

The predator activity landscape predicts the anti-predator behavior and distribution of prey in a tundra community

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Abstract. Predation shapes communities through consumptive and non-consumptive effects. In the latter case, prey respond to perceived predation risk through proactive or reactive risk management strategies occurring at different spatial and temporal scales. The predator–prey space race and landscape of fear concepts are useful to better understand how predation risk affects prey behavioral decisions and distribution. We assessed predation risk effects in a terrestrial Arctic community, where the arctic fox is the main predator of ground-nesting birds. Using high-frequency GPS data, we estimated a predator activity landscape corresponding to fox space use patterns and validated with an artificial prey experiment that this predator activity landscape correlated with the predation risk landscape. We then investigated the effects of the fox activity landscape on multiple prey species, by assessing the anti-predator behavior of a main prey (snow goose) actively searched for by foxes, and the nest distribution of several incidental prey species. We first found that snow geese showed a stronger level of nest defense in areas highly used by foxes, possibly responding with a reactive strategy to variation in predation risk. Then, nests of incidental prey reproducing in habitats easily accessed by foxes had a lower probability of occurrence in areas highly used by foxes, suggesting these birds may use a proactive risk management strategy by shifting their distribution away from risky areas. For incidental prey species nesting in microhabitat refuges difficult to access by foxes, probability of nest occurrence was independent of predation risk in the surrounding area, as they avoid risk at a finer spatial scale. By tracking all individuals of the dominant predator species in our study area, we demonstrated the value of using predator space use patterns to infer spatial variation in predation risk. Overall, we highlight the diversity of risk management strategies in prey sharing a common predator, hence refining our understanding of the mechanisms driving species distribution and community structure.

Key words: anti-predator behavior; arctic fox; artificial prey experiment; landscape of fear; nest distribution; predation risk; predation risk effects; predator activity landscape; predator–prey interactions; predator–prey space race.

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INTRODUCTION

Predation plays a central role in ecological and evolutionary processes (Menge and Sutherland

1976, Ford et al. 2014). It shapes communities through both direct killing of prey (consumptive effects) and non-consumptive, predation risk effects (Lima and Dill 1990, Cresswell 2008,

Laundré et al. 2010, Peacor et al. 2020). Non-consumptive effects of predation can be major drivers of food web structure and dynamics (Cresswell 2008, Teckentrup et al. 2018).

Prey respond to predation risk with various risk management strategies that are tailored to different spatial and temporal scales. Strategies are either proactive when behavior is adjusted to reduce risk prior to a predator encounter, or reactive when the threat is imminent (Lima and Dill 1990, Creel et al. 2014, Courbin et al. 2016). At broad spatial and temporal scales, predation risk associated with different areas may influence prey's choice of home range, such as the breeding home range of migrant birds (i.e., proactive home range selection or second-order habitat selection; Johnson 1980, Lima 2009, Morosinotto et al. 2010). At intermediate scales, spatial variation in predation risk within the home range of a prey may affect its space use, particularly during times of high risk (i.e., proactive patch selection or third-order habitat selection; Johnson 1980). For example, many bird species maximize their reproduction by nesting where predation risk is the lowest, either where the regional abundance of main predators is low (Forstmeier and Weiss 2004) or in habitats providing complete or partial refuge against predation (Anderson et al. 2015). At fine scales, in the direct presence of a predator, prey show reactive risk avoidance and use anti-predator behaviors such as escape behavior (Ydenberg and Dill 1986). In a breeding context, the threat posed by predators is often much higher for young than for adults (Rosenbaum 2018). Thus, in many species, parents (such as incubating birds) provide offspring defense rather than flee (Montgomerie and Weatherhead 1988, Lima 2009, Rosenbaum 2018).

Prey risk management strategies also depend on predator and prey encounter rates and on the outcome of the predator-prey space race, where predators are searching for prey and prey are moving to avoid predators (Sih 1984, 2005, Lima 2002, Smith et al. 2019). Indeed, space use patterns of predators and their main prey (which are often the most abundant and profitable prey) tend to correlate since predators actively search for them (Fortin et al. 2005, Arias-Del Razo et al. 2012). Thus, the main prey species can hardly avoid predation risk by shifting their distribution, and they lose the space race. This is also

most likely to occur when prey are relatively immobile (Sih 1984) since their distribution is predictable, such as in the case of breeding birds after nest establishment. Such prey will rather adopt reactive risk management strategies such as defense or vigilance behaviors. On the contrary, incidental prey species, which are consumed when encountered but are not affecting predator movements in the landscape, may win the predator-prey space race and manage the risk of predation proactively by avoiding areas highly used by predators (Forstmeier and Weiss 2004, Avgar et al. 2015).

The landscape of fear concept offers another useful framework to understand how predation risk affects prey behavior (Laundré et al. 2010, Gaynor et al. 2019, but see Peacor et al. 2020). Laundré et al. (2010) defined the landscape of fear as the spatial variation in prey perception of predation risk. Gaynor et al. (2019) then framed the landscape of fear as part of a series of interdependent landscapes. First, the physical landscape represents habitat features that interact with the biology (hunting mode, body size, etc.) of predators and prey to determine their distributions and interactions. These interactions then modulate the predation risk landscape and, accordingly, the landscape of fear. Finally, the landscape of fear determines the responses of prey to predation risk, which ultimately shape spatiotemporal variations in prey distribution and anti-predator behavior. Many studies have used proxies of predation risk, such as habitat features (Dupuch et al. 2014), or proxies of perceived predation risk, such as prey behavior (Willems and Hill 2009). Proxies are useful but they can also lead to circular reasoning (Gaynor et al. 2019).

For cursorial predators (in opposition to ambush or sit-and-wait predators), the space use of active individuals, which can be measured at a fine scale through GPS tracking, should closely approximate the landscape of predation risk since they continuously prowl in search of prey (Schmitz et al. 2004). Some landscape of fear studies measured predator movements to explain prey behavior while considering local density or space use of predators, but with only a limited number of locations (Thaker et al. 2011, Kohl et al. 2018). For very active predators, a detailed assessment of movements is required to infer the predation risk landscape (Poulin et al. 2021). Fortunately,

improved GPS telemetry (Wilmers et al. 2015) and modeling techniques (e.g., hidden Markov models; Patterson et al. 2017) now allow researchers to assess the behavior and active periods of predators from their fine-scale movements. However, the active periods of predators may sometimes be associated with activities other than hunting (such as long-distance movements); therefore, the correlation between fine-scale predator space use patterns and the predation risk landscape should be demonstrated.

