Predator activity, proactive anti-predator strategies, and nesting phenology produce a dynamic landscape of risk to tundra goose reproduction

Sean M. Johnson-Bice[1,3], Chloé Warret Rodrigues[1], Holly E.L. Gamblin[1], Frank B. Baldwin[2], James D. Roth[1]

[1]Department of Biological Sciences, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada
[2]Environment and Climate Change Canada, Canadian Wildlife Service, Winnipeg, Manitoba R3C 1M8, Canada
[3]Corresponding author. Email: s.johnsonbice@gmail.com

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Conflict of interest

The authors declare no conflict of interest.

Author contributions

S.M.J-B. led the data curation, data analysis, data visualization, and writing and editing of the manuscript. S.M.J-B., C.W.R., H.E.L.G., and J.D.R. helped collect the data. All authors contributed to the conceptualization, study design, and revising of the manuscript.

Statement on inclusion

All authors of our study are based in the same province and country where the research took place (Manitoba, Canada).

Data availability statement

All data and R code associated with this study will be permanently archived in the figshare data repository upon acceptance.

Abstract

Birds generally rely on proactive anti-predator strategies when selecting nest sites, as they have limited options to adapt to changing levels of risk once incubation begins. Arctic waterfowl often nest colonially as an anti-predator strategy but dispersed-breeding species may use other proactive strategies, such as nesting in less risky areas. However, empirical links between spatial patterns of predation risk and nest habitat selection or success are needed to better understand how predator activity shapes Arctic waterfowl reproduction. Using activity data from the main cursorial nest predators, Arctic and red foxes (*Vulpes lagopus*, *V. vulpes*), and activity data from aerial predators, we evaluate the influence predator activity has on Canada goose (*Branta canadensis interior*) nest habitat selection and success, and how nesting phenology mediates these effects. By comparing habitat selection models fit to i) goose nest locations and ii) fox locations obtained from GPS-collars, we show that geese and foxes display nearly opposite patterns of selection for the same landscape traits. Geese selected sites that appeared to minimize their probability of encountering foxes while also maximizing their ability to detect foxes. Spatial predictions of fox activity revealed nests located in areas with higher probability of fox use had lower nest success, indicating fox space-use patterns reflect predation risk. Nests initiated earlier had a greater probability of nest success, but these patterns strongly depended on location; the benefits of nesting early were largely lost in areas of high fox activity. We also found a negative relationship between clutch size and incubation date, suggesting nests incubated later had higher rates of failure likely due, in part, to geese being in poorer body condition. Although nest success was lower in areas with high aerial predator activity, fox activity likely has a greater influence on goose nest spatial patterns due largely to movement constraints imposed by tundra landscape features on foxes but not aerial predators. Our study demonstrates the mechanisms by which nesting phenology and predator activity interact to shape bird reproduction, and provides an empirical demonstration of the value of incorporating temporal dynamics into the "landscape of fear" framework.

Keywords: anti-predator behavior; Arctic fox; Canada goose; landscape of fear; movement ecology; nest success; predation risk; predator-prey interactions

Introduction

Responses to predation risk range from "reactive responses" of immediate, short-term risk to "proactive responses" to risk that occur before interacting with predators (Creel et al., 2014; Creel, 2018). Reactive responses typically involve actions that promote the prey's escape from an attacking predator, such as fleeing or exhibiting reciprocal aggressive behavior (Bêty et al., 2002; Courbin et al., 2016). Proactive responses are decisions that reduce the probability of interacting with predators, or increase the probability prey will survive an expected encounter (e.g., responses in areas of high predator activity). One way that prey proactively mitigate predation risk is by changing their space use patterns based on perceived patterns of risk (Lima, 2002). These behavioral responses of prey to predation risk underlie the "landscape of fear" concept, whereby the landscape interacts with predator space use and prey perception of risk to generate expected levels of predation risk across space and time (Laundré et al., 2010; Gaynor et al., 2019). While mobile prey may readily adapt their proactive antipredator responses to changing levels of risk, immobile prey have fewer options once they are anchored to a location.

Predation is a major source of failure and mortality for bird nests, and birds often use proactive strategies to manage risk when selecting nest sites. Proactive antipredator responses require knowledge of, or direct experience with, predation risk, and birds rely on numerous information sources to gauge risk (Lima, 2009; Chalfoun & Schmidt, 2012). For example, birds can obtain information on predation risk while moving throughout the breeding grounds (Reed et al., 1999) or gaining information from previous breeding attempts (Schmidt, 2001; Hoover, 2003). They can then incorporate this information into their nest site decision-making, such as by choosing nest sites in areas of low predator activity (Schmidt et al., 2006) or sites that promote other antipredator responses (e.g., characteristics that enhance predator detection; Amat & Masero, 2004; Keyel et al., 2013). Despite widespread recognition that predation is a strong selective pressure on bird nesting biology, empirical evaluations linking spatial patterns of risk to nest site selection and survival remain sparse (Lima, 2009; Clermont et al., 2021).

In tundra ecosystems, Arctic birds have adapted proactive antipredator responses that can cope with relatively high exposure to predators due to the short vegetation. Smaller Arctic birds can mitigate nest predation by having cryptically colored nests/eggs or concealing their nests in the short vegetation (e.g., Liebezeit et al., 2009; Ims et al., 2019), but these strategies are harder for larger species like waterfowl. Consequently, Arctic waterfowl commonly nest in large, dense colonies that offer antipredator benefits like predator swamping (Baldwin et al., 2011; Iles et al., 2013), and mutual vigilance and mobbing responses (Burger, 1981; Samelius & Alisauskas, 2001). However, some species, like the Canada goose (*Branta canadensis interior*), breed more dispersed. Although Canada geese nest in clumps at broader spatial scales, they exhibit strong territoriality and distance themselves from neighbors at smaller scales (Reiter & Andersen, 2013). This spacing strategy may help geese reduce encounters with predators by dispersing themselves throughout the landscape, while still being close enough to neighbors to obtain information on attacking predators. When available, Canada geese may select nest sites in microhabitat refuges that restrict terrestrial predators' access, such as on small islets, or within colonies of other species to presumably exploit the antipredator benefits these colonies offer (Baldwin et al., 2011). However, when these antipredator features are limited, geese often select nest sites in open areas that likely promote visual detection of predators (Miller et al., 2007).

Predation risk varies across time as well as space, indicating that an integrated spatiotemporal perspective may better characterize risk (Palmer et al., 2022). For instance, accounting for diel behavioral patterns revealed vicuñas (*Vicugna vicugna*) forage in areas of high predation risk from pumas (*Puma concolor*) during times they have learned are less risky (Smith et al., 2019). For Arctic waterfowl, clear temporal patterns in nesting success often emerge based on the date waterfowl begin nesting, with usually greater rates of nest survival the earlier nesting is initiated (Baldwin et al., 2011; Ross et al., 2017; Clermont et al., 2018). Thus, nesting phenology could potentially mediate spatial patterns of predation risk to breeding waterfowl.

The over-arching objective of this study was to evaluate how predator activity affects nest habitat selection and nesting success of a dispersed-nesting goose, and whether these effects are mediated by nesting phenology. To our knowledge there has been no direct evaluation assessing spatial patterns of predation risk on Canada goose nesting ecology, much less how the timing of nesting affects these dynamics, obscuring our understanding of the degree to which predation risk acts as a constraining influence and selective pressure on Canada goose reproduction. We first evaluated whether predator activity constrains the spatial distribution of Canada goose nests in the low-Arctic tundra by comparing habitat selection preferences from models—incorporating the same predictor variables—fit to (1) goose nest locations and (2) Arctic (*Vulpes lagopus*) and red fox (*V. vulpes*) locations obtained with GPS-collars. We hypothesized that geese select for nest sites in areas with a low probability of fox use to minimize encounters with foxes, and therefore predicted that habitat selection patterns would be nearly opposite for goose nest and fox locations. We then evaluated whether spatial patterns of predator activity (fox movement data and aerial predator counts) can predict the reproductive success of geese (i.e., evaluating whether nest success was lower in areas of high predator activity), and how nesting phenology affects nest survival rates across varying levels of expected predation risk. Together, this approach allowed us to evaluate to what degree predator activity acts as a selective pressure on goose reproduction by generating expected spatial variation in predation risk, and how incorporating temporal dynamics into these spatial patterns, characterized by nesting phenology, may improve our understanding of this predator-prey relationship.

