

Research Article

Experimental and field evidence indicate that islet-nesting tundra birds experience reduced nest predation and benefit indirectly from high snow goose densities

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Landscape features can shape the occurrence and strength of predator–prey interactions by influencing predation risk and prey distribution. In the High Arctic, some bird species select nesting sites with physical features that impede access for their main terrestrial predator, the Arctic fox. We investigated how nest microhabitat characteristics and prey availability modulate nest survival in tundra birds that select pond and lake islets as breeding sites. Over four summers, we analyzed survival of 132 cackling goose and 55 glaucous gull nests located on islets or pond and lake shores within a 150-km² area encompassing a snow goose colony on Bylot Island, Nunavut, Canada. Over three years, we also assessed the effect of microhabitat on predation risk using artificial nests. We found that islets act as partial prey refuges, with higher nest survival on islets than on pond and lake shores. Nest survival generally increased with islet distance from shore, but we found little evidence of this effect for cackling geese and glaucous gulls, which rarely nested on islets near shore. Moreover, water depth surrounding islets had little to no influence on any nest type. Nest survival on islets was much lower in a year with relatively low snow goose nest density, suggesting that geese may confer a short-term positive indirect effect on other bird species nesting on islets within or near the main goose nesting area. Since the Arctic fox was virtually the sole predator of artificial nests, our findings suggest that annual variation in nest survival on islets was driven by a shift in fox foraging behavior in response to changes in prey availability across the landscape. Our study, which integrates multi-year monitoring and field experiments, highlights the interplay between microhabitat selection and predator–multi-prey dynamics in the Arctic tundra.

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Introduction

Physical characteristics of the landscape can shape species relative abundance by influencing the occurrence and strength of interactions (Cherif et al. 2024). Landscape features can affect predator foraging behavior by modulating movement capacity, prey encounter rates, prey detection, and the probabilities of attack and capture (Shepard et al. 2013, Wootton et al. 2023, Beardsell et al. 2026). These factors collectively influence predation risk for prey (Atuo and O'Connell 2017), ultimately impacting prey distribution and persistence in the landscape (Lima 1998, Laundr   et al. 2010, Clermont et al. 2021).

Prey can select microhabitats that minimize the likelihood of being predated (Gaynor et al. 2019). These microhabitats, known as prey refuges, can enhance prey survival or reproduction compared to the surrounding habitat (Berryman and Hawkins 2006, Duchesne et al. 2021). The protective effect of refuges can arise from the limited use of these microhabitats by predators due to elevated short- and long-term fitness costs. These costs include reduced predation efficacy and efficiency (e.g. lower attack success, increased cost of transport), and a higher risk of injury (e.g. greater difficulty evading prey defenses, falling from steep terrain) (Mukherjee and Heithaus 2013, Shepard et al. 2013). The quality of refuges can vary, offering complete or partial protection depending on differences in their physical characteristics that influence the foraging behavior of predators and, thus, the associated predation risk (Velando and M  rquez 2002, Brown and Kotler 2004). Beyond physical characteristics, the quality of partial refuges may also be context-dependent (Lecomte et al. 2008, Batbayar et al. 2014). For instance, fluctuating local prey densities could modulate the energetic state of predators and, as a result, their willingness to pursue prey located in less accessible or riskier microhabitats (Berger-Tal et al. 2009). Integrating the interplay between physical landscape features and prey densities is therefore crucial for evaluating the quality of refuges and their role in shaping prey distribution and abundance in the landscape (Clermont et al. 2021, Duchesne et al. 2021, Beardsell et al. 2026).

The Arctic tundra provides an excellent system to study how the quality of refuges for prey can be modulated by both the physical characteristics of microhabitats and the food resources available to predators. The Arctic fox *Vulpes lagopus* is the main nest predator of tundra bird species, heavily influencing their reproductive success (B  ty et al. 2002, McKinnon and B  ty 2009). Its foraging behavior is strongly shaped by annual prey abundance, which can lead to fluctuations in predation pressure on nests (B  ty et al. 2002, Beardsell et al. 2022). Some bird species less effective in protecting their nest against foxes can select islets in ponds and lakes as nesting sites, where water barriers hinder fox access,

improving reproductive success compared to shore sites (Zoellick et al. 2004, Gauthier et al. 2015). Although foxes are capable swimmers (Strub 1992), their attack and success probabilities are likely lower for nests on islets because they cannot achieve the same speed or adopt the same offensive or defensive positions as they could on shore (Beardsell et al. 2026). Moreover, foxes must weigh the risk of injury posed by defensive birds, as even seemingly minor injury could prove life-threatening (Mukherjee and Heithaus 2013).