Conceptualization of the landscape of fear has generated hypotheses about the role of predation risk in driving animal behavior across contexts (Laundré et al. 2010, Gaynor et al. 2019). Empirical studies are needed to simultaneously evaluate how predators generate the distribution of predation risk and how different prey species respond proactively or reactively to this distribution. Arctic terrestrial food webs are good models to study vertebrate predator–prey interactions because they are relatively simple. One example is the tundra community of Bylot Island (Nunavut, Canada), where the arctic fox (*Vulpes lagopus*) is the main terrestrial predator. This canid is a cursorial, active hunting predator that travels extensive daily distances within its territory (Poulin et al. 2021). On Bylot, it feeds on lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*), which show annual density fluctuations (Gruyer et al. 2008). Apart from lemmings, arctic foxes prey on nesting birds and pose a greater threat to eggs and chicks (Bêty et al. 2001, McKinnon and Bêty 2009). During the nesting season, they collect eggs of the colonial nesting greater snow goose (*Anser caerulescens atlanticus*) (Bêty et al. 2001) and thus select both productive lemming habitats and patches of high snow goose nest density (Grenier-Potvin et al. 2021). While geese can decide where to nest, once this decision is made, they can no longer rely on proactive spatial avoidance of predators, since foxes seek out their nests. Highly conspicuous snow geese, however, actively defend their nests when closely approached by a fox (Bêty et al. 2002). This defense strategy is effective as long as geese remain close to their nest during incubation (Reed et al. 1995, Bêty et al. 2002). Foxes also opportunistically prey upon nests of other ground-nesting birds and are their main nest predator (McKinnon and Bêty 2009, Gauthier

et al. 2011). These incidental prey mainly nest in mesic tundra, but some of them nest in micro-habitat patches that constrain fox movements and can thus offer protection. For example, islets of just a few square meters located in ponds may serve as refuges in the tundra landscape (Gauthier et al. 2015).

We assessed the effects of the predation risk landscape in the tundra community of Bylot Island. We first defined and assessed empirically the *predator activity landscape*, that is the utilization distribution of active foxes, using high-frequency GPS data coupled with hidden Markov models. We then experimentally tested whether this predator activity landscape predicted (P1) the probability of consumption of artificial prey, thus reflecting the predation risk landscape. Then, we investigated the effect of the fox activity landscape on risk management strategies of the bird community. We assessed the nest defense behavior of a main prey (snow geese), predicting (P2) that nest defense when approached by a potential predator should be stronger in areas most used by foxes, where predation risk of unattended nests is higher. We also assessed the effect of the predator activity landscape on the nest distribution of incidental prey, composed of bird species from different guilds, and predicted (P3) that the probability of nest occurrence should be lowest in areas most used by foxes.

METHODS

Study system

We conducted fieldwork during May–July 2019 in the southwest plain of Bylot Island (72°53'N, 79°54'W), in Sirmilik National Park of Canada, Nunavut (Appendix S1: Fig. S1). The ecosystem is characterized primarily by mesic tundra and polygonal wetlands (Grenier-Potvin et al. 2021). In this system, arctic fox pairs have virtually no predators and are territorial. Territories of all studied individuals overlapped a snow goose colony composed of >20,000 nesting pairs distributed over 70 km² (Bêty et al. 2001, 2002).

Fox captures and movement tracking

During May and June 2019, we captured 13 foxes using Softcatch #1 padded leghold traps

(Oneida Victor Ltd., Cleveland, Ohio, USA). These foxes represented six neighboring territorial pairs and one additional individual, whose small home range overlapped two territories (Fig. 1). Each fox was marked with colored ear tags allowing identification at a distance and was fitted with a GPS collar (95 g, 2.6–3.3% of body mass; Radio Tag-14, Milsar, Poland) equipped with rechargeable batteries, a solar panel, and UHF transmission allowing remote data download. We used a GPS fix interval of 4 min, and average GPS location error was 11 m (Poulin et al. 2021). The six fox territories comprise our study area. The general contour of the study area was drawn using the concave hull of fox GPS data (QGIS, version 3.8.3; QGIS Development Team 2019), excluding a few extra-territorial trips (Fig. 1). For each individual, we used locations from 10 d at the end of June. These ten days correspond to a major part of the laying and incubation periods of tundra nesting birds and are of utmost importance for their annual reproductive success. Data sets were synchronized (± 2 d depending on capture day and the timing of missing data; the 2 d following capture were excluded). Daily observations and automated cameras at fox dens confirmed that we tracked all foxes foraging in the study area. Of the six monitored fox pairs, five reproduced.

Capture techniques and immobilization procedures were approved by the UQAR Animal Care Committee (CPA-64-16-169 R3), and field research was approved by the Joint Park Management Committee of Sirmilik National Park of Canada (SIR-2018-28021).

Artificial prey experiment

We conducted an artificial prey experiment using 8-g pieces of dried beef liver (measuring ca. $0.5 \times 2 \times 2$ cm; Benny Bullys Sales, Ontario, Canada; hereafter baits) to assess predation risk. Predation on artificial prey is a good proxy for predation risk on bird nests, as probability of predation approximates 100% when a fox initiates an attack on an unattended goose nest or on any passerine or shorebird nest (Beardsell et al. 2021). Like baits, most nest contents are thus readily available once detected. The experiment started on 4 July, after we had tracked fox movements. We placed in each of the six fox territories six to eight lines of ca. 10 baits each (total of 428

baits distributed in 44 curved lines each measuring 293 ± 77 m (mean \pm SD); see bait locations in Appendix S1: Fig. S2A). Each bait line was located in a homogeneous habitat patch, and bait lines were distributed equally between wetland polygons and mesic tundra patches, at least 300 m from the study area limits. Avoiding study area borders ensured that baits could not be taken by unknown foxes from adjacent territories. Distance between adjacent baits within bait lines was 79 ± 7 m and distance between adjacent lines was 297 ± 118 m. We covered baits with moss or lichen to exclude predation by avian predators (as done for artificial nests; Léandri-Breton and Bêty 2020) and visited baits after 4 d to assess their removal by foxes. A piece of orange flag placed under each bait became visible when a bait had been removed, thus facilitating the assessment of predation events. To confirm that foxes were the only bait consumers, we placed some camera traps during 5 ± 2 d after the experiment at six locations (in three fox territories) to monitor the fate of baits, which were replaced if consumed. Thirteen baits were taken, all by foxes.

