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

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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 areas perceived to be safer. 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 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. We compared habitat selection models fit to i) goose nest locations and ii) fox locations obtained from GPS collars and found that geese and foxes display nearly opposite patterns of selection for the same landscape traits. Geese selected sites that minimized 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. Landscape heterogeneity influenced both fox and goose nest habitat selection patterns and, consequently, spatial variation in predation risk and reproductive success. Aerial predators appeared to have a lesser effect on spatial patterns of goose nest habitat selection and success. Spatial patterns of nest success were, however, strongly influenced by nesting phenology. Nests initiated earlier had a greater probability of successfully hatching, but these patterns depended on location; the benefits of nesting early decreased in areas of high fox activity. Our study demonstrates the mechanisms by which nesting phenology, predator activity, and landscape heterogeneity interact to shape bird reproduction, and provides an empirical demonstration of how our understanding of predation risk is enhanced by integrating both spatial and temporal dynamics.

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” to 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 landscape characteristics, predator space use, and prey perception of risk interact 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 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 to 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 (~20–50 m; 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; Corbeil-Robitaille et al., 2024). 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). Canada geese also show reactive anti-predator responses to predators by aggressively defending their nests from detected predators, with increasing aggression closer to the hatch date (Clermont et al., 2019b).

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 perceived as less risky (Smith et al., 2019). For Arctic waterfowl, clear temporal patterns in nest 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). Seasonal decline in nest success can be attributed to factors such as the mother's age and experience (older/more experienced birds tend to nest earlier and have greater nest success; Finney & Cooke, 1978; Raveling, 1981; Forslund & Larsson, 1992; Clermont et al., 2019a) or body condition (birds that nest later tend to be in worse body condition and have lower rates of nest success; Bêty et al., 2003; Descamps et al., 2011). Predators may, in turn, be better able to predate nests incubated by geese that are younger, less experienced, or in worse body condition. Thus, nesting phenology—which may reflect seasonal variation in factors like the vulnerability of nesting birds—may interact with predator activity to result in variation in spatial patterns of predation risk across the breeding season. In other words, the probability a nest successfully hatches may depend jointly on when the nest is initiated and the perceived (or real) risk of predation at that nest site.

The over-arching objective of this study was to evaluate how predator activity affects nest habitat selection and nest success of a dispersed-nesting goose, and whether these effects are mediated by nesting phenology. To our knowledge no direct evaluation has assessed 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 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 predator-prey dynamics in tundra ecosystems.

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 86 known fox dens within the Wapusk tundra, nearly all of which are located on beach ridges (Roth, 2003; Johnson-Bice et al., 2023). Within and around the goose nesting study area (~32 km^2), there are 22 known fox dens, with occupancy rates during the incubation season averaging 0.43 (range: 0.24–0.57; Johnson-Bice et al., 2024).

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 (generally at least 20–50 m from nearest neighbors; Reiter & Andersen, 2013). 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 Pérouse Bay snow goose colony ~12 km west of our core study area (which has declined dramatically in abundance over the past several years; Hudson Bay Project, 2024), but parts of our study area have been altered by goose foraging. Approximately 97% of goose clutches detected in our study area were laid by Canada geese, 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. Though red fox abundance in the region has remained relatively stable, their presence on the tundra has increased in recent years as Arctic fox abundance has declined (Moizan et al., 2023; Verstege et al., 2023). Rodents (namely collared lemmings *Dicrostonyx richardsoni* and meadow voles *Microtus pennsylvanicus*) tend to be the primary prey for foxes in this area (Dudenhoeffer et al., 2021), but geese are an important seasonal secondary prey (McDonald et al., 2017). Herring gulls (*Larus argentatus*) are the most common aerial nest predator, but other aerial predators like glaucous gulls (*L. hyperboreus*), parasitic jaegers (*Stercorarius parasiticus*), common ravens (*Corvus corax*), bald eagles (*Haliaeetus leucocephalus*), and sandhill cranes (*Grus canadensis*) are also relatively common.