Methods

Study area

Our study was conducted in Wapusk National Park in northeastern Manitoba, Canada, along the coast of Hudson Bay (Fig. 1). The Wapusk tundra is typified by large swaths of fen, lakes and ponds, and elevated beach ridges formed by isostatic rebound that run approximately parallel to the coastline (Ritchie, 1956; Sella et al., 2007). There are 85 known fox dens within the Wapusk tundra, nearly all of which are located on beach ridges (Roth, 2003; Johnson-Bice et al., 2023, Chapter 3).

The most common goose species are the lesser snow goose (*Chen caerulescens caerulescens*) and the Canada goose. These two species exhibit somewhat different nesting strategies: lesser snow geese nest in large colonies, while Canada goose nests are dispersed. The Wapusk lesser snow goose population dramatically increased in abundance from the 1960s through the 2010s, causing well-documented and widespread changes in tundra vegetation throughout the area (e.g., Cargill & Jefferies, 1984; Jano et al., 1998; Jefferies et al., 2006). During spring, snow geese grub for roots and rhizomes, causing vegetative losses and alterations to the soil sediments (Kerbes et al., 1990). These vegetation changes are most pronounced near the La Pèrouse Bay snow goose colony ~12 km west of our core study area, but parts of our study area were also altered by goose foraging. Approximately 95% of goose nests in our core study area are Canada goose nests, so we excluded snow goose nests here for simplicity.

Arctic and red foxes are the primary cursorial (i.e., ground-based) goose nest predators in the area, along with occasional predation from polar (*Ursus maritimus*) and grizzly (*U. arctos*) bears. Red fox presence in the study area has increased in recent years as Arctic fox abundance has declined, in part due to climate change (Moizan et al., 2023; Verstege et al., 2023). Herring gulls (*Larus argentatus*) are the most common aerial nest predator, but other aerial predators like glaucous gulls (*L. hyperboreus*), parasitic (*Stercorarius parasiticus*) and long-tailed (*S. longicaudus*) jaegers, common ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), and sandhill cranes (*Grus canadensis*) are also relatively common.

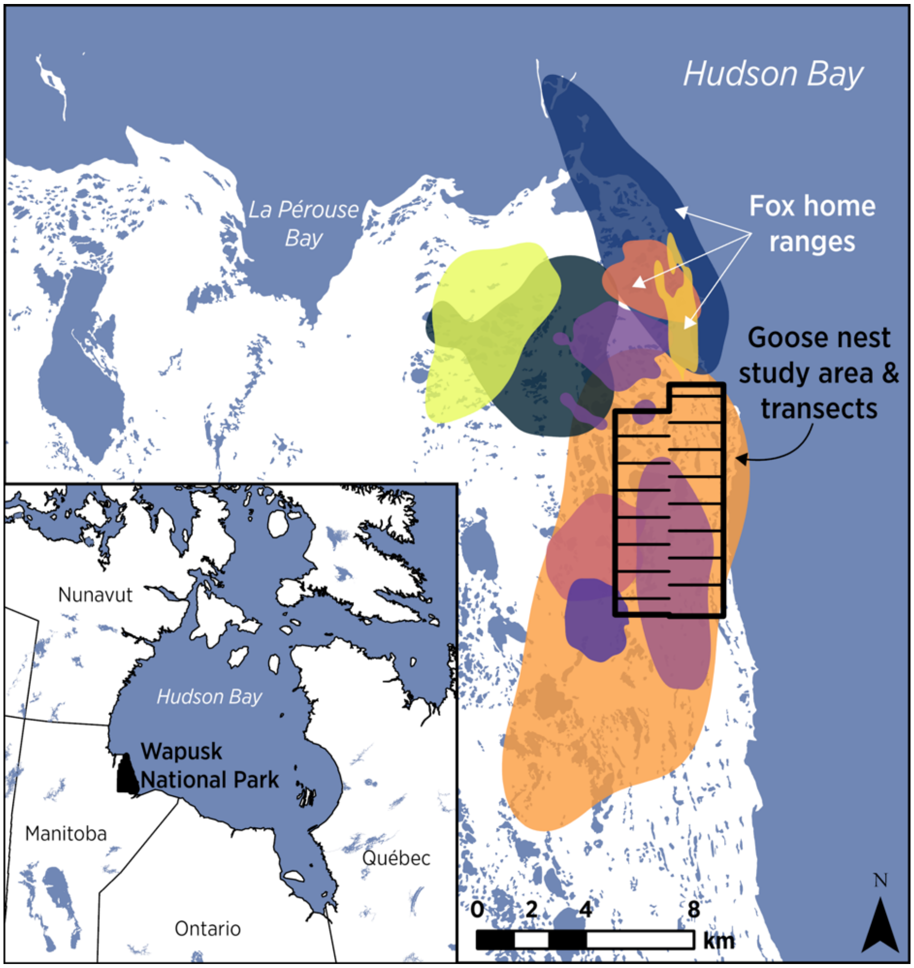

Figure 1. Study area within Wapusk National Park, Manitoba, Canada, along the western coast of Hudson Bay. Each of the 10 colored polygons represent the home range of a collared Arctic (*Vulpes lagopus*) or red (*V. vulpes*) fox. The black polygon outline denotes the boundary of the goose nest study area, with the 15 transects from one year shown. (Note: the large home range in orange is from a non-breeding Arctic fox that roamed throughout the study area).

Goose nest surveys and assessing nest fate

We conducted goose nest surveys between June 8 and 18, 2014–2023 (excluding 2020) using line-transect methods. Each year, we located goose nests along 15 2-km long transects spaced 1 km apart (7 transects in the west portion of the study area, 8 transects in the east, offset by 500m; Fig. 1). The transects were oriented east-west, generally perpendicular to the beach ridges. The northing value of the northernmost transect was randomly generated each year, resulting in slightly different transects to obtain full coverage of the study area across all study years.

During surveys, 3–5 observers walked along each transect and searched for goose nests using binoculars. Once a nest was detected, we slowly approached the nest until the goose flushed, then recorded the clutch size and nest location using a handheld GPS unit. Nest processing was done as rapidly as possible (usually <2 min) to minimize disturbance. If eggs were present we recorded float stage, reflecting development age, which we later used to estimate incubation initiation date (hereafter "incubation date") assuming a 28-day incubation period (Reiter & Andersen, 2008). If eggs were pipped or goslings were present, we assumed incubation began 28 days prior to the survey date. If a nest contained fresh down but no eggs, we assumed the nest had either been depredated or the eggs had already hatched. We determined the fate of nests from the presence (hatched) or absence (depredated) of large pieces of membrane (corresponding to at least one hatched egg) in or near the nest (Reiter & Andersen, 2011). Nests were revisited in late July to early August to assess nest fate, although nest fate data was sporadically collected until 2021. We also recorded the number of aerial predators observed on each transect as an index of aerial predator activity.