Snow goose nest defense behavior

Flushing distance from an approaching human is often used to assess a prey's anti-predator strategy (Blumstein 2003) and represents a good proxy for nest defense intensity. We measured the flushing distances of 458 incubating females as an indicator of their level of nest defense (see nest locations in Appendix S1: Fig. S2B). We chose sampled nests randomly within sites visited during fieldwork activities. A small flushing distance (the observer is close to the nest when the female leaves) indicates a high level of nest defense (Clermont et al. 2019). An observer approached a focal nest by walking silently at a slow and constant pace, in a straight line, and measured flushing distance with a telemeter or handheld GPS. To limit potential effects of incubation stage on goose nest defense (Clermont et al. 2019), we performed 85% of flushing distance measures within 5 d from 14 June to 18 June (we did remaining measures in the following days), which corresponds to the first half of the incubation period. We also assessed clutch size as it generally influences nest defense intensity (Montgomerie and Weatherhead 1988), and we measured the starting distance of the

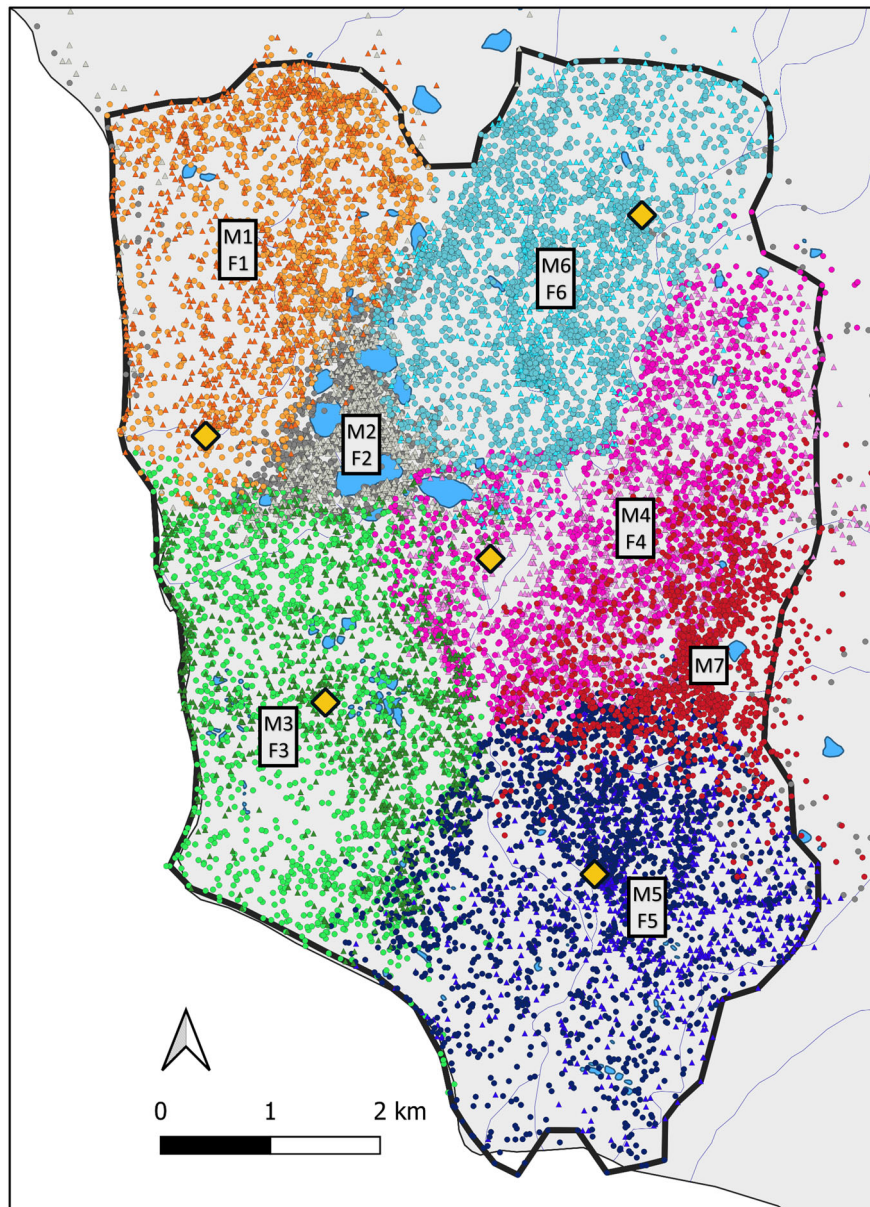


Fig. 1. Study area on Bylot Island (Nunavut, Canada) featuring GPS locations (dots for males and triangles for females) of 13 arctic foxes tracked during 10 d at the end of June 2019. Foxes occupied six territories (M7 had a small home range overlapping two territories), and pair members have related colors, as detailed in Appendix S1: Table S1. GPS locations were collected at 4-min fix intervals, and the 20,961 data points shown are those classified in the active state by a hidden Markov model. Yellow diamonds locate the five reproductive dens (M2, F2, and M7 did not reproduce). The thick black line is the contour of the study area. Lakes and large ponds are in blue. See Appendix S1: Fig. S1 for the geographical context of the study area.

approach as it affects flushing distance (Blumstein 2003). Starting distance ranged from 15 to 508 m and was assessed with a telemeter or handheld GPS. Focal nests were located at least 300 m from

the study area limits, thus ensuring that fox activity around nests was not underestimated due to visits by uncollared foxes from adjacent territories.

Nest distribution of incidental prey

During the incubation period, we conducted thorough searches of bird nests other than snow geese (i.e., incidental prey). In June, we walked repeatedly throughout the study area to detect signs of reproductive birds (calling, distraction displays, bird flushing at close distance). We did this through transect surveys conducted in mesic tundra, and intensive nest searches performed in wetland patches, stony riverbanks, and slopes, which are all easily accessible to foxes. We also inspected microhabitats surrounded by water (hereafter refuges, mostly islets in ponds), which are not easily accessed by foxes. We georeferenced 377 islets in the study area (Appendix S1: Fig. S3).

We found 109 nests from 13 species in the study area (see nest locations in Appendix S1: Fig. S2C). A total of 44 nests from 10 species were located in areas easily accessible to foxes: common-ringed plover (*Charadrius hiaticula*, $n = 3$), American golden plover (*Pluvialis dominica*, $n = 9$), white-rumped sandpiper (*Calidris fuscicollis*, $n = 2$), arctic tern (*Sterna paradisaea*, $n = 2$), rough-legged hawk (*Buteo lagopus*, $n = 1$), lapland longspur (*Calcarius lapponicus*, $n = 16$), parasitic jaeger (*Stercorarius parasiticus*, $n = 1$), long-tailed jaeger (*Stercorarius longicaudus*, $n = 6$), long-tailed duck (*Clangula hyemalis*, $n = 1$), and king eider (*Somateria spectabilis*, $n = 3$). A total of 65 nests from three species were located in refuges: cackling goose (*Branta hutchinsii*, $n = 38$), glaucous gull (*Larus hyperboreus*, $n = 11$), and red-throated loon (*Gavia stellata*, $n = 16$).

Predator activity landscape

We defined the predator activity landscape as the utilization distribution of all foxes in the active state within the study area. For opportunist active hunting predators such as arctic foxes, all traveling phases can be associated with hunting; therefore, we used a hidden Markov model (HMM) to assign GPS locations to an active or resting state (R package moveHMM; Michelot et al. 2016). HMM decomposes GPS tracks into sequences associated with different behavioral states, which differ from one another in their step lengths and turning angles (Langrock et al. 2012). The active state is characterized by long step lengths and small turning angles, and the resting state, by short step lengths and large turning angles. The HMM included time of the day as a covariate to reflect the circadian rhythm of foxes

(Grenier-Potvin et al. 2021). Models using a Weibull distribution for step lengths and a wrapped Cauchy distribution for turning angles yielded the most parsimonious model (HMM construction and model selection is detailed in Grenier-Potvin et al. [2021]).