The quality of islets as refuges in the tundra landscape may depend on their physical characteristics. For instance, glaucous gulls *Larus hyperboreus*, cackling geese *Branta hutchinsii* and red-throated loons *Gavia stellata* tend to nest on islets farther from shore and surrounded by deeper water (Corbeil-Robitaille et al. 2024), potentially to reduce predation risk from terrestrial predators (Gauthier et al. 2015). Furthermore, the relative protection offered by islets may also vary depending on the density of prey available to Arctic foxes (Gauthier et al. 2015). In most tundra ecosystems, foxes heavily rely on lemmings, whose populations undergo large-amplitude cycles (Giroux et al. 2012, Fauteux et al. 2015). When lemming abundance is low, predation pressure on nesting birds generally increases (Summers et al. 1998, B  ty et al. 2001, Beardsell et al. 2022). Colonial-nesting birds, like snow geese, can also constitute a significant portion of the diet of Arctic foxes, primarily through the consumption of their eggs and chicks (Giroux et al. 2012). Fox density is increased in these large bird colonies due to a reduction in their home range size, thereby increasing predation pressure on vulnerable tundra-nesting birds (Dulude-de Broin et al. 2023).

Through field observations and experiments, we assessed the effectiveness of islets as refuges for nesting birds in the tundra ecosystem of Bylot Island (Nunavut, Canada), where lemmings and colonial snow goose populations exhibit strong inter-annual variation in abundance. We examined how nest microhabitat (i.e. fine-scale characteristics measured within a few meters of the nest site, classified here as islet or shore nesting habitat), islet characteristics (distance to shore and water depth), and main prey densities influence nest survival of cackling geese and glaucous gulls. Unlike snow geese, individuals from these species are commonly found on islets, but also actively defend their nests with aggressive behavior, creating a potential risk of injury for foxes (Beardsell et al. 2026). We also conducted field experiments using artificial nests to provide a standardized measure of predation risk that excludes the potential effects of nest defense ability and parental quality (McKinnon et al. 2010). We hypothesized that both natural and artificial nest survival would be higher for nests less accessible to foxes, predicting (P1) greater survival on islets than on shore, and (P2) increased survival on islets with greater distance from shore and water depth, as these factors could increase risks for foxes and reduce their

predation efficiency. As foxes are more likely to target prey in less accessible microhabitats when their energy acquisition rate is lower (Beardsell et al. 2026), we also predicted that (P3) nest survival would decrease in years of low lemming and low snow goose nest densities.

Material and methods

Study system

We conducted fieldwork in summers 2018, 2019, 2022, 2023, and 2024 in a ~ 150-km² study area located on the southwest plain of Bylot Island (72°88'N, 79°84'W), in Sirmilik National Park, Nunavut, Canada (Fig. 1). This area is mainly characterized by mesic tundra and polygonal wetlands interspersed with streams, shallow ponds, and lakes (Gauthier et al. 2024). A total of 355 islets has been geolocated in these small waterbodies. These islets are mostly

formed through ice-wedge polygon degradation and are therefore vulnerable to climate change (Corbeil-Robitaille et al. 2024). The majority (> 80%) remain unoccupied by birds during the summer (Corbeil-Robitaille et al. 2024), with red-throated loons, glaucous gulls, and cackling geese being the main species selecting islets as nesting sites (Fig. 2).

Vertebrate biodiversity is dominated by birds, with over 35 species observed nesting (Moisan et al. 2025). The greater snow goose is the most abundant avian species in the study area, typically breeding each summer in a vast colony of approximately 25 000 pairs, mostly concentrated within an area of about 75 km² (Moisan et al. 2025) (Fig. 1). Snow goose eggs provide an abundant and predictable food source for predators, as the breeding population size and spatial extent have remained relatively stable over the past decades (Duchesne et al. 2021, Moisan et al. 2025). However, in 2022, due to a very late spring and delayed snowmelt, the snow goose breeding population reached an unprecedented