Fox capture, collaring, and home range analysis

We captured Arctic and red foxes during 2017–2023 using padded leghold and Tomahawk live traps (for details on captures and collaring see (Warret Rodrigues & Roth, 2023a, b). Foxes were fit with GPS collars that recorded locations every 1.5 or 2 h during the goose nesting season (Iridium satellite collars #4170 or 4270, Telonics, Mesa, Arizona, USA). Foxes captured during 2022–2023 (n=5) were fit with collars that recorded locations every 15 min (0.25 hr) during one 6-hr period each day, with the 6-hr period changing daily to ensure locations were recorded across the full 24-hr diel period. We thinned the locations obtained from these foxes to one location every 1.5 hr to match fix rates of the other foxes. For this study, we included only foxes with home ranges near the goose nesting study area (n=10 foxes; 2 red and 8 Arctic, Fig. 1) during the primary nesting period. All handling procedures were approved by the University of Manitoba Animal Care Committee (Protocol F17-012). Research permits were obtained from Parks Canada (WAP-2017-25781, WAP-2018-27938), Manitoba Wildlife (WB18911, WB20226, WB21856, WB25383, WB25857), and Environment and Climate Change Canada (14-MB-SC002, 21-MB-SC001).

We constructed home ranges for each collared fox to delineate boundaries within which 'available' locations would be generated for the used–available habitat selection analysis. We first retained only GPS locations collected during the goose nesting period (defined as May 15–June 30), and then generated 95% autocorrelated kernel density home ranges for each fox following guidelines from the *ctmm* R package (see Calabrese et al., 2016 for details).

Goose nest and fox habitat selection study design

We compared fox and goose nest habitat selection by fitting two separate models incorporating the same landscape variables in a used–available study design. For both models, we randomly generated 100 available locations for every used (observed) location. Fox available locations were generated within each fox's home range. Goose nest available locations were generated within 300 m of the survey transects (~97% of nests found during surveys were located within this threshold). Some nests were used in multiple years, so only the first observation of a nest was included in the habitat selection model. We excluded all nests categorized as 'open water' from the land cover data set (~12%), as these nests were largely located on small islets within lakes/ponds and the spatial resolution of our habitat data precluded evaluating whether/how geese select for islets. Although islets can be refuges from terrestrial predators (Clermont et al., 2021; Duchesne et al., 2021), our data indicated there was likely no substantial difference in nest success (0.56 vs. 0.51 average success).

We used the same four variables for both habitat selection models to allow for direct comparison: land cover type, distance to nearest patch of open water, distance to nearest beach ridge, and an index of terrain ruggedness. Since geese should select for areas that reduce the likelihood of nest depredation, we predicted geese select nest sites that were close to open water, which would reduce the number of directions from which foxes could approach the nests and also limit the distance females needed to travel to drink. We also predicted geese would nest in relatively flat areas, to aid in visual detection of predators, and far from beach ridges that contain almost all of the fox dens in the area and also function as wildlife corridors (beach ridges are one of the few dry habitats).

We used a 5-m resolution data set developed for Wapusk National Park as our land cover data (Ponomarenko et al., 2014), reclassified into 7 different categories (Appendix 4, Table S.1): 'Fen', 'Goose-affected', 'Dryas heath', 'Shallow water/sedge fen', 'Unvegetated', 'Shrub/willow', and 'Open water'. Goose-affected areas were generally 'Fen' cover types that had been altered by goose foraging, typically characterized with sparse vegetation interspersed with mudflats. Since geese nest on land, we excluded 'Open water' areas from the goose nest analyses but retained it for the fox model, as lakes/ponds are often still frozen during parts of the nesting period and foxes can theoretically swim in these features when unfrozen. Land cover type was then extracted for each used/available point. We also calculated the Euclidean distance (in meters) between each point and the nearest open water patch and beach ridge (*Supporting Information*). We used the 30-m resolution FABDEM elevation data set (Hawker et al., 2022) to create a 5x5 window terrain ruggedness index (TRI) raster using the 'tri' function from the *spatialEco* R package (Evans & Murphy, 2021). Lower TRI values indicate relatively flat areas, whereas higher TRI values indicate relatively uneven ("rugged") areas.

Statistical analyses

Habitat selection models

We compared fox movement and goose nest locations with random (available) locations using binomial generalized linear mixed effects models (GLMMs) with a logit link. Available locations were assigned a weight of 5000, while used locations a weight of 1 (Fieberg et al., 2021). In each model, we log+1 transformed the continuous variables (distance to water, distance to beach ridge, TRI) due to the data being heavily skewed and having some values of 0. 'Fen' was the reference land cover type (categorical variable) as it is the most common cover type in the study area. For the fox movement model, we included a random intercept for 'fox ID' and random slopes to allow all continuous covariates to vary by 'fox ID' (Muff et al., 2020). For the goose nest model, we included a random intercept term for 'year'; model fitting issues precluded also including random slopes (likely due to a negligible effect of 'year'). We verified each fitted model had no collinearity issues (variance inflation factors were <2 for each variable). We evaluated the importance of individual covariates with an $\alpha=0.05$ and whether the 95% confidence intervals overlapped 0. We used spatial (goose nest model) and individual (fox model) blocking cross-validation methods ($n=5$ folds) to evaluate the fit of each habitat selection model (Boyce et al., 2002; Roberts et al., 2017; see *Appendix 4* for full details).

We visualized and compared model results by calculating the relative selection strength (RSS) for each continuous variable from each model (Avgar et al., 2017; Fieberg et al., 2021). RSS is a quantitative measure of the relative magnitude of selection of a given location in relation to another location(s) (Avgar et al. 2017; Fieberg et al. 2021; Northrup et al. 2022), calculated as $\exp(\beta_1 \times X_1 + \beta_2 \times X_2 + \beta_3 \times X_3 + \ldots)$ from each fitted model, where β_1 is the coefficient estimate of variable X_1, β_2 is the coefficient estimate of variable X_2, etc. (i.e., exponentiated model predictions without the intercept term). We calculated RSS scores across a range of values for each covariate relative to the mean value of that covariate from the goose nest data set, with all other variables fixed. This approach allowed us to make direct comparisons of selection strength between the two models under identical conditions. We used the natural log of RSS values for plotting the effects. Log-RSS values >0 show selection for those conditions relative to the mean, whereas values <0 show avoidance relative to the mean.

Nest fate and clutch size analyses

We tested the relationship between goose nest success and relative probability of fox use at each nest site using a binomial GLMM with a logit link (hatched nests=1, failed nests=0). Throughout the study area, we generated estimates of log-RSS values predicted from the fitted fox movement model, and then used the estimated log-RSS value from each nest location as a predictor variable in the nest success model. We included incubation date as another predictor variable, plus an interaction term between incubation date and log-RSS value. Including incubation date meant we excluded depredated clutches that were detected during surveys (~13%). However, given the importance of nesting phenology from previous research, we elected to focus our analysis on nests for which we could estimate incubation date. To evaluate how aerial predator activity influenced nest fate, we included the number of aerial predators observed on the transect as another predictor variable (log-transformed). We included 'year' as a random intercept term; model fitting issues precluded also including random slopes (likely due to a negligible effect of 'year'). We did not include a random intercept term for 'nest ID' (to account for clutches at the same site from multiple years) due to the low number of repeated nest sites in our data (<10%).

We also investigated whether clutches incubated later in the breeding season have smaller clutch sizes, which could be an indirect sign that geese are in worse body condition and likely more vulnerable to depredation. Since we were primarily interested in the over-arching pattern, rather than intra-annual patterns, of how clutch size changes with incubation date, we pooled all years of data and evaluated the relationship between clutch size and incubation date (ordinal day) using a generalized linear model. Clutch size is non-zero integer count data and the data also showed a left skew, so we used a truncated Conway-Maxwell Poisson distribution to obtain a suitable model fit. We performed residual diagnostic checks using the *DHARMa* R package (Hartig, 2022).

