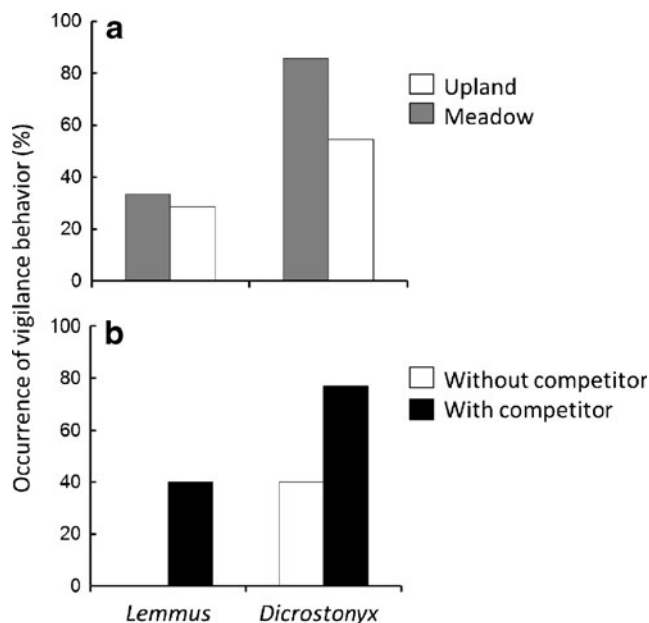

Fig. 3 Occurrence of vigilance behavior (estimated as the percentage of patches where vigilance behavior was observed on at least one photograph) in *Lemmus* and *Dicrostonyx* in upland (*white bar*) and meadow (*gray bar*) habitats (**a**) and in the presence (*black bar*) versus absence (*white bar*) of the competitive species within a patch (**b**) at Walker Bay (Nunavut, Canada) in 2011

Lemmus images between covered and open patches in upland tundra in 2011 was different from that in 2010. Our data reject both mechanisms. There was no difference in *Lemmus* use of covered and open patches in the upland tundra (Fig. 1). We conclude that the well-documented and density-dependent habitat preference by lemmings is a consequence of competition (Morris et al. 2000; Ale et al. 2011; Morris and Dupuch 2012) rather than predation risk (see also Dupuch et al. 2013).

Risk was manifested at smaller spatial scales within habitats. Both lemming species increased their activity under cover compared to open patches. The response, however, was similar between species and habitats. It would be a mistake to imagine that the two lemming species respond to risk in identical ways. Time allocation and vigilance are also prominent mechanisms allowing prey species to reduce risks from predation (Brown and Kotler 2004) and, by inference, from other causes. Both lemming species increased the level of vigilance in the presence of their interspecific competitor within a patch. Vigilance behavior was similar in both meadow and upland habitats and was not influenced by variation in putative predation risk (cover treatment). These results are consistent with our interpretation that interspecific competition is an important determinant of lemming foraging behavior and spatial distribution at Walker Bay.

Our results also revealed that *Dicrostonyx* was, on average, more vigilant than *Lemmus*. Two likely causes come to mind: (1) *Dicrostonyx* vigilance is directed toward the aggressive