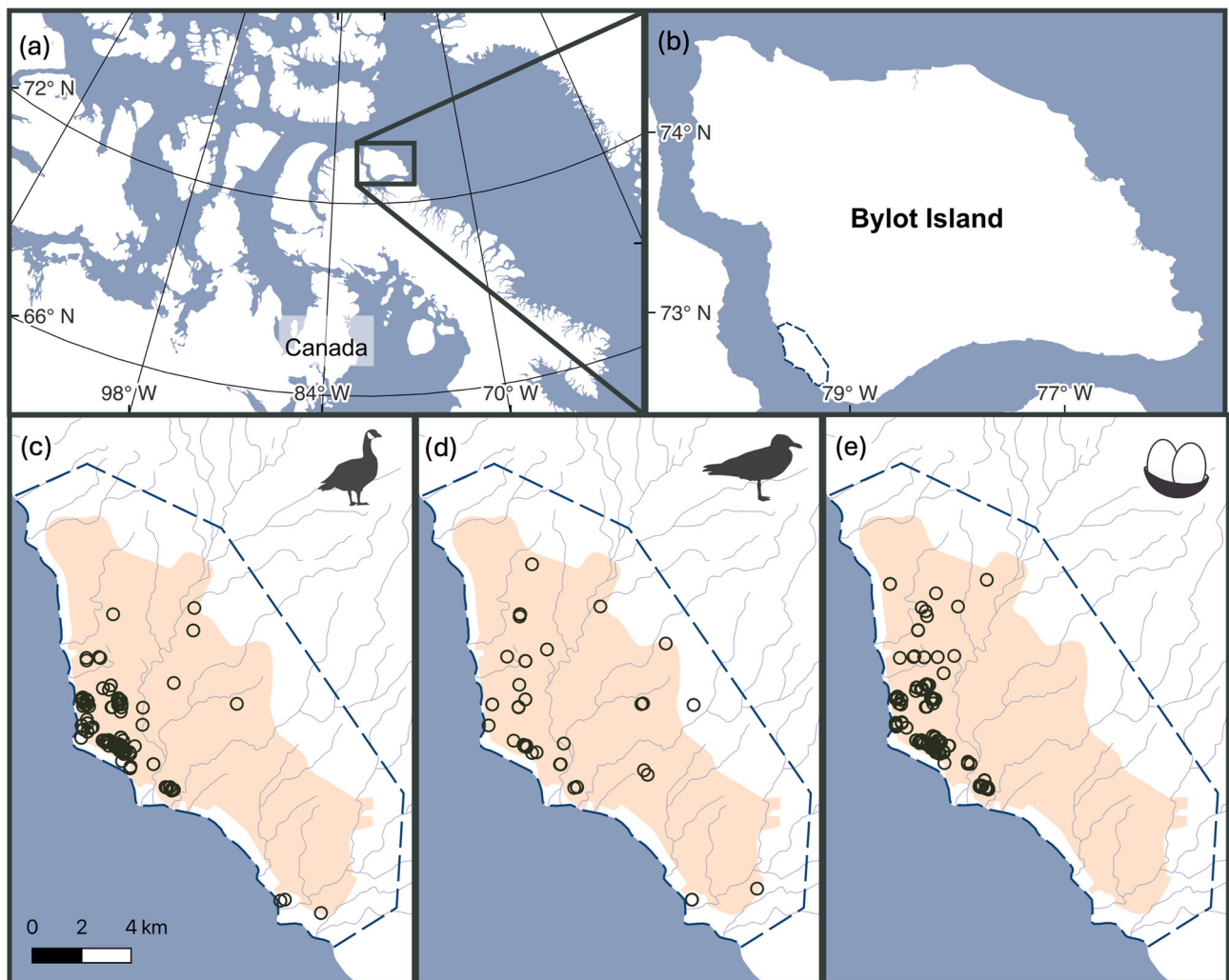


Figure 1. Top panels (a), (b) show the study location on Bylot Island, Nunavut, Canada. Bottom panels show the study area (outlined by dashed lines; ~ 150 km²), including the main snow goose nesting area (orange polygon) and the spatial distribution of nests (hollow circles) used in survival analyses: (c) cackling goose nests (n=132), (d) glaucous gull nests (n=55), and (e) artificial nest experimental units (n=190), each consisting of a triad of artificial nests.