All models were fit using the *glmmTMB* R package (Brooks et al., 2017), and we estimated and visualized the marginal effects of predictor variables from the nest fate and clutch size models using the ‘ggemmeans’ function from the *ggeffects* R package (Lüdecke, 2018). All analyses were carried out using R version 4.3.1 (R Core Team, 2023).

Results

During 2014–2023, we detected 697 Canada goose clutches from 559 unique nesting sites. Of the 559 sites, 69 were classified as “open water” and were subsequently excluded from the analyses, leaving 490 sites for the remaining analyses. We assessed the hatching fate (successful/failed) of 422 clutches from these sites, 311 of which we also estimated incubation date and recorded the number of aerial predators observed during the survey. The majority of nests with a known hatch fate but unknown incubation date were nests that were already depredated when detected during surveys (n=56).

We collected 2,048 locations from 10 different GPS-collared foxes (range: 78–397 locations per fox) in the goose nesting study area and nearby vicinity. We detected an average of 14.3 avian predators along each transect (SD=10.8, range: 1–58).

Habitat selection analysis

Overall, Canada geese selected nest sites (n=490) in areas that were predicted to be less used by foxes. Geese selected sites that were close to open water (β=–0.233, z=–6.03, p<0.001). Although foxes showed no significant response to water (β=0.045, z=0.60, p=0.552), the 95% confidence intervals of the coefficient estimates and log-RSS predictions did not overlap between the two models (Fig. 2a). Goose nests tended to be farther from beach ridges (β=0.272, z=6.94, p<0.001), whereas foxes selected for areas close to beach ridges (β=–0.134, z=–2.37, p=0.018; Fig. 2b). Geese selected nest sites located in relatively flat areas (i.e., lower terrain ruggedness index values; β=–0.755, z=–5.97, p<0.001), whereas foxes selected for relatively uneven areas (β=0.579, z=3.82, p<0.001; Fig. 2c).

Foxes and geese also showed different selection preferences for land cover types. Nests were disproportionately located within areas affected by goose foraging (i.e., goose-affected areas; Fig. 2d,e). Geese tended to avoid building nests in Dryas heath, unvegetated, and shrub/willow cover types (Fig. 2d,e). Foxes tended to select land cover types in similar frequencies to their availability, with the notable exception of shrub/willow land cover types and open water (Fig. 2d). The random intercept/slope terms of ‘fox ID’ were influential in the fox movement model, whereas the random intercept term of ‘year’ in the goose nest model had no effect (Appendix 4, Table S.2).

When comparing spatial predictions of areas likely to be used by foxes and geese, the generally opposite patterns of selection become evident (Fig. 3). There was a strong negative correlation between fox movement log-RSS values and goose nest log-RSS values from across the goose nest study area (R^2=0.45, p<0.001).

Cross-validation results indicated both habitat selection models were excellent fits to the data. Across testing folds, the fox movement model had an average Spearman’s *r* value of 0.896 (range: 0.802–0.964) and the goose nest model had an average Spearman’s *r* value of 0.926 (range: 0.878–0.976).

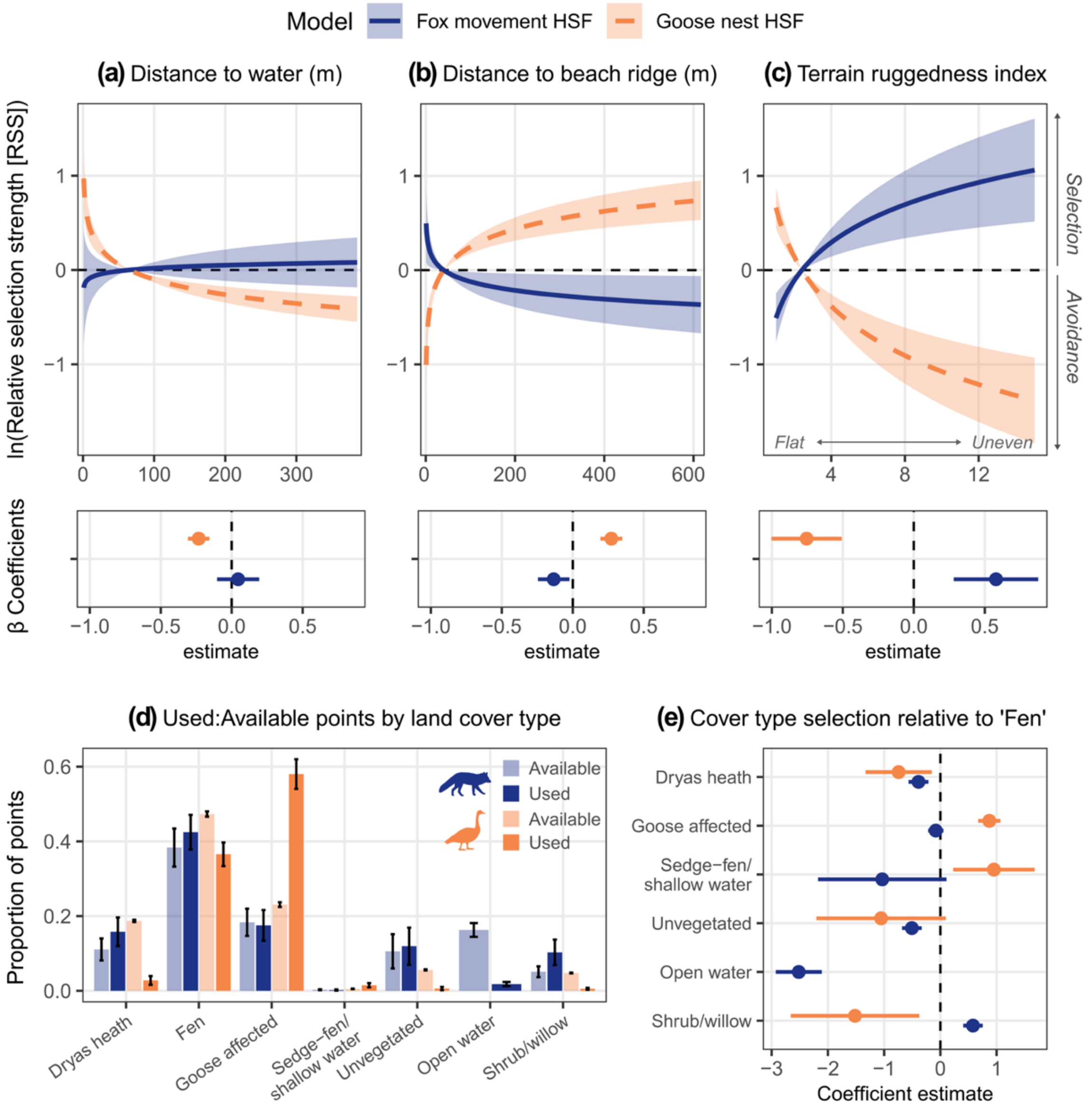

Figure 2. Results from the habitat selection models (HSF) demonstrating how foxes (blue) and geese (orange) showed nearly opposite patterns of selection for the same landscape features in Wapusk National Park, Manitoba, Canada. Panels (a–c) show the log-relative selection strength values (+/-95% confidence intervals [CI]) relative to the mean x-covariate value from the goose nest data (all other covariates were fixed at their mean). Values greater than 0 show selection, whereas values less than 0 show avoidance (model predictions cross 0 at the mean of each x-covariate). Coefficient estimates (+/-95% CI) are shown below in sub-panels. Panel (d) shows the mean (+/- std. error) proportion of used and available points from each land cover type across all 10 foxes (light/dark blue) and all eight years of goose nests. Panel (e) shows the coefficient estimates (+/-95% CI) of each land cover type relative to 'Fen', the reference level used in both fox movement and goose nest habitat selection models.