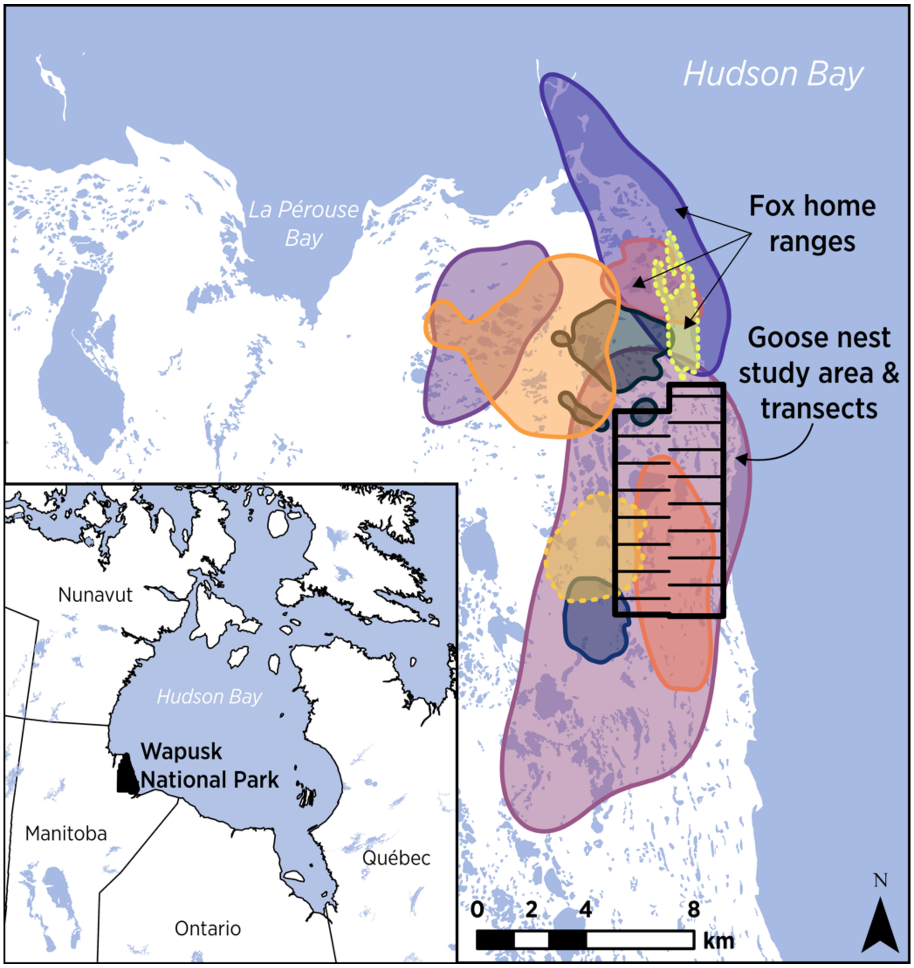

Fig. 1. Study area within Wapusk National Park, Manitoba, Canada, along the western coast of Hudson Bay. Each of the 10 colored polygons represents the home range of a collared Arctic fox (*Vulpes lagopus*, solid outlines) or red fox (*V. vulpes,* dashed outlines). The black polygon outline denotes the boundary of the goose nest study area, with the 15 transects from one year shown. (Note: the large home range in purple 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, 2014–2024 (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 (usually within 300 m of the transect), 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 on the nest, 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 collected on a random subset of nests before 2018. 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 2018–2023 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 (within 6–8 km, Fig. 1; *n*=10 foxes, 2 red and 8 Arctic) during the primary nesting period. All handling procedures were approved by the University of Manitoba Animal Care Committee (Protocols F17-012, F22-004). Research permits were obtained from Parks Canada (WAP-2017-25781, WAP-2018-27938, WAP-2021-38241, WAP-2022-41740), 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 (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; Corbeil-Robitaille et al., 2024), our data indicated there was likely no substantial difference in nest success (0.57 on islets 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 close to open water, which would reduce the number of directions from which foxes could approach the nests and potentially 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 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 (Table S1): '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 (i.e., calculating relative difference in elevation from a central cell with the neighboring cells within a 5x5 grid) 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 and 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'. 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 *Supporting Information* for full details).

We visualized and compared model results by calculating the relative selection strength (RSS) for each continuous variable from each model, where RSS is a quantitative estimate of the relative magnitude of selection for a given location compared to another location(s) (Avgar et al., 2017; Fieberg et al., 2021). 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 analysis

We tested the relationship between goose nest success and relative probability of fox use at each nest site using a binomial GLMM with a complementary log-log ("cloglog") 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 (~11%). 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 accounted for the fact that nests were found at different points during incubation using the logistic-exposure method (Shaffer, 2004). Exposure period for successful nests was calculated as the number of days between the date the nest was found and expected hatch date, whereas exposure period for failed nests was calculated as the midpoint between those two dates. The log of exposure period was then included as an offset term in the model (de Zwaan et al., 2022). We included ‘year’ as a random intercept term but 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 (~18%).

We verified each fitted model had no collinearity issues (variance inflation factors were <2 for each variable) and visually inspected model residuals to assess model fits. We evaluated the importance of individual covariates with an $\alpha=0.05$ and whether the 95% confidence intervals overlapped 0. All generalized linear mixed effects 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 model using the ‘predict_response’ function from the *ggeffects* R package (Lüdecke, 2018). All analyses were carried out using R version 4.4.1 (R Core Team, 2023).

Results

During 2014–2024, we detected 801 Canada goose clutches from 632 unique nesting sites. Of the 632 sites, 75 were classified as “open water” and were subsequently excluded from the habitat selection and nest fate analyses, leaving 557 sites for these analyses. We assessed the nest fate (successful/failed) of 526 clutches from these sites, 428 of which we also estimated incubation date and recorded the number of aerial predators observed during the survey. Most clutches with a known hatch fate but unknown incubation date were clutches that were already depredated when detected during surveys ($n=55$).