Then, we used kernel density estimation (QGIS Heatmap plugin) to map the fox utilization distribution (UD) using only active locations. UD quantifies the intensity of space use (from low to high probability density of GPS locations) by tracked animals and thus identifies areas where animals are most likely to be found (Fortin et al. 2005, Thaker et al. 2011). We used 10×10 m pixels to map UD scores, allowing fine spatial scale assessment of variation in fox UD, and a fixed UD smoothing parameter (called radius in QGIS, which is equivalent to the kernel bandwidth) to specify the distance at which GPS locations influence UD scores. As the choice of the UD smoothing parameter can affect prediction tests, we performed a sensitivity analysis. We ran statistical models (presented in the following section) for five UD smoothing parameters ranging from 200 to 400 m (50-m increments). As foxes in their active state traveled 232 ± 145 m (mean \pm SD; see *Results*) between GPS fixes obtained at 4-min intervals, the chosen range of smoothing parameters yielded fine resolution activity landscapes that reflected the scale of our data. Using smaller parameter values would have underestimated the use of areas located between GPS locations, whereas using larger parameter values would have overestimated the use of areas located on each side of the fox track. UD scores were standardized from 0 to 1 in each of the five UD.

Statistical models

We tested the effect of the fox activity landscape on the probability of predation of baits (P1), snow goose nest defense behavior (P2), and the nest distribution of fox incidental prey (P3). The first step consisted in extracting the fox UD score at all locations used in the models, that is, locations of baits, nests of tested snow geese, and nests and available nesting locations of incidental birds.

Probability of predation of baits.—We used a generalized linear mixed model (R package lme4; Bates et al. 2015) with a logit-link function and a

binomial distribution to test the effect of fox UD score on the probability of predation of baits (0 = not predated, 1 = predated), with the ID of the bait line nested in the ID of the fox territory as random effects. We fitted one model for each

of the five UDs defined with different smoothing parameters.

Snow goose nest defense behavior.—We used a linear mixed model to test the effect of fox UD score on goose flushing distance. We square-root-

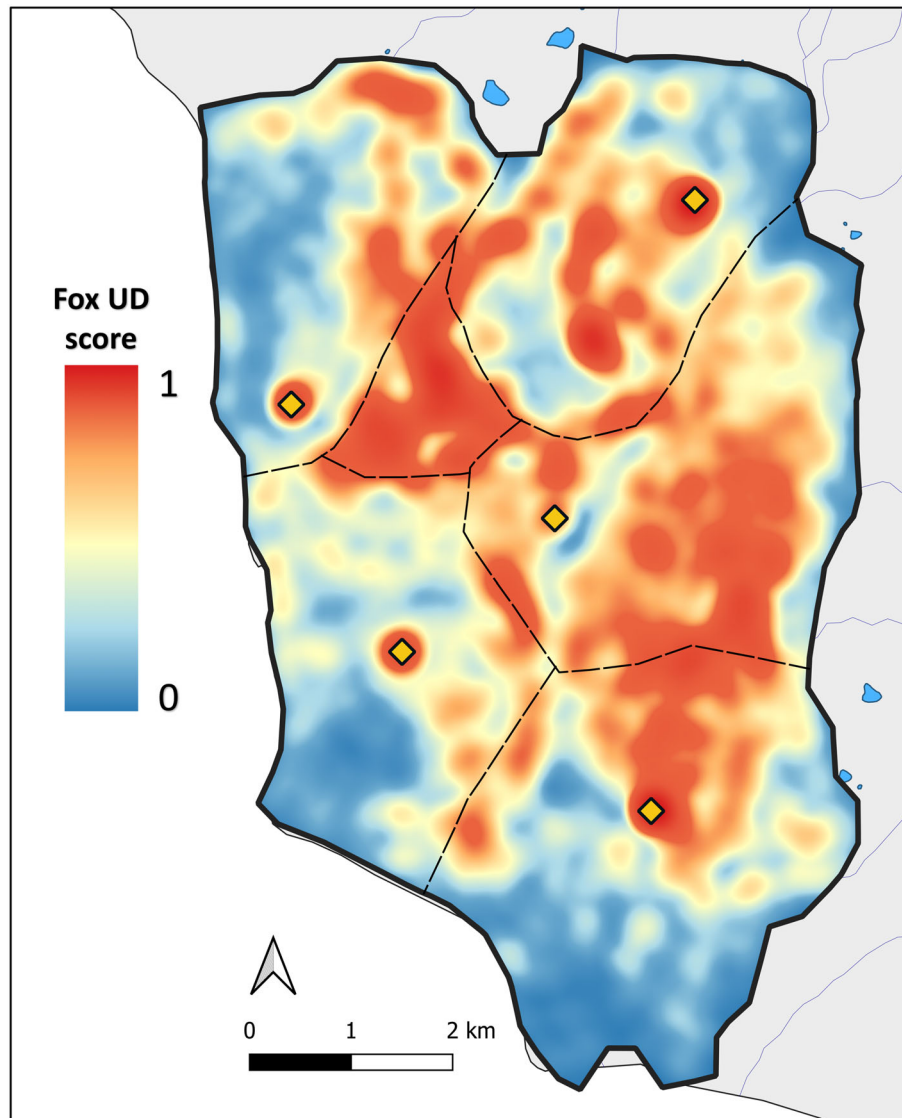


Fig. 2. Arctic fox activity landscape generated from 20,961 GPS locations classified in the active state by a hidden Markov model. The activity landscape reflects fox utilization distribution (UD) based on data from 13 individuals living in six territories and tracked during 10 d at the end of June 2019, on Bylot Island. A UD smoothing parameter of 300 m was used to generate this activity landscape (see Appendix S1: Fig. S4 for activity landscapes generated from other smoothing parameters). The color scale reflects fox UD score (from 0 to 1) and thus probability of the presence of an active fox. Yellow diamonds locate the five reproductive dens, dashed lines identify the approximate boundaries of fox pair territories, and the thick black line is the contour of the study area.

transformed goose flushing distance to respect the assumption of normality and homoskedasticity in models' residuals. The other fixed effects included in the models were clutch size, starting distance of the approach, and date of observation. All covariates were centered and standardized to facilitate the interpretation of model estimates (Schielzeth 2010). We included as random effects the ID of the fox territory and the ID of the observer performing the approach. We fitted one model for each of the five UD. As the effect of fox UD score on flushing distance was weak (see *Results*), we investigated whether a few influential points were driving the relationship. We identified outliers using the R package *car* (Fox and Weisberg 2020) and tested models without those points, which yielded results similar to those we present.