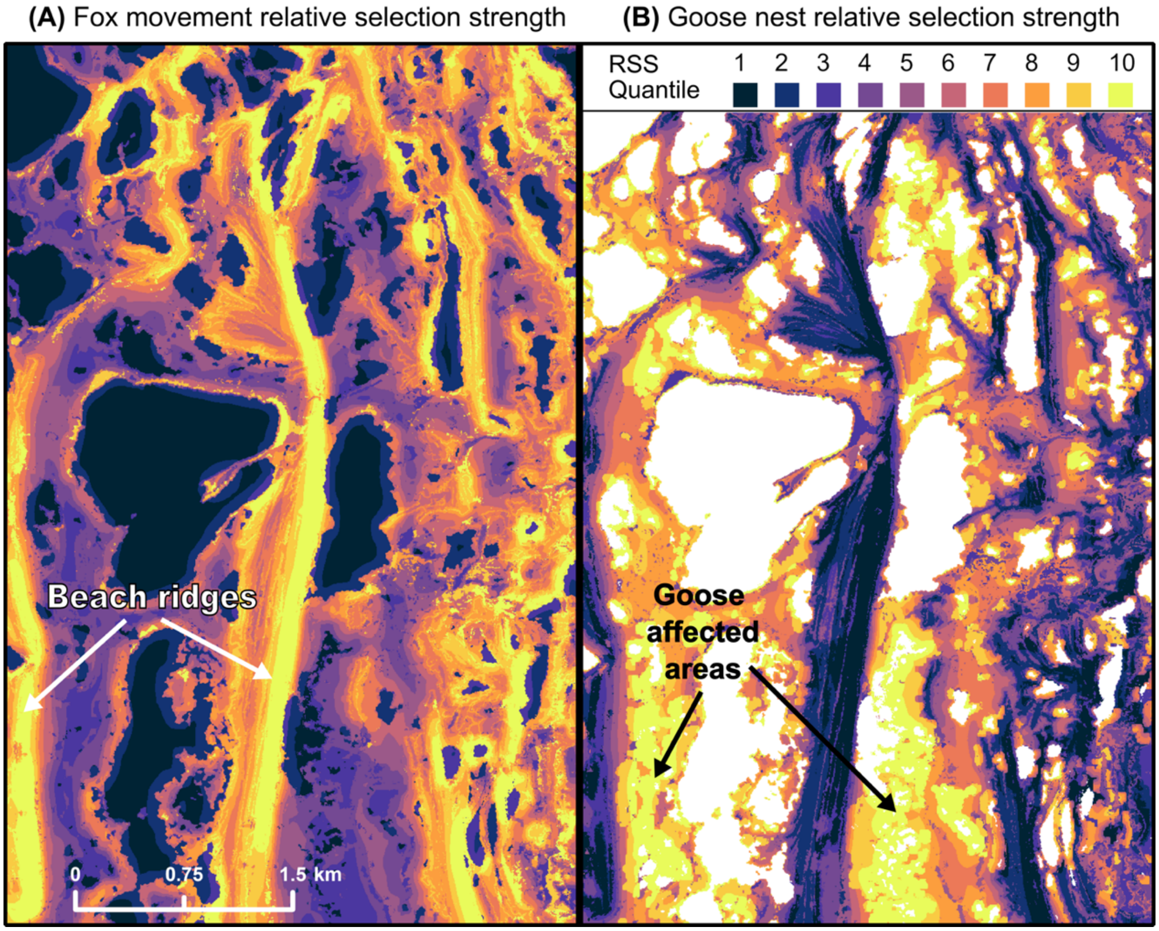

Figure 3. Relative probability of use generated from the fox movement (left) and goose nest (right) habitat selection models. Predictions from both models were binned into 10 equal-sized quantiles. Areas with a low relative selection strength (RSS) are shown in blue/purple and areas with a high RSS value are shown in orange/yellow. The plots show how foxes generally select to move along beach ridges, whereas geese avoid beach ridges and select for goose-affected areas (darkest blue areas in left panel/white areas in right panel are open water, which were excluded in the goose nest model).

Nest fate and clutch size analyses

Annual Canada goose nest success averaged 0.51 (SD=0.25, range: 0.18–0.93). Average incubation date across all nests was May 28, with the average annual start of incubation date ranging from May 19 (2023) to June 5 (2021).

Both avian predator activity and fox activity affected nest success (*n*=311 nests). Predicted fox activity, represented by the estimated log-RSS value from the fox movement model at each nest location (mapped in Fig. 3), was negatively related to the probability of nest success (β=–21.02, *z*=–2.07, *p*=0.038; Table S3). Incubation date had the greatest relative influence on nest success, with clutches incubated earlier having a greater probability of success (β=–0.180, *z*=–

6.10, $p<0.001$). However, these results depended on nest location, as there was a significant interaction between fox log-RSS value and incubation date ($\beta=0.142$, $z=2.09$, $p=0.037$): the benefits of nesting earlier dissipated in areas of high fox activity (Fig. 4a,b). We also found a negative relationship between aerial predator activity (i.e., the number of aerial predators observed during the survey transect) and the probability of nest success ($\beta=-0.372$, $z=-2.11$, $p=0.035$; Figs. 4.4c, 4.5).

Results from the clutch size analysis showed a significant negative relationship between incubation date and clutch size ($\beta=-0.011$, SE=0.003, $z=-4.29$, $p<0.001$, 95% CI: [–0.017, –0.006]; Fig. 6).

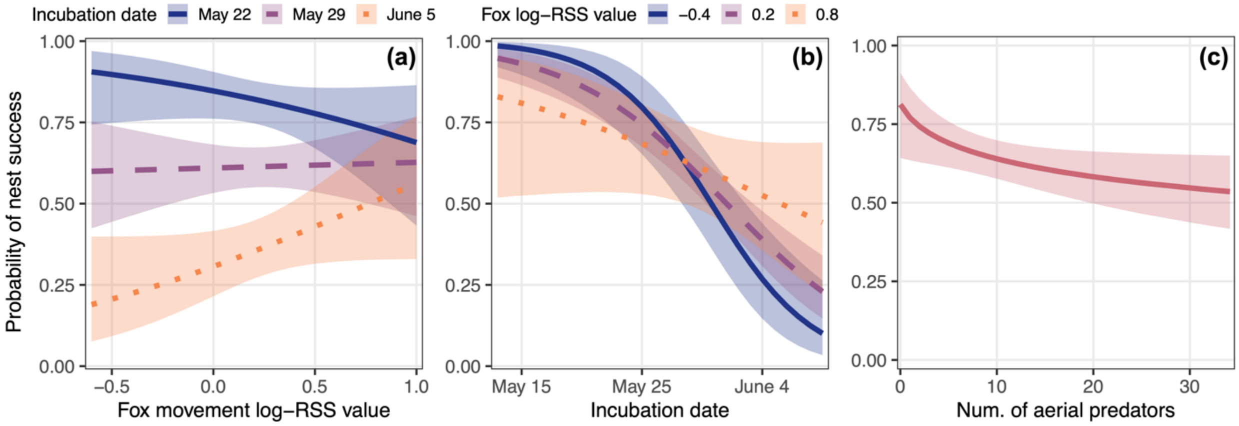

Figure 4. Results from the model evaluating Canada goose nest success (n=311 clutches) in Wapusk National Park, Manitoba, Canada. Panel (a) shows the effects of fox activity (estimated log-relative selection strength [RSS] values) on the probability of nest success at three different goose incubation initiation dates (mean incubation date: May 29, +/- 1 std. deviation). Panel (b) shows the predicted effects of incubation date on the probability of nest success at three different levels of predicted fox activity (low, medium, high). Panel (c) shows the marginal effects of aerial predator activity on the probability of nest success, predicted from the nest fate model. Ribbons represent +/-95% confidence intervals of each estimate.