We collected 2,048 locations from 10 different GPS-collared foxes (range: 78–397 locations per fox) in the goose nesting study area and vicinity. We detected an average of 12.0 avian predators along each transect (SD=9.5, range: 1–58).

Habitat selection analysis

Overall, Canada geese selected nest sites ($n=557$) in areas that were predicted to be less used by foxes. Geese selected sites that were close to open water ($\beta=-0.241$, $z=-6.68$, $p<0.001$). Although foxes showed no significant response to water ($\beta=0.045$, $z=0.60$, $p=0.552$), 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 ($\beta=0.265$, $z=7.26$, $p<0.001$), whereas foxes selected for areas close to beach ridges ($\beta=-0.134$, $z=-2.37$, $p=0.018$; Fig. 2b). Geese selected nest sites located in relatively flat areas (i.e., lower terrain ruggedness index values; $\beta=-0.736$, $z=-6.21$, $p<0.001$), whereas foxes selected for relatively uneven areas ($\beta=0.579$, $z=3.82$, $p<0.001$; 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 (Table S2).

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 ($r=-0.684$, $p<0.001$).

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 0.948 (range: 0.915–0.976).

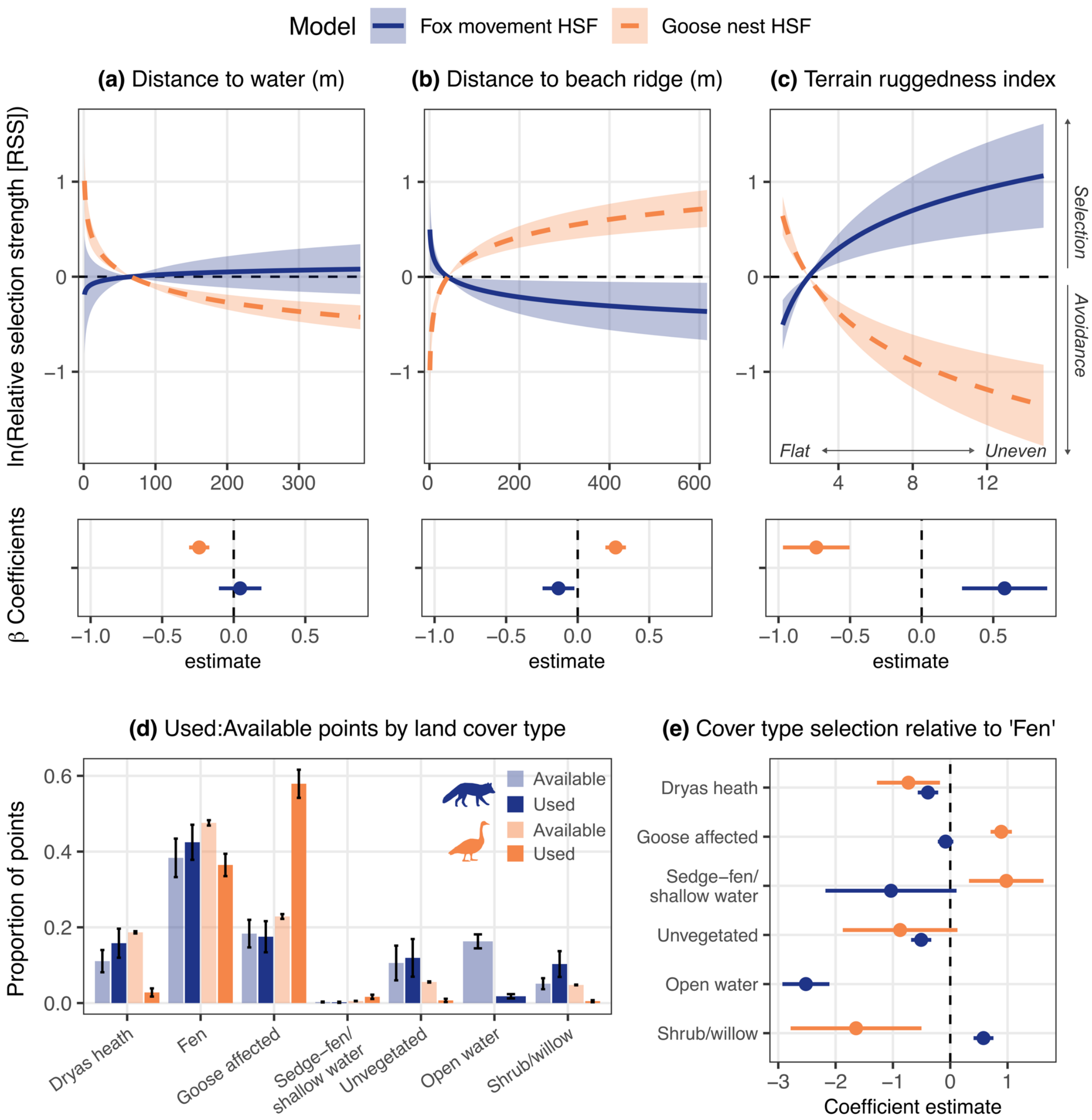

Fig. 2. Results from the habitat selection function (HSF) models demonstrating how foxes (blue) and geese (orange) showed nearly opposite patterns of selection for the same landscape features in Wapusk National Park, Manitoba, Canada. Panels (a–c) show the log-relative selection strength values (±95% 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 ten 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 HSF models.

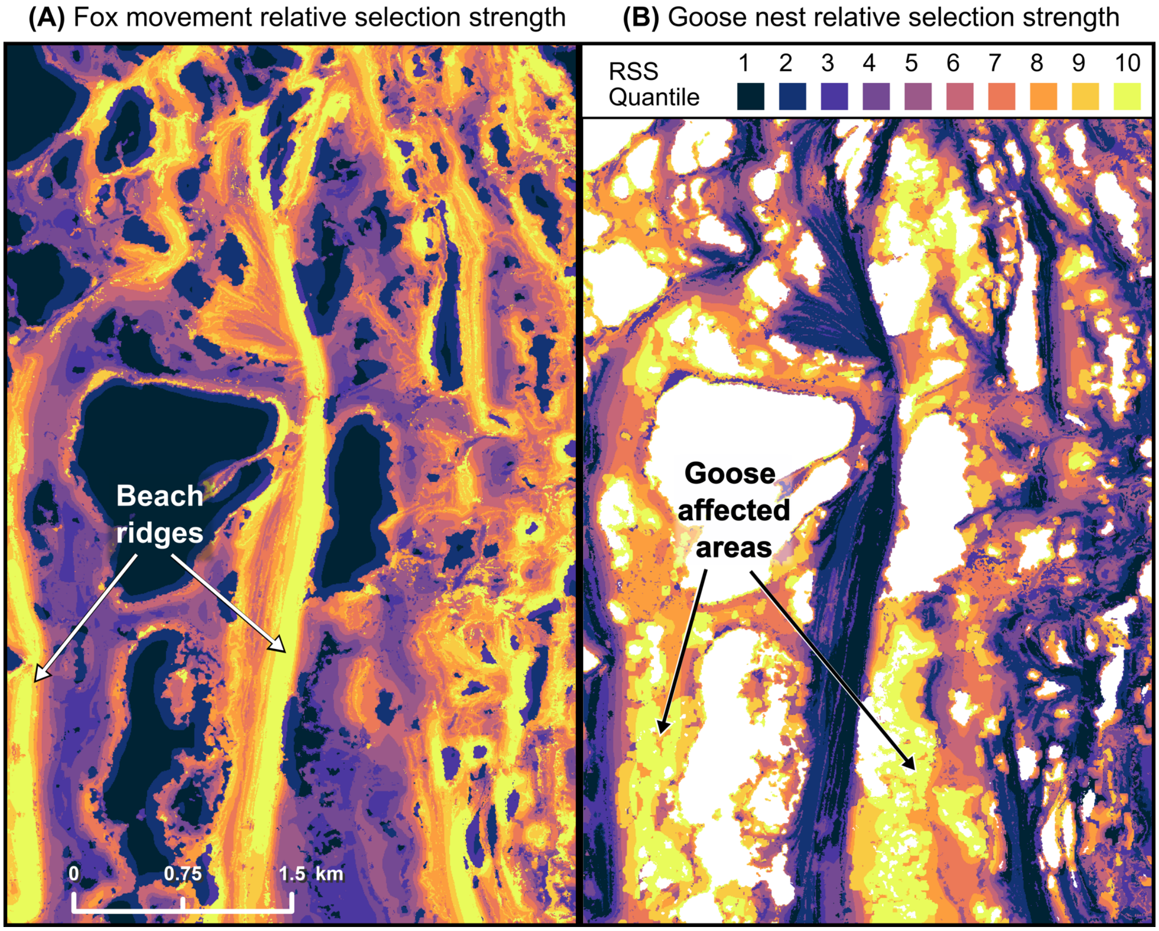

Fig. 3. Relative probability of use generated from the fox movement (left) and goose nest (right) habitat selection function (HSF) models. Predictions from both models were binned into 10 equal-sized quantiles. Areas with a low relative selection strength (RSS) are shown in blue/purple and areas with 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 HSF model).

Nest fate analysis

Annual Canada goose nest success averaged 0.57 (SD=0.23, range: 0.18–0.96). Average incubation date across all nests was May 28 (ordinal day 148), with the average annual start of incubation date ranging from May 19 (2023) to June 4 (2021).