Nest distribution of incidental prey.—We used conditional logistic regressions with a use-available design (function *clogit* in R package *survival*; Therneau et al. 2020) to test the effect of fox UD score on the distribution of bird nests of fox incidental prey species (P3). Since fox UD scores are smoothed values obtained from locations with a ± 11 m error and collected at 4-min intervals, they reflect a spatially averaged fox utilization of the area rather than microhabitat use. Hence, the UD score of an islet could be >0 even if no fox visited this small patch, and the spatial resolution of the fox activity landscape was unable to reflect the fine spatial scale of refuges. We thus analyzed separately species nesting in

habitats easily accessible to foxes (first set of models) and species nesting in microhabitat refuges (second set of models).

In the first set of models, we compared fox UD scores at bird nests (used locations) with fox UD scores at potential nesting sites (available locations). We considered as available locations a set of random sites located in the study area and out of water bodies. We paired each bird nest location to 50 random locations drawn from an area surrounding the nest (hereafter the *nest area*). As tundra nesting birds have various natural histories, including nesting habitat and social system, they likely select nesting sites at different spatial scales, which are unknown. Hence, we could not justify a priori a single radius for the nest area. We therefore repeated analyses after forcing random locations within five radii varying from 1000 to 3000 m (increments of 500 m), thus fitting 25 models (5 UD \times 5 nest area radii).

In the second set of models, we again compared fox UD scores at bird nests (used locations) with fox UD scores at available sites. However, we used as available locations potential nesting sites located in the study area and surrounded by water, drawing from our 377 georeferenced islets. We paired each bird nest location to 50 islets chosen randomly from the area surrounding the nest. Less than 50 islets were sometimes available within the nest area, so we assessed whether this affected results (Appendix S2). As for the first set of models, we fitted 25 models (5 UD \times 5 nest area radii).

Table 1. Results from binomial mixed models testing the effect of fox UD score on the probability of predation of baits, with patch ID nested in territory ID fitted as random effects, for the five UD with smoothing parameters ranging from 200 to 400 m ($n = 428$ baits).

UD smoothing parameter (m)	Fixed effect	Estimate [95% CI]	<i>z</i>	<i>P</i>
200	(Intercept)	−0.25 [−1.17, 0.68]	−0.60	0.546
	Fox UD score	3.56 [−0.02, 7.45]	1.91	0.056
250	(Intercept)	−0.35 [−1.29, 0.60]	−0.82	0.414
	Fox UD score	3.28 [0.31, 6.49]	2.12	0.034
300	(Intercept)	−0.48 [−1.44, 0.49]	−1.07	0.284
	Fox UD score	3.24 [0.59, 6.09]	2.36	0.013
350	(Intercept)	−0.61 [−1.61, 0.38]	−1.31	0.191
	Fox UD score	3.23 [0.79, 5.84]	2.56	0.011
400	(Intercept)	−0.73 [−1.77, 0.29]	−1.50	0.133
	Fox UD score	3.18 [0.89, 5.62]	2.69	0.007

Note: See Appendix S1: Table S2 for variance values of random effects.

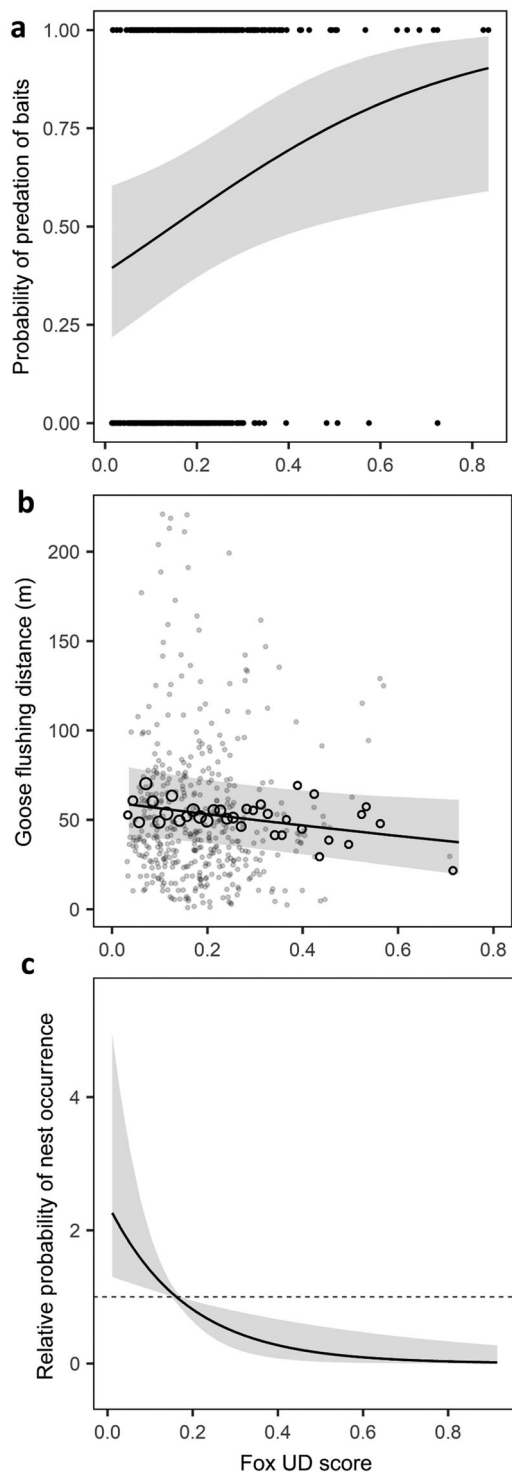


Fig. 3. Predicted effect of fox UD score on (a) probability of predation of baits (0 = bait not eaten, 1 = bait

(Fig. 3. *Continued*)

eaten, $n = 428$), (b) goose flushing distance ($n = 458$), and (c) relative probability of occurrence of nests from birds nesting in habitats easily accessible to foxes ($n = 44$ nests from 10 species). In (b), we back-transformed goose flushing distance and fox UD score before plotting (goose flushing distance had been square-root-transformed, and fox UD score had been centered and standardized in linear models). Dots are raw data, and circles are partial residuals divided in 50 bins of equal fox UD score interval after accounting for the effects of the number of eggs, the observer's starting distance, and the date. Circle size is proportional to the number of observations in each bin. In (c), the dashed horizontal line represents a relative probability of occurrence of 1, with values below and above 1 indicating lower and higher probabilities of occurrence than random, respectively. The gray area represents the 95% confidence interval of (a) the fitted logistic regression, (b) the linear regression, and (c) the relative probability of occurrence obtained by bootstrap. For these representations, we used fox UD scores generated with an intermediate smoothing parameter of 300 m, and (c) nest areas generated with an intermediate radius of 2000 m.

All analyses were conducted in R (version 3.6.1; R Development Core Team 2019). We validated the assumptions of normality, homoskedasticity, non-collinearity among fixed effects, and independence of residuals for all models. Values are expressed as mean \pm SD.