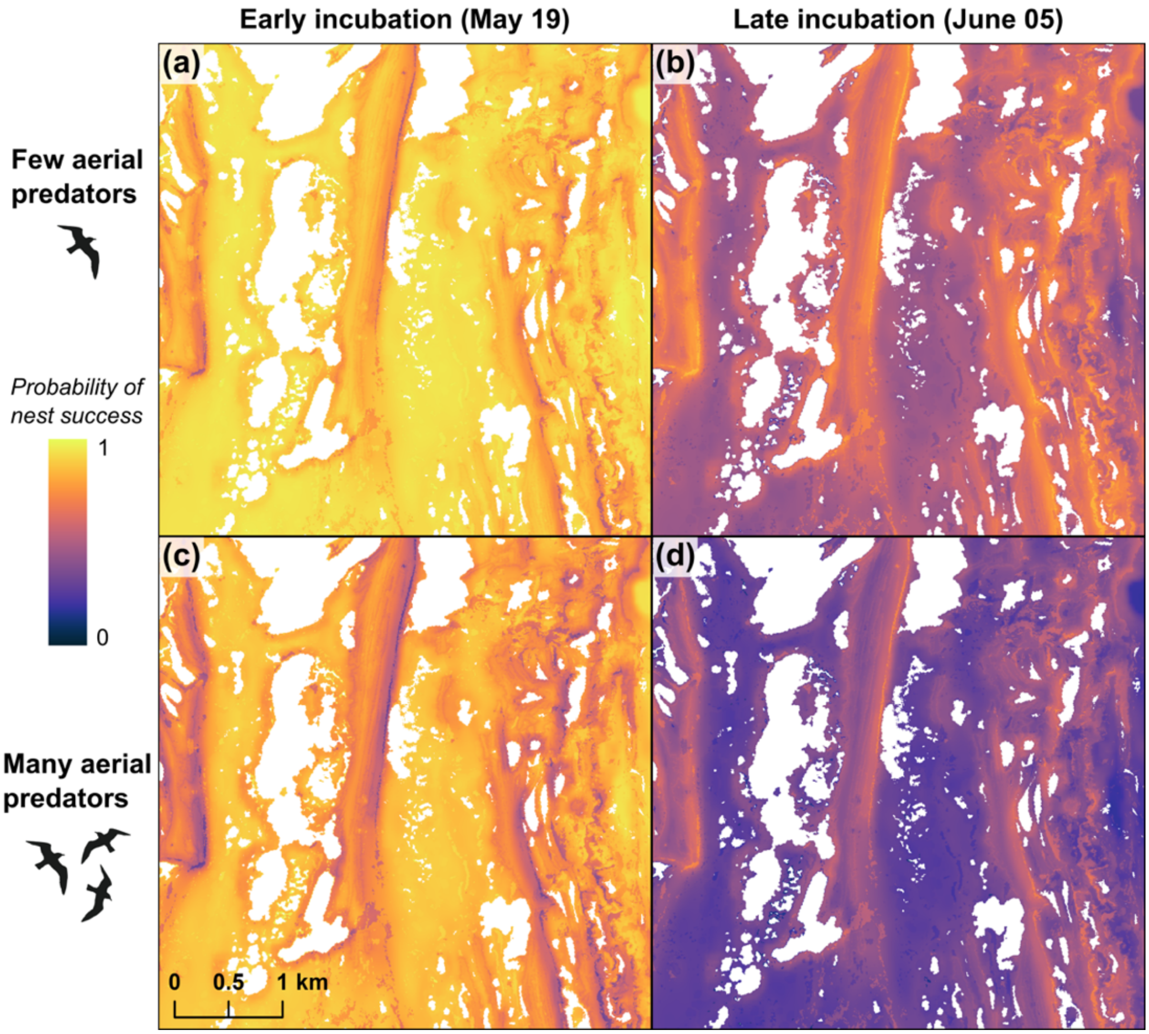

Figure 5. Predicted spatial patterns of Canada goose nest success within the study area, demonstrating the dynamic landscape of risk to goose reproduction that is produced by nesting phenology and predator activity (both fox and aerial predators). The figure depicts the probability of nest success under four different scenarios: few aerial predators (mean – 1 std. deviation) with early (a) and late (b) nest incubation, and many aerial predators (mean + 1 std. deviation) with early (c) and late (d) incubation. Incubation dates selected were the earliest (May 19) and latest (June 5) average incubation dates during our study period.

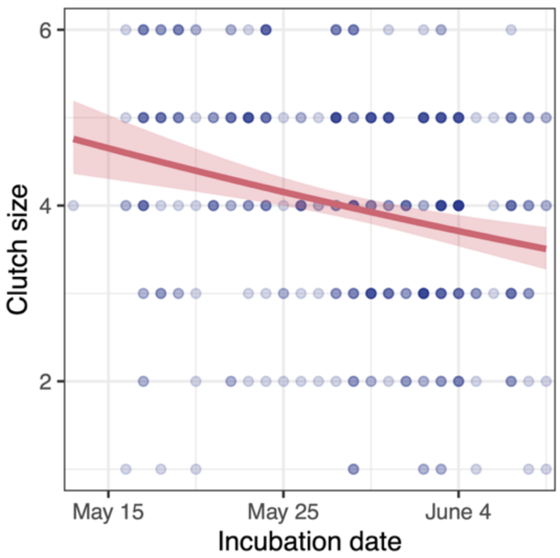

Figure 6. Negative relationship between incubation date and size of clutches laid by Canada geese. The red line and ribbon depict the effects of incubation date on clutch size estimated from a generalized linear model (+/- 95% confidence interval), and the blue points are the observed data (darker points = more clutches; *n*=351 clutches).

Discussion

Using movement data from the dominant cursorial nest predators, Arctic and red foxes, plus aerial predator activity data obtained during nest surveys, we demonstrate that predator activity has a strong effect on the spatial distribution and reproductive success of a dispersed-breeding goose on the Arctic tundra. As expected, habitat selection preferences of Canada geese were nearly opposite those of foxes, indicating that geese select nest sites in areas that minimize interactions with foxes. Goose nest success was lower, on average, in areas with a greater probability of use by foxes, although these effects were strongly mediated by the date geese started incubation. Our study provides a novel spatiotemporal perspective on how predator activity influences the reproduction of prey in a heterogenous tundra landscape.

Geese selected nest sites in areas that would likely minimize their probability of encountering foxes while also maximizing their ability to detect foxes. Goose nests tended to be located near water, within flat areas, and far from beach ridges (Fig. 2a–c). These patterns were generally opposite to fox selection patterns, and also likely reflect landscape traits that would aid in the detection and/or defense of hunting foxes. Nesting close to water limits the range of view incubating geese need to search for predators (i.e., foxes will not attack nests from within a lake) and likely reduces the time that incubating geese spend off nest to drink water (Lecomte et al., 2009). Nesting in relatively flat areas also probably enhances the ability of geese to visually detect incoming predators (Miller et al., 2007). Similarly, beach ridges are the only elevated features in the study area, so geese may avoid nesting near ridges as these features may obscure their ability to detect predators on the far side of ridges. Beach ridges are also home to fox dens and often used as movement corridors for other wildlife (Zhao et al., 2022), so it is probably beneficial to nest farther from predator activity centers. It is also possible that some of the observed selection patterns reflect goose preferences for other resources (e.g., proximity to food or water). However, incubating females typically spend <5% of their time away from nests (Aldrich & Raveling, 1983) and nesting geese in this study showed strong selection for areas with degraded food resources (‘goose-affected areas’), suggesting these other resources likely have a lesser role than predation risk in structuring the spatial distribution of nests.