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 (*n*=428 clutches, β=–15.76, *z*=–2.84, *p*=0.005; Table S3). Incubation date had the greatest relative influence on nest success, with clutches incubated earlier having a greater probability of success (β=—0.192, *z*=—9.71, *p*<0.001). However, these results depended on nest location, as there was a significant interaction between fox log-RSS value and incubation date (β=0.105, *z*=2.76, *p*=0.006): the benefits of nesting earlier dissipated in areas of high fox activity (Fig. 4a,b). There was a tendency for nest success to be lower in areas with higher counts of aerial predators but this effect did not reach statistical significance (β=—0.218, *z*=—1.74, *p*=0.081; Fig. 4c).

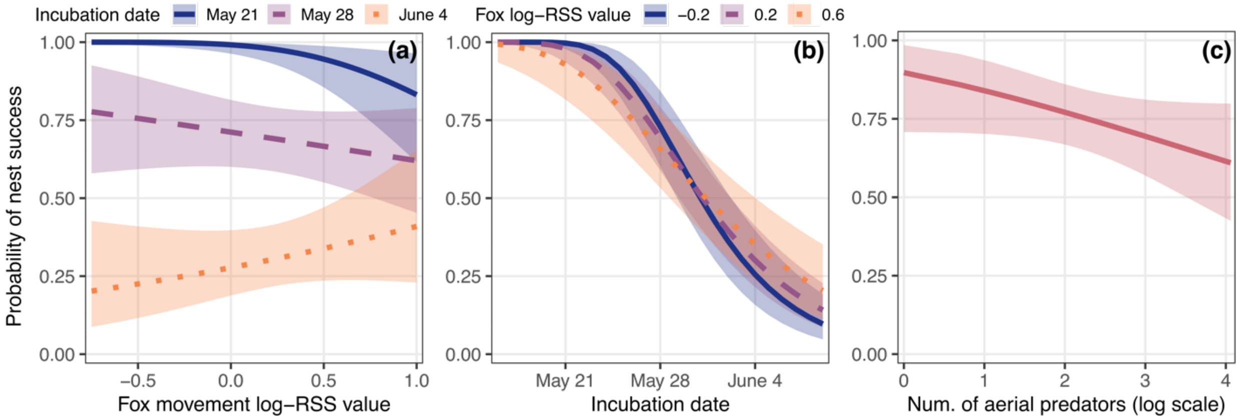

Fig. 4. Results from the model evaluating Canada goose nest success (*n*=428 clutches) in Wapusk National Park, Manitoba, Canada. Panel (a) shows the effects of fox activity (estimated log-relative selection strength [RSS] values) on the probability of nest success at three different goose incubation initiation dates (mean incubation date: May 28, ±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 (not statistically significant). Ribbons represent ±95% confidence intervals of each estimate. All predictions were conditioned on the mean average exposure duration (9.7 days).