RESULTS

Fox activity landscape

We acquired a total of 45,140 fixes for 13 foxes tracked for 10 d (Fig. 1). The active behavioral state was assigned to $46 \pm 9\%$ of locations per individual (range 31–60%; Appendix S1: Table S1) for a total of 20,961 GPS locations. Average step length and turning angle were 232 ± 145 m and 55° for active locations, and 9 ± 9 m and 116° for resting locations (see Grenier-Potvin et al. 2021). Representations of the fox activity landscape show heterogeneity in the intensity of space use by foxes that remained

as smoothing parameters varied from 200 to 400 m (Fig. 2, Appendix S1: Fig. S4). The predator activity landscape identified areas intensively used by some foxes, such as the small central territory of M2 and F2 and the space that M7 shared with the M4-F4 or M5-F5 pairs (Figs. 1, 2).

Probability of predation of baits

The artificial prey experiment showed that the predation risk landscape was positively linked to the predator activity landscape. Baits were more likely to be consumed where fox UD score was high (Table 1, Fig. 3a), whatever the UD smoothing parameter (Table 1).

Snow goose nest defense behavior

Snow geese showed higher level of nest defense when nesting in areas of high predation risk, as shown by the negative relationship

between flushing distance and fox UD score (Table 2, Fig. 3b). Although slope estimates were consistently negative for the five UD, the slope lessened and lost its significance as the UD smoothing parameter increased, suggesting that geese only responded to risk at the finest spatial scales that we explored. Geese also showed a weaker level of nest defense when they had a relatively small clutch and saw the observer approaching from far away, as shown by the significant effects of clutch size and starting distance on flushing distance (no effect of smoothing parameter; Table 2). Flushing distance did not vary with observation date.

Nest distribution of incidental prey

For bird species nesting in habitats easily accessible to foxes, nests were more likely to occur where fox UD score was low, compared with random locations (Table 3, Fig. 3c). The

Table 2. Results from linear mixed models testing the effect of fox UD score on goose flushing distance.

UD smoothing parameter (m)	Fixed effect	Estimate [95% CI]	df	<i>t</i>	<i>P</i>
200	(Intercept)	7.34 [5.98, 8.74]	2.79	11.7	0.002
	Fox UD score	-0.26 [-0.47, -0.04]	417.61	-2.36	0.019
	Number of eggs	-0.30 [-0.48, -0.11]	424.33	-3.15	0.002
	Starting distance	1.46 [1.25, 1.67]	265.55	13.72	<0.001
	Date	-0.17 [-0.46, 0.10]	42.69	-1.29	0.203
250	(Intercept)	7.34 [5.98, 8.74]	2.79	11.71	0.002
	Fox UD score	-0.25 [-0.47, -0.03]	410.57	-2.25	0.025
	Number of eggs	-0.3 [-0.49, -0.11]	424.34	-3.15	0.002
	Starting distance	1.45 [1.25, 1.67]	264.14	13.7	<0.001
	Date	-0.17 [-0.45, 0.11]	42.14	-1.27	0.211
300	(Intercept)	7.33 [5.99, 8.71]	2.78	11.87	0.002
	Fox UD score	-0.23 [-0.45, 0.01]	402.52	-1.98	0.049
	Number of eggs	-0.3 [-0.49, -0.11]	424.37	-3.15	0.002
	Starting distance	1.46 [1.25, 1.67]	264.68	13.69	<0.001
	Date	-0.16 [-0.45, 0.11]	42.35	-1.21	0.230
350	(Intercept)	7.33 [6.01, 8.68]	2.78	12.08	0.002
	Fox UD score	-0.20 [-0.42, 0.04]	396.55	-1.69	0.091
	Number of eggs	-0.30 [-0.48, -0.11]	424.42	-3.13	0.002
	Starting distance	1.46 [1.25, 1.67]	266.50	13.67	<0.001
	Date	-0.16 [-0.44, 0.12]	43.01	-1.17	0.250
400	(Intercept)	7.33 [6.03, 8.66]	2.78	12.25	0.002
	Fox UD score	-0.17 [-0.39, 0.07]	392.59	-1.46	0.146
	Number of eggs	-0.30 [-0.48, -0.11]	424.48	-3.12	0.002
	Starting distance	1.46 [1.25, 1.68]	268.83	13.67	<0.001
	Date	-0.15 [-0.44, 0.12]	43.69	-1.13	0.265

Notes: Number of eggs, starting distance of the observer, and date were included as covariates. Territory ID and observer ID were fitted as random effects, and models were repeated for the five UD with smoothing parameters ranging from 200 to 400 m ($n = 458$ goose nests). All fixed effects are centered and standardized. Significant effects are in bold. See Appendix S1: Table S3 for variance values of random effects.

Table 3. Results from conditional logistic regressions with a use-available design testing the effect of fox UD score on the nest distribution of (A) birds nesting in habitats easily accessible to foxes ($n = 44$ nests from 10 species) and (B) birds nesting in microhabitats providing a refuge against foxes ($n = 65$ nests from 3 species).

Radius of nest area (m)	UD smoothing parameter (m)	(A) Nests in easily accessible habitats			(B) Nests in refuges		
		Coefficient [95% CI]	z	P	Coefficient [95% CI]	z	P
1000	200	-9.81 [-18.42, -1.20]	-2.23	0.026	0.93 [-7.36, 9.23]	0.22	0.826
	250	-7.12 [-13.86, -0.39]	-2.07	0.038	0.50 [-6.14, 7.13]	0.15	0.884
	300	-5.58 [-11.17, -0.002]	-1.96	0.050	1.13 [-5.45, 5.70]	0.04	0.965
	350	-4.46 [-9.23, 0.32]	-1.83	0.067	-0.20 [-5.06, 4.67]	-0.08	0.937
	400	-3.53 [-7.69, 0.63]	-1.66	0.097	-0.46 [-4.84, 3.92]	-0.20	0.838
1500	200	-10.61 [-18.60, -2.61]	-2.60	0.009	4.43 [-1.66, 10.52]	1.43	0.154
	250	-7.70 [-13.82, -1.57]	-2.46	0.014	3.24 [-1.47, 7.96]	1.35	0.178
	300	-6.04 [-11.05, -1.04]	-2.37	0.018	2.40 [-1.49, 6.30]	1.21	0.226
	350	-4.89 [-9.13, -0.66]	-2.26	0.024	1.79 [-1.54, 5.12]	1.05	0.293
	400	-4.01 [-7.68, -0.34]	-2.14	0.032	1.36 [-1.58, 4.31]	0.91	0.365
2000	200	-9.87 [-17.33, -2.41]	-2.59	0.009	3.50 [-1.79, 8.78]	1.30	0.195
	250	-7.04 [-12.67, -1.41]	-2.45	0.014	2.44 [-1.64, 6.51]	1.17	0.241
	300	-5.42 [-9.95, -0.88]	-2.34	0.019	1.74 [-1.63, 5.11]	1.01	0.312
	350	-4.29 [-8.07, -0.50]	-2.22	0.026	1.28 [-1.60, 4.16]	0.87	0.385
	400	-3.44 [-6.68, -0.21]	-2.09	0.037	0.97 [-1.56, 3.50]	0.75	0.453
2500	200	-8.05 [-14.82, -1.28]	-2.33	0.020	3.47 [-1.82, 8.76]	1.29	0.199
	250	-5.68 [-10.77, -0.59]	-2.19	0.029	2.55 [-1.51, 6.60]	1.23	0.218
	300	-4.35 [-8.44, -0.26]	-2.08	0.037	1.92 [-1.41, 5.25]	1.13	0.258
	350	-3.45 [-6.86, -0.04]	-1.98	0.048	1.47 [-1.38, 4.31]	1.01	0.312
	400	-2.78 [-5.69, 0.14]	-1.87	0.062	1.15 [-1.36, 3.64]	0.90	0.371
3000	200	-7.03 [-13.61, -0.45]	-2.10	0.036	3.78 [-1.48, 9.05]	1.41	0.159
	250	-4.99 [-9.90, -0.08]	-1.99	0.047	2.79 [-1.21, 6.80]	1.37	0.171
	300	-3.83 [-7.75, 0.09]	-1.91	0.056	2.16 [-1.11, 5.43]	1.30	0.195
	350	-3.02 [-6.28, 0.23]	-1.82	0.068	1.70 [-1.07, 4.48]	1.20	0.229
	400	-2.42 [-5.19, 0.35]	-1.71	0.087	1.37 [-1.06, 3.80]	1.11	0.269