Fig. 4 Diel pattern of activity (patch use; estimated as the mean number of sequences·camera^{-1}·h^{-1}) for *Dicrostonyx* (**a**, **b**) and *Lemmus* (**c**, **d**) in the presence and absence of cover, in upland (**a**, **c**) and meadow habitats (**b**, **d**) at Walker Bay (Nunavut, Canada) in 2011
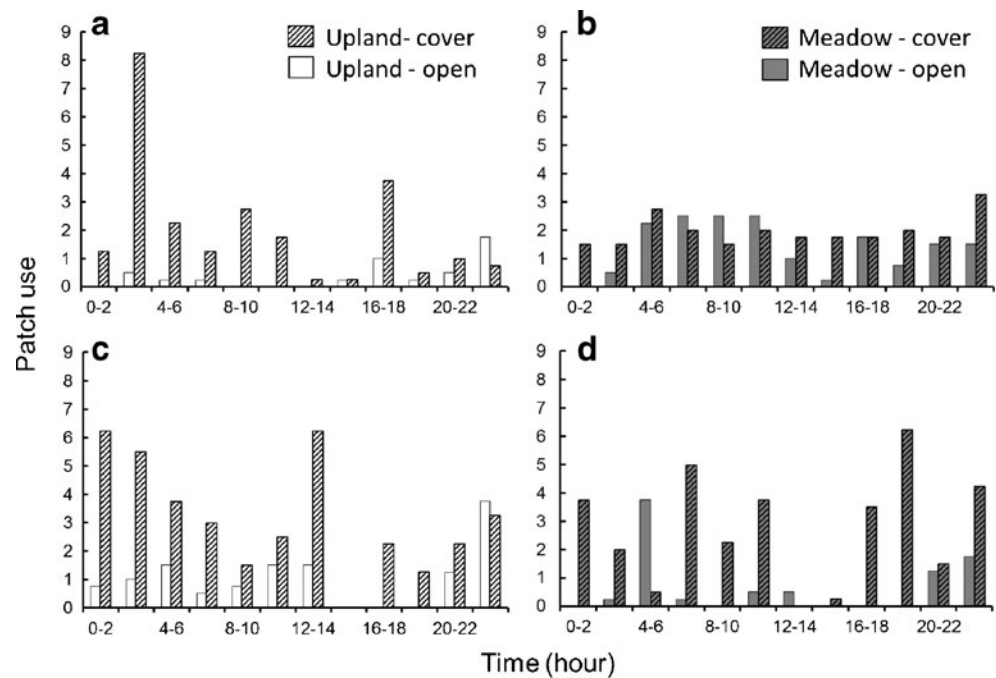
competitive superiority of *Lemmus* (Morris et al. 2000) or (2) toward a higher perception of predation. Whichever the cause, *Dicrostonyx* has a demonstrated ability to use both vigilance and protective cover in order to reduce risk, a strategy observed equally in both meadow and upland habitat. *Lemmus*, on the other hand, appears far less likely to employ vigilance as a predator deterrent than does *Dicrostonyx*.

Lemmus' less vigilant foraging appears to constrain its activity to more protective patches in both upland and meadow habitats and to restrict its activity during the afternoon. Conversely, *Dicrostonyx's* use of vigilance allows it to forage more safely in the open area during all hours of the day in meadow, but not in upland where its activity in open patches is reduced in the morning (differential patterns of air temperature between open and covered areas, and between habitats, cannot account for the diel patterns; Electronic supplementary resource 2). Unfortunately, our data are insufficient to test the tantalizing hypothesis that the diel differences in patch use reflect underlying temporal differences between species in predation risk.

Although each species used vigilance to help manage competitive risks, differences between species might nevertheless influence their vulnerability to predators and impact on predators' numerical and functional responses. Arctic foxes in Siberia responded numerically to *Lemmus* with a specialized type II functional response, but did not respond numerically to *Dicrostonyx*, for which they possessed a generalized type III functional response (Angerbjörn et al. 1999). Type III functional responses can emerge via effective vigilance if it causes predators to switch prey, or induces longer handling times, at low prey densities. Thus, the high

vigilance that we document for *Dicrostonyx*, in comparison to that for *Lemmus*, could explain the interspecific difference of Angerbjörn et al. (1999) in functional responses by Arctic foxes. A similar type III functional response has been observed among predators preying on *Dicrostonyx* in Greenland (Gilg et al. 2006) where Schmidt et al. (2008) reported that *Dicrostonyx* spent approximately 50 % of the time being vigilant while outside its burrows.

Differences in vulnerability to predators and habitat preference, combined with the effects of competition between prey species sharing the same predators, may help explain rodent population oscillations and observed shifts in the relative abundance of prey species (Hanski and Hentonnen 1996). If the competitively superior species is also more vulnerable to predation, then the subordinate species can increase in abundance when predation is concentrated on its competitor (apparent competition, Holt 1977). *Lemmus* is competitively superior to *Dicrostonyx* (Morris et al. 2000), and *Dicrostonyx* is typically more abundant than *Lemmus* at Walker Bay. *Lemmus*, however, is occasionally more numerous than *Dicrostonyx* (Morris et al. 2012). The patterns of varying abundance are consistent with Hanski and Hentonnen's (1996) results if *Lemmus* is more vulnerable to predation than *Dicrostonyx* at Walker Bay.