The negative correlation between fox space use and goose nest locations could suggest foxes devote little time to hunting goose nests. However, our fox habitat selection model included locations of foxes in all behavioral states (including resting or tending to offspring at dens), not just foraging. From the prey’s perspective, this temporal component of predator space use—i.e., where predators spend most of their time, not only where they spend time hunting geese—is likely an important consideration when selecting nest sites. Building nests on or near ridges would be risky since foxes spend so much time there. Even though part of the selection strength for beach ridges and uneven terrain by foxes could be related to hunting other preferred prey like lemmings (McDonald et al., 2017), foxes are generalist predators that could easily switch to hunting geese if they encounter a nest in these areas. Our study did not account for indirect interactions between geese and other prey of foxes, which can influence the reproductive success of geese in tundra ecosystems (e.g., Bêty et al., 2001; Bêty et al., 2002; Juhasz et al., 2020). However, previous work from our study area found no link between rodent abundance and Canada goose nest success (Reiter & Andersen, 2011). Moreover, the negative relationship between goose nest success and the probability of space use by foxes (Fig. 4a,b) indicates our index of fox activity adequately reflects spatial variation in predation risk (Clermont et al., 2021). Fox activity therefore seems to generate predictable spatial patterns in predation risk that influence goose nesting decisions (i.e., a "landscape of fear"; Laundré et al., 2010; Gaynor et al., 2019).

Although geese appear to favor proactive antipredator strategies when selecting nest sites, it remains unclear what information they use to assess risk. Foxes are already localizing at their dens when Canada geese arrive in early May (Neufeld, 2021; Moizan et al., 2023), indicating geese have time to gather information on fox activity before nesting begins 10+ days later. Canada geese are also a long-lived species that breed for many years and the outcomes of previous breeding attempts can provide information on the relative safety of potential nest sites. Indeed, goose nesting success is lower for young individuals (Raveling, 1981; Rockwell et al., 1993), suggesting geese learn how to better protect their reproductive investments as they age. Geese may also incorporate information from conspecific neighbors when choosing nest sites and assessing risk, as interactions with neighbors can influence the spatial distribution and nesting success of Canada geese (Reiter & Andersen, 2013). We could not adequately evaluate neighbor effects in this study since we used line-transect survey methods rather than full census methods (i.e., not all neighbors were accounted for in our study).

Our study provides a novel perspective on how goose reproductive ecology is affected by the interplay of predator activity and nesting phenology, the latter of which is changing in a warming Arctic. Nest survival decreases the later nests are incubated (Fig. 4a,b; Baldwin et al., 2011; Ross et al., 2017; Clermont et al., 2018), likely due in part to geese being in poorer body condition later in the breeding season (as indicated by the observed negative relationship between clutch size and incubation date; Fig. 6). Geese that lay nests later tend to be in poorer body condition either due to environmental conditions on the breeding grounds that inhibit energy gain (e.g., late snow cover), because they arrived to the breeding grounds in worse condition and must spend more time acquiring food resources, or some combination of both (Bêty et al., 2003; Madsen et al., 2007). Incubating females in worse body condition tend to leave their nests more frequently, and for longer periods of time, to feed (Aldrich & Raveling, 1983), and geese with smaller clutches also tend to return to their nests slower after being disturbed (Miller et al., 2013), both of which leave their nests more vulnerable to predation (Samelius & Alisauskas, 2001; Bêty et al., 2002). As spring phenology advances in a warming Arctic, geese are also faced with increasing pressure to arrive early enough to acquire sufficient food resources for nesting, and to time their nesting with peak vegetation productivity (Nolet et al., 2020) – a task that is particularly difficult for geese in Wapusk as they are forced to acquire food in a highly degraded landscape. Goslings that hatch later have lower survival rates in large part because of a mismatch with peak vegetative productivity, which is exacerbated if spring phenology advances faster than reproductive phenology (Ross et al., 2018). Like many Arctic regions (reviewed in Nolet et al., 2020), geese in our study area have advanced their timing of nesting (MacInnes et al., 1990; Rockwell et al., 2011). However, our results suggest a major caveat with these phenological patterns, as we found the importance of nesting phenology on nest survival depended on local levels of cursorial predator activity (Fig. 5). Nesting early provided benefits to geese only in areas of low fox activity, whereas predation risk to nests in areas of high fox activity were similar regardless of incubation date (Fig. 4a,b). Collectively, this study thus sheds light on how predator activity and nesting phenology interact to shape goose nesting patterns, and provides a valuable case study on how incorporating temporal dynamics into spatial patterns of predation risk can provide a better understanding of predator-prey relationships (Palmer et al., 2022).

Sources of mortality other than fox predation seem to be responsible for the influence of nesting phenology in areas of predicted low fox activity, and we suggest that predation by avian predators likely explains at least part of this pattern. Despite the coarser resolution of avian predator activity data relative to fox activity, we found goose nesting success was lower in areas with more aerial predators (Fig. 4c). Predation by migratory avian predators seems a reasonable alternative mortality source (along with e.g., weather conditions; Juhasz et al., 2020) since nests incubated later would be exposed to more predators as birds arrive onto the breeding grounds. However, regardless of their influence on nest success, avian predators likely have a lesser influence on Canada goose nest habitat selection in this system than foxes. If avian predator activity strongly affected nest site selection we may have expected geese to select sites that offer concealment, as previously observed (Miller et al., 2007). However, geese tended to avoid land cover types that would offer the best overhead concealment (i.e., shrub/willow cover types; Fig. 2d,e). Prey often adapt antipredator behavior more strongly to one predator over others in multi-predator systems (Relyea, 2003; Morosinotto et al., 2010), and geese appear to respond more strongly to predation risk from foxes than avian predators (Lecomte et al., 2008). Unlike foxes, avian predators generally pose little predation risk to adult geese. Additionally, the distribution of lakes, ponds, wetlands, and beach ridges in the area imposes movement constraints on foxes that are not imposed on avian predators, and this heterogeneity influences where foxes move and spend time. Ultimately, landscape composition and fox locomotion interact to create high spatial variation in perceived predation risk, which geese, in turn, use to inform nesting decisions as they navigate this “landscape of fear”. Our study thus provides evidence that landscape features can mediate relative predation risk, and responses to perceived risk, from aerial and cursorial predators on the Arctic tundra.

Concluding remarks

Without the ability to easily move nests in response to changing levels of risk, birds often employ proactive antipredator responses to guide nesting decisions and maximize their reproductive success. Using movement data from the dominant nest predators in our system, our study provides an empirical link between predator activity, spatial patterns of predation risk, and the breeding ecology of a tundra-nesting bird. We showed how the landscape interacts with predator movements to create predictable spatial patterns of predation risk, which we validated by demonstrating a relationship between probability of predator use and reproductive success. Our finding that geese preferentially selected nest sites in areas with a low probability of predator use indicates geese perceive these spatial patterns of predation risk and respond proactively by constructing nests in predator activity refuges. However, we also demonstrated nesting phenology mediated the effects of spatial variation in predation risk. Our study provides an empirical demonstration of how integrating time into the "landscape of fear" framework enhances our understanding of the reproductive ecology of birds.