Notes: Coefficient estimates are presented for 25 models, each reflecting a given size of the nest area (from 1000 to 3000 m) and UD smoothing parameter (from 200 to 400 m). Significant effects are in bold.

probability of nest occurrence declined steeply as fox UD score increased (Fig. 3c). The effect of fox UD score on nest distribution was significant or almost significant (with P values only slightly over 0.05 and the upper limit of confidence intervals slightly over 0) for all five fox activity landscapes (smoothing parameters of 200–400 m) and five nest area sizes (radii of 1000–3000 m) (Table 3). Coefficient estimates were larger for the smallest UD smoothing parameters (Table 3), suggesting that risk was more likely to affect bird nest distribution at the finest spatial scales.

For bird species nesting in refuges, fox UD score did not affect the probability of nest occurrence, whatever the smoothing parameter or nest area radius (Table 3). Fox UD scores of nesting locations were not statistically different from those of random islets (Table 3). Variation in the

number of random islets available for testing did not affect results (Appendix S2).

DISCUSSION

The diversity of prey risk management strategies in a heterogeneous landscape needs to be considered to fully assess the ecological context of the landscape of fear (Gaynor et al. 2019). Using high-resolution arctic fox GPS data, behavioral observations, and field experiments, we demonstrated that fine-scale variation in space use of active predators accurately reflects spatial variation in predation risk, and explains anti-predator behavior of a main prey and nest distribution of some incidental prey species in an Arctic terrestrial community (Fig. 4). More specifically, our results demonstrate how a main prey, which is easy to detect and cannot avoid predators in

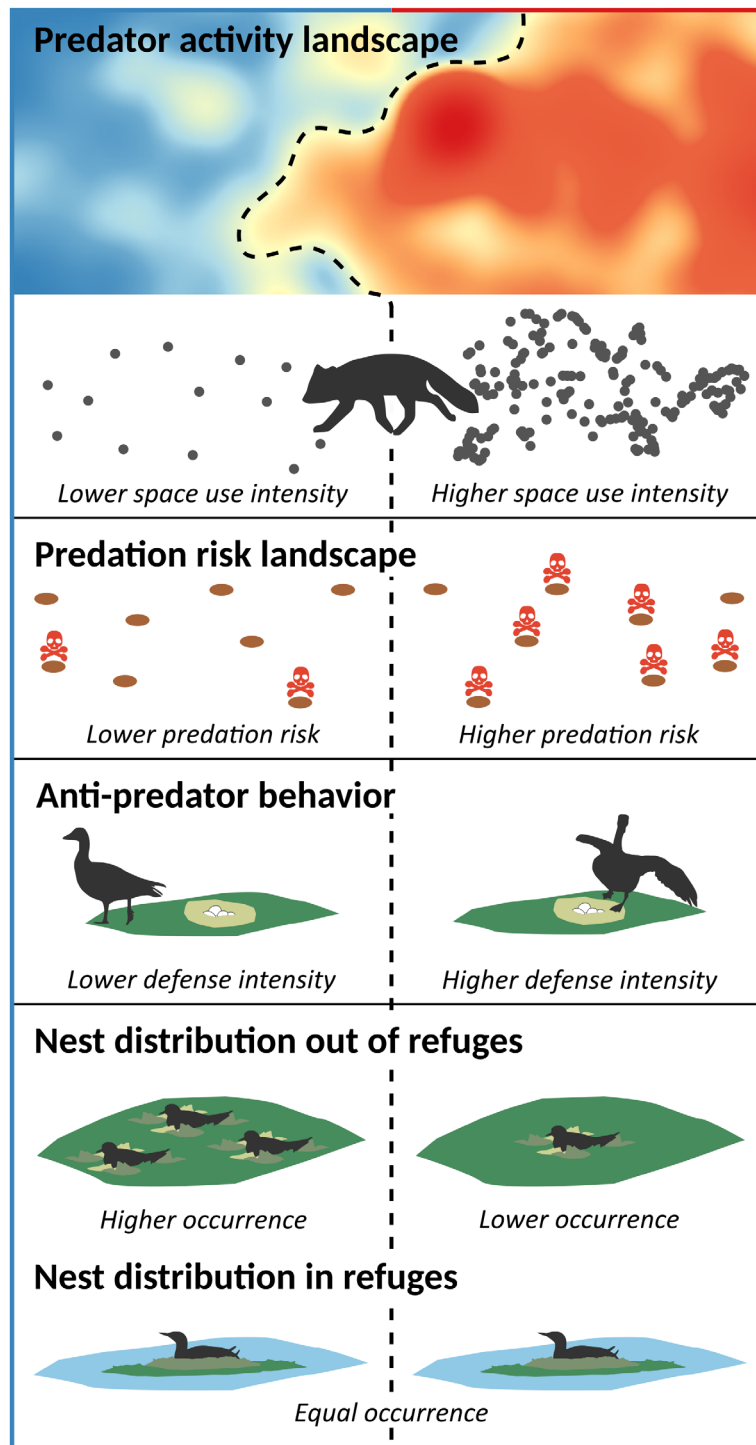


Fig. 4. Landscape of fear context in a terrestrial Arctic community. The predator activity landscape generates a space, rely on reactive anti-predator behavior and incidental prey that do not nest in refuges are located in areas of lowest fox utilization, while show more intense nest defense in areas of highest risk. In contrast, we found that species of incidental prey that do nest in refuges may be

(Fig. 4. *Continued*)

landscape of predation risk and predicts anti-predator response and distribution of some prey species. The illustrated predator activity landscape shows the multiple spatial gradients of intensity in arctic fox space use (low in blue, high in red). The relationship between the predator activity landscape and the predation risk landscape is demonstrated by an artificial prey experiment. The predator activity landscape predicts anti-predator behavior of a main prey (here, snow goose) and nest distribution of incidental prey (here, a shorebird) nesting in habitats easily accessed by foxes. However, the nest distribution of incidental prey (here, a loon) nesting on small patches surrounded by water (i.e., islets acting as refuges) is independent of the predator activity landscape, which reflects fox utilization of the surrounding area rather than microhabitat use.

found in areas of high risk because they avoid risk at finer spatial scales. This suggests that some incidental prey that are consumed only opportunistically may be able to win the predator-prey space race. Overall, our study examining predation risk effects generated by predator activity on multiple prey species highlights the diversity of prey responses that occur at various spatial scales.