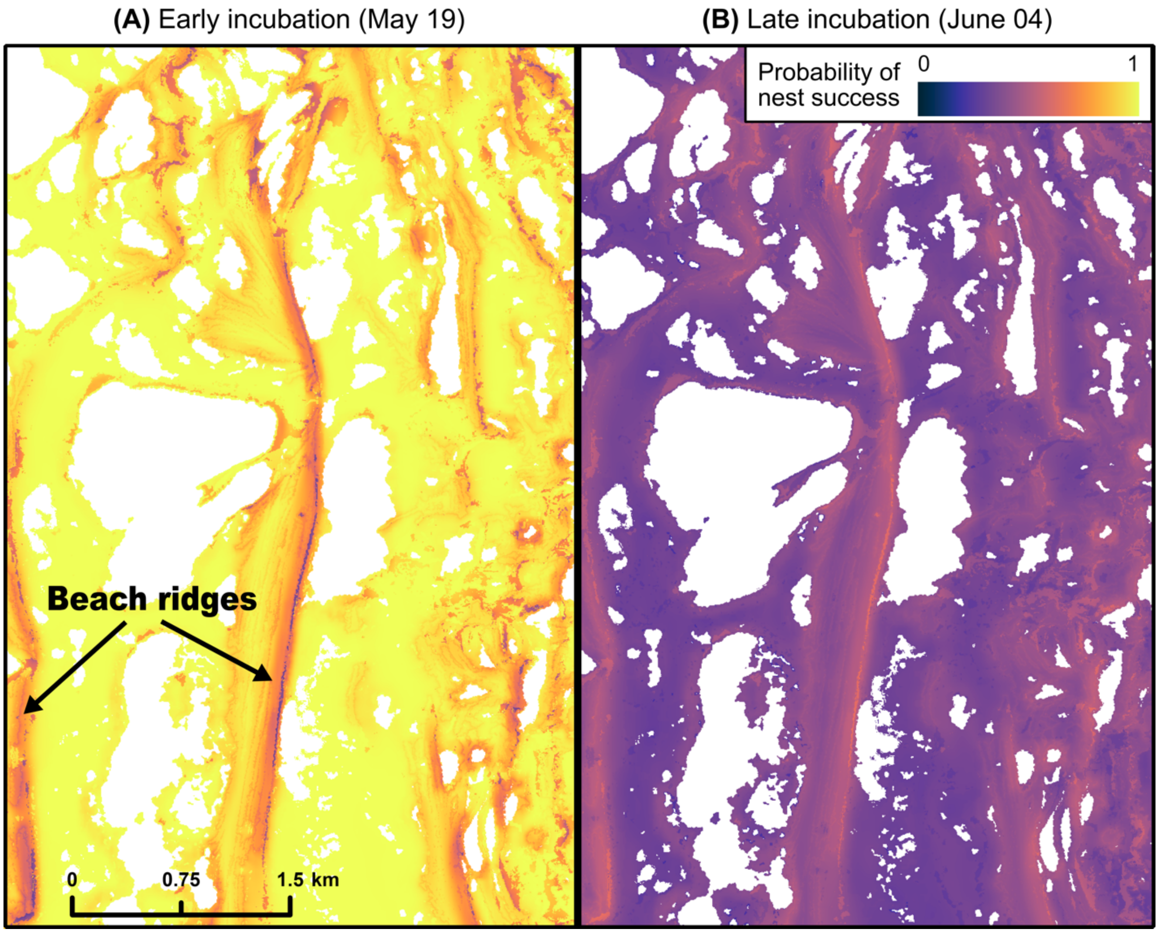

Fig. 5. Predicted spatial patterns of Canada goose nest success within the study area, demonstrating the dynamic landscape of risk to goose reproduction that is produced by nesting phenology and spatial variation in fox activity. The figure depicts the probability of nest success within a portion of the study area for nests that were incubated relatively early (a) or late (b). Variation in the probability of nest success within each panel reflects spatial variation in risk derived from the fox habitat selection model.

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, suggesting 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.

Proactive anti-predator nesting decisions in response to predator space use

Goose nest habitat selection patterns likely reflect an anti-predator strategy to minimize predation risk from foxes, while also enabling geese to meet their physiological demands during incubation. Goose nests tended to be located near water, within flat areas, and far from beach ridges (Fig. 2a–c), landscape traits that likely aid in the detection and/or defense of hunting foxes. Foxes often circle goose nests during an attack (Bahr, 1989), so nesting close to water or on peninsulas should restrict the number of directions from which foxes can attack nests (i.e., foxes will not attack nests from within a lake), whereas nesting in relatively flat areas 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), which may create predictable sites of higher predation risk that geese adaptively respond to (Thomson et al., 2006). However, it is also likely that some of the observed selection patterns reflect goose preferences for other resources, particularly proximity to open water. Foxes are more successful predating nests when the incubating goose is taking a recess from their nest than when they are incubating (Bêty et al., 2002), and drinking is a primary reason incubating geese leave their nests (Lecomte et al., 2009). Though incubating females typically spend <5% of their time away from nests (Aldrich & Raveling, 1983), nesting close to water would reduce the length of time incubating geese spend off nest and thus reduce their vulnerability to predation. We speculate food demands likely play a lesser role in influencing goose nesting decisions, as Canada geese rely heavily on body reserves for energy while incubating (Murphy & Boag, 1989) and nesting geese in this study showed strong selection for areas with degraded food resources (‘goose-affected areas’).

Results from our fox habitat selection analysis indicated foxes spent most of their time on and around elevated beach ridges in our study area, habitat features where most of their reproductive dens and primary prey (lemmings) are generally concentrated (Johnson-Bice et al., 2023). Our analysis did not parse out fox habitat selection preferences based on behavioral state (e.g., foraging vs. resting), so the results reflect time spent by foxes attending home sites and hunting all summer prey species (rodents, Canada geese, snow geese, etc.). Previous research has shown that foxes select different habitat features based on their behavioral state (Grenier-Potvin et al., 2021), so it is likely that fox and goose nest habitat selection patterns may be more similar when foxes hunt geese (i.e., foxes selecting habitats where nesting geese are located). However, rather than focusing on fox habitat selection preferences when hunting, our primary interest in this study was to evaluate goose nesting decisions in response to general space use patterns of predators. From the prey's perspective, the full temporal budget of predator space use, not only time spent hunting, is likely important to consider when selecting nest sites. Independent of the fox's behavioral state, building nests on or near beach ridges would be risky since foxes spend so much time there and foxes, as generalist predators, can easily switch to hunting geese if they were to encounter a nest. The negative correlation between fox and goose habitat selection from this study then should not imply foxes devote little time to hunting goose nests, but rather that geese end up selecting nest sites in areas foxes use less across all behavioral states.