Regardless of the influence of predation risk on lemming population dynamics, both species prefer to be active under cover when given the opportunity, a result suggesting that they live in a fearsome landscape, but one where neither upland tundra nor sedge meadow provides a safer refuge for active lemmings. We do not know whether the higher vigilance by *Dicrostonyx* is effective at reducing predation at Walker Bay

because the detailed functional responses of predator species to each lemming species are unavailable for this area. One might expect, on the other hand, that the higher vigilance by *Dicrostonyx* reduces its foraging efficiency (Dall et al. 2001; Brown and Kotler 2007). It is thus possible that differences in vigilance and diel patterns of activity also help to explain the coexistence of the two lemming species. Nevertheless, both species appear to live in a flattened landscape of fear at Walker Bay where their suite of predators is equally dangerous in both habitats.

A flattened landscape of fear could emerge by several nonexclusive processes including fine-grained predators using different patches in proportion to their abundance and by adaptive predator–prey habitat selection games played among habitats with similar inherent "riskiness" (Hugie and Dill 1994). Predator–prey foraging games that include vigilance should, however, yield a landscape where increased risk in productive patches is neutralized by increased prey vigilance (Brown and Kotler 2007). This prediction will likely be more complicated when predators forage on two or more prey species that differ in the effectiveness of vigilant behavior. In the case of arctic lemmings, if *Dicrostonyx* is more capable of reducing predation risk through vigilance, then less vigilant *Lemmus* could cause predators to value *Lemmus'* preferred meadow habitat more than if only *Dicrostonyx* is present. Thus, *Lemmus* could elevate fear indirectly in meadow through increased predation risk as well as heightening vigilance there through competitive dominance. According to this predation and competitive risk hypothesis, *Dicrostonyx* vigilance in upland habitat would be directed mainly toward reducing predation risk while similar vigilance in meadows would be targeted toward reducing risks associated with predation as well as competitive interactions with *Lemmus*. *Lemmus*, with less ability to modify its safety through vigilance, can nevertheless also manage risk through its preference for cover and possibly through its temporal pattern of activity.

The main point is that a prey species' contours of fear, whether flat or not, emanate from responses toward predators, competitors, and their functional, spatial, and temporal interactions with one another. Landscapes of fear are thus likely to also vary, in space and through time, with the composition and abundance of the predator–prey community. Snowy owls, arctic foxes, jaegers, and other migratory predators that were common at Walker Bay during the 1996 lemming peak (Wilson et al. 1999; Wilson and Bromley 2001) have been mostly absent during 2010–2011 (small numbers of snowy owls, arctic foxes, jaegers, and rough-legged hawks have been observed but without consistent evidence of breeding). When predation risk is uniformly low, as it may have been during our assessment of risk at Walker Bay (Dupuch et al. 2013), prey distribution may reflect the missed opportunity costs associated with searching other food patches

and of engaging in activities that reduce competition (Eccard and Liesenjohann 2008). In this context, future studies should aim to map the contours of fear while controlling for competition among prey when predation risk is suspected to be relatively low.

As the densities of predators and the associated risk to prey increase, trade-offs between food and safety should shift to elevate prey vigilance toward predators. Such fear-driven systems generate complex predator–prey isoclines (Brown and Kotler 2007) that may help to explain the ongoing and occasionally tempestuous debate on top-down versus bottom-up control in terrestrial arctic ecosystems (e.g., Gauthier et al. 2009; Oksanen et al. 2009). It will thus be informative to reevaluate lemming vigilance and patch use in systems, or at times, when predators are more abundant than they have been recently at Walker Bay. We suspect that there is much to be learned from studies that delve more deeply into the causes, consequences, and temporal dynamics of fear.

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