The predator activity landscape as a predation risk landscape

We obtained a predator activity landscape that robustly depicted fine-scale variation in fox intensity of space use, thanks to the use of fox movement data collected at a high frequency in combination with the identification of active and resting behavioral states (see Grenier-Potvin et al. 2021, for what underlies variation in arctic fox space use). An artificial prey experiment using baits demonstrated that predation risk was highest in areas highly used by foxes and therefore that predation risk for prey was related to spatial variation in fox space use. Our sensitivity analyses also confirmed the robustness of our results, which were consistent across our range of UD smoothing parameters (Tables 1, 2, and 3).

Obtaining a good map of predation risk requires accurate spatial modeling of predator density, which is difficult to do from a limited number of predator locations or from proxies of predator space use, such as habitat features. Our study demonstrates the value of using fine-scale predator movements to characterize the landscape of predation risk in landscape of fear studies. Also, multi-predator systems impose multiple and contrasting landscapes of risk to prey (Thaker et al. 2011, Gaynor et al. 2019). In

this study, we were able to accurately depict spatial variation in predation risk because all foxes living in our study area were collared, and foxes are the main predators of nesting birds (McKinnon and Bêty 2009, Gauthier et al. 2011).

The predator activity landscape explains goose nest defense intensity

Nesting snow geese can hardly use spatial avoidance to reduce predation risk, since active foxes select patches where goose nest density is highest (Grenier-Potvin et al. 2021). Geese nonetheless use nest defense when predation risk of their nest is imminent (Bêty et al. 2002, Lima 2009). We found that this reactive risk management strategy was related to the level of risk, as snow geese nesting in areas highly used by foxes showed the highest level of nest defense. Indeed, geese nesting in high fox use areas face greater risks of nest predation when leaving their nest unattended (due to a greater density of foxes) and should thus defend their nest more intensely when approached by a potential predator (here, a human). The relationship between goose nest defense and the predator activity landscape likely results from plastic adjustments of anti-predator behavior in response to variation in predation risk, as in female ungulates that are more vigilant where wolf presence is highest (Laundré et al. 2001). Assessing anti-predator behavior on the same individuals along a gradient of predation risk (Fontaine and Martin 2006, Mathot et al. 2011) would, however, be required to fully understand the underlying mechanisms explaining the observed patterns. Nonetheless, our results suggest that predator space use influences prey behavior, with potential benefits to prey fitness (Cresswell 2008).

The effect of local fox activity on goose flushing distance was moderate compared with the effect of the observer's starting distance, and model outputs slightly differed according to UD smoothing parameter (Table 2). Variables not considered may further explain variation in goose nest defense, such as the presence of conspecifics (Kazama et al. 2011), prey physiological state, or timing of breeding that affects the expected fitness value of the clutch (Béty et al. 2003). Finally, nest visibility in the landscape may also affect perception of predation risk level and response to the predator activity landscape (Gaynor et al. 2019).

Microhabitats modulate the effect of the predator activity landscape on the distribution of incidental prey

We found that the physical landscape, along with the nesting behavior of prey, intervened in the ecological context of the landscape of fear. Microhabitats modulated the effects of the predator activity landscape on the distribution of incidental prey, as species proactively mitigated predation risk at different spatial scales, either by nesting in microhabitat refuges or by nesting in areas of low predator activity. Indeed, cackling geese, glaucous gulls, and red-throated loons nest essentially on islets serving as refuges against fox predation (Gauthier et al. 2015). Accordingly, we found that the probability of nest occurrence of these birds was independent of the predator activity landscape, which at its measured spatial resolution reflected fox utilization of the surrounding area rather than the nest location per se. In fact, species using microhabitat refuges can likely better afford to have their nest surrounded by a relatively risky landscape, because they avoid predation risk at a finer spatial scale. On the contrary, species nesting in habitats easily accessible to foxes may perceive predation risk and avoid nesting in areas highly used by foxes, possibly by shifting location when encountering predators during nest building (Peluc et al. 2008). The ability to choose a safe nest location can also be adaptive, such as in shorebirds nesting strictly on stony shores (Léandri-Breton and Béty 2020), which are avoided by active foxes (Grenier-Potvin et al. 2021). However, nest distribution away from risky areas may also result from consumptive effects of predation, as nests located in areas highly used by

foxes may have been preyed upon before we detected them. Monitoring fine-scale bird movements during nest establishment (Gilbert et al. 2016) and locating nests before any predation occurs would help investigating the ability of nesting birds to perceive and respond to predation risk, and thus win the predator-prey space race.

In this study, we assessed nest distribution of passerines, shorebirds, ducks, geese, and birds of prey, and grouped species according to whether they used microhabitat refuges or not. Although all species share arctic fox as their main predator and are thus functionally linked, they also differ in their nesting ecology and different variables may influence their nest distribution. It will thus be interesting to replicate our work with increased sample sizes to test hypotheses about potential differences in the way species respond to the predator activity landscape. Finally, animals face a variety of physiological, phylogenetic, and ecological constraints that limit their ability to assess predation risk and respond to the landscape of fear (Jordan and Ryan 2015, Gaynor et al. 2019). Directly measuring how prey perceive predation risk would increase our understanding of the complex relationships linking predation risk and prey responses, despite the challenges that this approach entails (Gaynor et al. 2019).

Conclusion

Our study demonstrates predation risk effects resulting from the movements of an active predator shared by a community of nesting birds. We showed how prey that are searched for by predators and cannot avoid them in space mitigate risk reactively through anti-predator behavior, while prey that are consumed only opportunistically can win the space race by avoiding risk proactively through habitat selection occurring at different spatial scales. Assessing the landscape of fear context in an animal community allows to better understand prey species behavior and distribution, thus clarifying key aspects of the structure and functioning of ecosystems.

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J. Clermont, J. Bêty, and D. Berteaux conceived the study with contributions from coauthors. All authors contributed to field planning or data acquisition. J. Clermont conducted statistical analyses, with significant help from A. Grenier-Potvin and contributions from coauthors. J. Clermont led the writing, with contributions from coauthors.

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DATA AVAILABILITY

Arctic fox GPS data are available from Movebank: https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study1241071371

Other data sets (artificial prey experiment, goose behavior and bird nest distribution) are available from Dryad: <https://doi.org/10.5061/dryad.vdncjsxvd>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3858/full>