In support of predictions from the "landscape of fear" concept (Laundré et al., 2010; Gaynor et al., 2019), heterogeneity in the physical landscape appears to play a key role in influencing spatial variation in predation risk, and consequently nest success, by mediating the habitat selection of both nesting birds and their predators. Landscape features like beach ridges, lakes, and wetlands influence fox movement and space use decisions (Grenier-Potvin et al., 2021), and this heterogeneity also clearly influences goose nest habitat selection (Fig. 2). Whether geese select areas less used by foxes because they are relative predator refuges or because they offer better opportunities to fend off predators once an attack is launched, the underlying motivation is to minimize predation risk. Although nest success tended to be lower in areas with higher avian predator activity (Fig. 4c), avian predators likely have a lesser influence on Canada goose nest habitat selection than foxes. The same landscape features that influence fox movements (topography, beach ridges, wetlands) pose little constraint to avian movements, thereby plausibly resulting in less predictable spatial variation in avian predator activity. If avian predator activity strongly affected nest site selection we may have expected geese to select sites that offer concealment (Miller et al., 2007), but geese in this study tended to avoid cover types that would offer overhead concealment (i.e., shrub/willow cover types; Fig. 2d,e). Prey often adapt anti-predator behavior more strongly to one predator over others in multi-predator systems (Relyea, 2003; Morosinotto et al., 2010), and our findings suggest that heterogeneity in the physical landscape may influence the relative strength of prey responses to multiple predators by differentially affecting predator movement patterns (Lecomte et al., 2008).

Proactive selection of nest sites in areas perceived to be safer implies that birds have obtained information on predation risk and used that information to guide nesting decisions in a way that presumably increases their fitness. Geese appear to favor proactive antipredator strategies by selecting nest sites in areas generally less used by foxes, a process that seems to be reinforced by fox predation acting as a selective pressure on goose reproduction. The negative relationship between goose nest success and fox space use indicates the latter adequately predicts spatial variation in predation risk (Clermont et al., 2021), and therefore fitness is likely higher for geese that select nest sites less used by foxes. However, it remains unclear what information geese use to assess risk. Geese may obtain information on fox activity during the period between arrival on the tundra and incubation begins (10+ days in our area; Neufeld, 2021), use information from previous breeding attempts (as evidenced by older geese generally having higher rates of nest success; (Raveling, 1981; Rockwell et al., 1993), or obtain information from conspecific neighbors, which often affect the spatial distribution and success of clustered nests (Reiter & Andersen, 2013).

Spatial patterns of predation risk to nesting birds and the value of integrating time

With predation being a leading cause of nest failure (Lima, 2009), interest in understanding how predation and spatial patterns of predation risk affect nesting birds has increased recently alongside maturation of the "landscape of fear" concept. Most studies evaluating how spatial variation in predator activity affects bird reproduction, however, have used relatively coarse indices of predator activity or abundance (e.g., track plates, traps, and other methods that estimate occupancy and relative abundance; Schmidt et al., 2006; Davis et al., 2019). Advancements in biologging technology offer opportunities to evaluate how bird nesting decisions are influenced by predator movements, which can provide different inferences of wildlife–habitat relationships than occupancy-based approaches (Bassing et al., 2023). For instance, GPS-collar data from mammalian mesopredators was used to demonstrate how predator habitat selection influences the success and spatial distribution of nesting bobwhite (*Colinus virginianus*) (Harris & O'Connell, 2023). Our general approach of comparing predator and prey habitat selection, and assessing how predator space use affects prey reproduction, is now common in studies of mammalian predator–prey dynamics. We suggest this approach is generalizable and underused in many avian systems. Greater research effort evaluating both predator movements and bird nesting biology will provide insight into how reliable predator activity (and predator behavioral state) can predict reproductive success, and ultimately a more mechanistic understanding of how nesting birds assess and respond proactively to perceived spatial variation in predation risk.

Despite increasing recognition that spatial patterns of predation risk often change across time periods (Palmer et al., 2022), most studies evaluating spatial or temporal patterns of bird nest success tend to evaluate these factors in isolation. Seasonal decline in bird nest success is well-documented across numerous ecosystems due to factors such as seasonal variation in breeding experience or body condition of nesting birds (e.g., Finney & Cooke, 1978; Raveling, 1981; Bêty et al., 2003; Descamps et al., 2011), but intraseasonal changes in predator behavior or abundance may also alter predation risk patterns. Across the nesting season, predators may increase their foraging activity (Sperry et al., 2008; Bonnefond et al., 2025), show seasonal increases in abundance (e.g., in systems with migratory predators; Lameris et al., 2019), or develop their search image for nests (Husby & Verdal, 2024), all of which may result in temporal variation in predation risk across the landscape. Here, we showed that the probability of nest success for a given nest site varied across the nesting season, where the benefits of nesting early declined in areas most used by foxes (Fig. 4a,b). To our knowledge, this study is one of the first to empirically show that spatial patterns in predation risk to nesting birds vary temporally, though we doubt this pattern is unique to our system. Studies evaluating how spatial patterns of predation risk vary across the nesting season will help assess how common these patterns are and provide a better understanding of predation's role in bird reproduction.