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Appendix 1

Supplemental information for: "Predator activity, proactive anti-predator strategies, and nesting phenology produce a dynamic landscape of risk to tundra goose reproduction"

Additional details on landscape traits used for the habitat selection analyses

Distance to nearest open water (m) was calculated as the Euclidean distance between each point and the nearest water feature >0.001 km^2 (as determined from the land cover data set). To assess the effect of proximity to beach ridges on fox movement and goose nest selection, we first defined the boundaries of beach ridges using the land cover data set, such that contiguous areas >0.01 km^2 comprised of 'Unvegetated' and/or 'Dryas heath' cover types were classified as beach ridges. We then calculated the Euclidean distance (meters) from each point to the nearest beach ridge. The areas used to define water patches and beach ridges were informed based on our expert knowledge of the study area: water patches <0.001 km^2 in area are typically tiny ponds/puddles on the landscape that likely have a negligible influence on wildlife space use, while no fox dens occur on beach ridges <0.01 km^2 in area.

Full details on how land cover types were re-classified are presented in Table S1.

Table S1. Land cover types used in the fox movement and goose nest habitat selection analyses, re-classified from (Ponomarenko et al., 2014).

Original land cover type	Re-classified cover type
Coastal fen	Fen
Poor sedge fen	Fen
Ridge sedge fen	Fen
Shrub sedge fen	Fen
Emerging sedge fen/shallow water	Emerging sedge fen/shallow water
Coastal tall willow	Shrub/willow
Coastal low willow	Shrub/willow
Riparian tall willow	Shrub/willow
Lichen dwarf shrub	Shrub/willow
Shrub-moss-lichen	Shrub/willow
Spruce larch forest*	Shrub/willow
Lichen spruce woodland*	Shrub/willow
Moist rhododendron-Dryas	Dryas heath
Dry Dryas Heath	Dryas heath
Mild goose affected	Goose affected
Severe goose affected	Goose affected
Unvegetated	Unvegetated
Water	Water

*in our study area, these habitats are functionally shrub height

Cross-validation methods for habitat selection models

We used cross-validation methods to evaluate the fit of each habitat selection model (Roberts et al., 2017). This process involved fitting 80% of the data to each model, testing model performance on the withheld 20% of data, and repeating that process four more times until all portions had been tested. For the fox movement model, we split the data using a random individual blocking method (i.e., training data sets had data from eight foxes, testing data sets had data from remaining two foxes). We used a spatial blocking method to split the goose nest data into training/testing data sets, whereby the goose nest study area was divided into five equal-sized areas (nests from one area were withheld as each of five testing folds). We then binned predicted results from each testing fold into 10 equal-sized, frequency-adjusted quantiles and performed Spearman-rank correlation analysis on these quantiles (Boyce et al., 2002).

Relationship between survey date and aerial predators observed on the transect

Since aerial predators in our study area are migratory, it is theoretically possible that the number of aerial predators observed along goose nest survey transects could have been influenced by survey date (with likely more predators observed on later transects). However, the relationship between transect survey date and aerial predator counts indicates there was no evidence that aerial predator counts were greater at later survey dates (Fig. S1). Our results should therefore not be affected by the date the survey occurred.

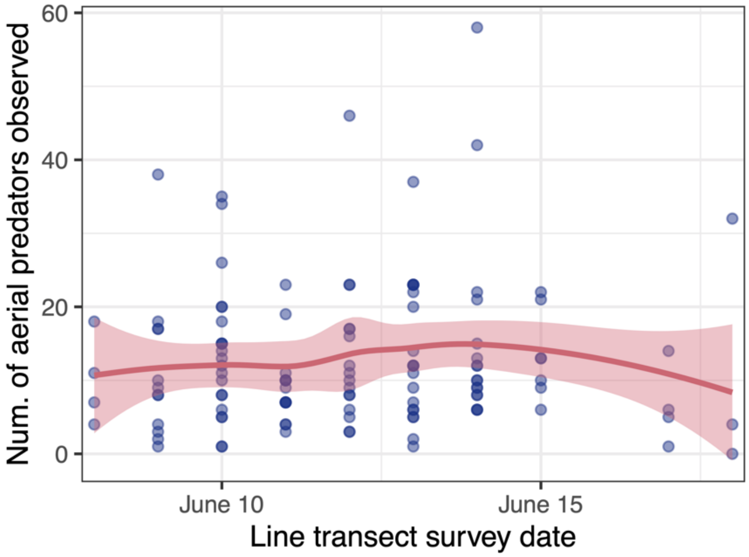

Fig. S1. Relationship between the date that goose nest transects were surveyed (range: June 8–18) and the number of predators observed on the transect, fit with a Loess smoother (+/-95% confidence intervals). Each point is a single transect.

Full habitat selection and nest fate model results

Full results from both habitat selection models (goose nest and fox movement models) are presented in Table S2. Full model results from the nest fate analysis are in Table S3.

Table S.2. Results from the fox movement and goose nest habitat selection analyses. Parameters in bold were significant at the α=0.05 level (excluding the intercept). SE= standard error, LC=land cover type.

	Fox movement HSF						Goose nest HSF					
Term	Estimate	SE	Z	*p*	Conf. low	Conf. high	Estimate	SE	Z	*p*	Conf. low	Conf. high
(Intercept)	–13.22	0.481	–27.46	<0.001	–14.17	–12.28	–13.10	0.315	–41.65	<0.001	–13.72	–12.49
LC: Dryas heath	–0.389	0.091	–4.28	<0.001	–0.567	–0.210	-0.742	0.301	-2.47	0.014	-1.332	-0.152
LC: Goose affected	0.081	0.069	-1.18	0.239	-0.217	0.054	0.870	0.101	8.61	<0.001	0.672	1.068
LC: Sedge fen/water	-1.034	0.583	-1.77	0.076	-2.177	0.110	0.952	0.369	2.58	0.010	0.228	1.676
LC: Unvegetated	-0.507	0.090	-5.64	<0.001	-0.683	-0.331	-1.054	0.587	-1.79	0.073	-2.205	0.098
LC: Water	-2.518	0.209	-12.04	<0.001	-2.928	-2.108	-	-	-	-	-	-
LC: Willow	0.580	0.089	6.55	<0.001	0.406	0.754	-1.518	0.583	-2.61	0.009	-2.661	-0.376
Dist. Water (log)	0.045	0.076	0.60	0.552	-0.103	0.193	-0.233	0.039	-6.03	<0.001	-0.308	-0.157
Dist. Ridge (log)	-0.134	0.057	-2.37	0.018	-0.245	-0.023	0.272	0.039	6.94	<0.001	0.195	0.349
Terrain ruggedness log TRI)	0.579	0.152	3.82	<0.001	0.282	0.877	-0.755	0.126	-5.98	<0.001	-1.003	-0.508
σ_{Fox} / σ_{Year}	1.366	-	-	-	0.758	2.462	<0.001	-	-	-	-	-
$\sigma_{\text{Dist\_water}}$	0.223	-	-	-	0.127	0.389	-	-	-	-	-	-
$\sigma_{\text{Dist\_ridge}}$	0.169	-	-	-	0.103	0.276	-	-	-	-	-	-
σ_{TRI}	0.430	-	-	-	0.250	0.741	-	-	-	-	-	-

Table S.3. Results from the nest fate analysis model. Parameters in bold were significant at the α=0.05 level (excluding the intercept). SE=standard error.

Term	Estimate	SE	Z	*p*	Conf. low	Conf. high
(Intercept)	28.20	4.444	6.35	<0.001	19.49	36.91
Fox movement log-RSS value	–21.03	10.15	–2.07	0.038	–40.91	–1.14
Incubation date (ordinal day)	–0.180	0.030	–6.10	<0.001	–0.238	–0.122
Avian predator count (log)	–0.372	0.176	–2.11	0.035	–0.718	–0.027
Interaction term: fox movement log-RSS*incubation date	0.142	0.068	2.09	0.036	0.009	0.275
σ_{Year}	<0.001	-	-	-	-	-

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