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, we showed how the landscape and predator movements interact to create predictable spatial patterns of predation risk, which geese in our system seemed able to perceive and respond proactively to by constructing nests in areas perceived to be safer. These spatial patterns of predation risk, however, were strongly mediated by nesting phenology, indicating this landscape of risk is temporally dynamic. Our study thus provides an empirical demonstration of how our understanding of bird reproduction, and predator–prey ecology in general, is enhanced by integrating both spatial and temporal dynamics.

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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.

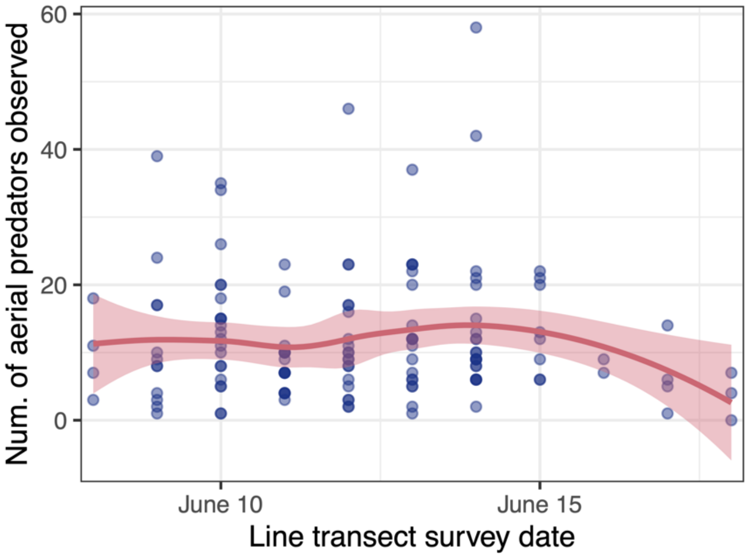

Fig. S1. Relationship between the date that goose nest transects were surveyed (range: June 8–18) and the number of predators observed on the transect, fit with a Loess smoother (+/-95% confidence intervals). Each point is a single transect.

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 S2. 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, *σ*=random effect standard deviation.

	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	–13.06	0.294	–44.48	<0.001	–13.64	–12.49
LC: Dryas heath	**–0.389**	**0.091**	**–4.28**	**<0.001**	**–0.567**	**–0.210**	**-0.729**	**0.281**	**-2.60**	**0.009**	**-1.279**	**-0.179**
LC: Goose affected	0.081	0.069	-1.18	0.239	-0.217	0.054	**0.890**	**0.095**	**9.38**	**<0.001**	**0.704**	**1.076**
LC: Sedge fen/water	-1.034	0.583	-1.77	0.076	-2.177	0.110	**0.972**	**0.332**	**2.95**	**0.003**	**0.327**	**1.627**
LC: Unvegetated	**-0.507**	**0.090**	**-5.64**	**<0.001**	**-0.683**	**-0.331**	-0.875	0.510	-1.71	0.087	-1.875	0.126
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**	**-1.643**	**0.582**	**-2.82**	**0.005**	**-2.784**	**-0.502**
Dist. Water (log)	0.045	0.076	0.60	0.552	-0.103	0.193	**-0.241**	**0.036**	**-6.68**	**<0.001**	**-0.312**	**-0.170**
Dist. Ridge (log)	**-0.134**	**0.057**	**-2.37**	**0.018**	**-0.245**	**-0.023**	**0.265**	**0.037**	**7.26**	**<0.001**	**0.194**	**0.337**
Terrain ruggedness log TRI)	**0.579**	**0.152**	**3.82**	**<0.001**	**0.282**	**0.877**	**-0.736**	**0.119**	**-6.21**	**<0.001**	**-0.969**	**-0.504**
σ_{Fox}	1.366	-	-	-	0.758	2.462	-	-	-	-	-	-
σ_{Year}	-	-	-	-	-	-	<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 S3. Results from the nest fate analysis model. Parameters in **bold** were significant at the α=0.05 level (excluding the intercept). SE= standard error, *σ*=random effect standard deviation.

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	**–15.76**	**5.55**	**–2.84**	**0.005**	**–26.64**	**–4.88**
Incubation date (ordinal day)	**–0.192**	**0.020**	**–9.71**	**<0.001**	**–0.231**	**–0.153**
Avian predator count (log)	–0.218	0.125	–1.74	0.081	–0.462	–0.027
Interaction term: fox movement log-RSS*incubation date	**0.105**	**0.038**	**2.76**	**0.006**	**0.030**	**0.179**
σ_{Year}	0.384	-	-	-	0.200	0.738

References cited in supplemental information

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