Figure 2. The wetlands of the study area comprise numerous ponds and lakes scattered with islets (a), which serve as nesting sites for a few bird species, including the cackling goose (b). Arctic foxes can reach these islets by swimming (c) or by jumping when the islet is located close to the shore. Photos by: (a) Jeanne Clermont, (b) Yannick Seyer, and (c) Louis-Pierre Ouellet.

low, with only ~ 4500 pairs and most nests concentrated in a reduced area of 40 km² (Moisan et al. 2025). In parallel, predators in the system also heavily rely on small mammals. The brown *Lemmus trimucronatus* and collared lemming *Dicrostonyx groenlandicus* show synchronized abundance cycles of 3–5 years, with much greater amplitude in the brown lemming's cycle (Gruyer et al. 2008).

The Arctic fox is the main terrestrial predator in the study area, feeding heavily on lemmings and snow geese (primarily eggs and goslings) during the summer (Bêty et al. 2002, Gauthier et al. 2011). Foxes also prey on the eggs of various nesting birds, including glaucous gulls and cackling

geese. Avian predators such as glaucous gulls, long-tailed *Stercorarius longicaudus* and parasitic jaegers *S. parasiticus*, and common ravens *Corvus corax* may occasionally depredate eggs from undefended nests (Bêty et al. 2001, McKinnon and Bêty 2009). However, their influence on the breeding success of cackling geese and glaucous gulls is likely limited, as these avian predators rarely displace large birds from their nests (Inglis 1977).

In the study area, Arctic foxes typically maintain the same home range throughout the summer (Clermont et al. 2021) and generally remain faithful to these home ranges during winter (Rioux et al. 2017). Although access may vary spatially

and between years, all foxes in the study area have access to snow goose eggs, as their summer home ranges fully or partially overlap the goose nesting area (average home-range size ranging from 11 to 22 km²; Giroux et al. 2012, Dulude-de Broin et al. 2023). Annual variation in snow goose nest density can therefore influence summer prey availability for all foxes foraging within our study area.

Study design

We analyzed natural and artificial nest survival to assess islet refuge protective quality based on physical characteristics and biological context. Between microhabitats, we compared nest survival on islets and on pond and lake shores for cackling geese (Fig. 3a) and artificial nests (Fig. 3b). We could not conduct this analysis for glaucous gulls as only three nests were monitored on the shore (see the Supporting information for annual sample sizes). Between islets, we evaluated how nest survival was influenced by distance from shore and water depth surrounding islets for cackling geese (Fig. 3c), glaucous gulls (Fig. 3d), and artificial nests (Fig. 3e). For natural nests, all analyses included both main prey annual densities (lemmings and snow goose nests). Natural nest monitoring and robust prey density estimates were unavailable for 2024 due to logistical constraints that prevented us from conducting fieldwork during the birds' incubation period. However, we still deployed artificial nests that year. Consequently, we could not include annual main prey density estimates in artificial nest analyses but nonetheless tested for annual variation in nest survival (Fig. 3b, e), as we could still infer general main prey availability. Moreover, we did not collect data in 2020 and 2021 due to the COVID-19 pandemic.

Main prey availability

We estimated lemming density in 2018, 2019, 2022, and 2023 from live-trapping sessions conducted in the Qarlituvik Valley (73°08'N, 80°08'W). Although separated by 30 km, fluctuations in summer lemming density are synchronized between the main snow goose nesting area and Qarlituvik Valley (Fauteux et al. 2018, Dulude-de Broin et al. 2023). Three sessions were conducted each summer (mid-June, mid-July, and mid-August) in two 11-ha permanent grids, one in mesic tundra and one in wetland habitat. Each grid contained 144 Longworth traps, spaced 30 m apart. Sessions lasted three days, with traps checked every 12 h. Captured lemmings were identified to species level and marked with passive integrated transponder (PIT) tags before release. Using the mark–recapture method (Fauteux et al. 2015), we estimated annual lemming density as the mean of June and July densities for each species and grid, a period which corresponds to the incubation period for both cackling goose and glaucous gull.

We estimated snow goose nest density in the study area in 2018, 2019, 2022, and 2023 following a multi-step process presented in Moisan et al. (2025). Within the main snow goose nesting area (inside orange polygon Fig. 1c–e), whose outline was delimited annually using a GPS receiver aboard a helicopter, we assessed nest densities separately in wetlands and mesic habitats, as geese generally nest more densely in wetlands on Bylot Island (Lecomte et al. 2008). First, wetlands were delineated through photointerpretation of high-resolution (~ 30 cm) satellite images. Habitat not classified as freshwater or wetlands were considered mesic. Second, we calculated nest density in mesic habitat using systematic nest sampling and observations of breeding individuals, whereas

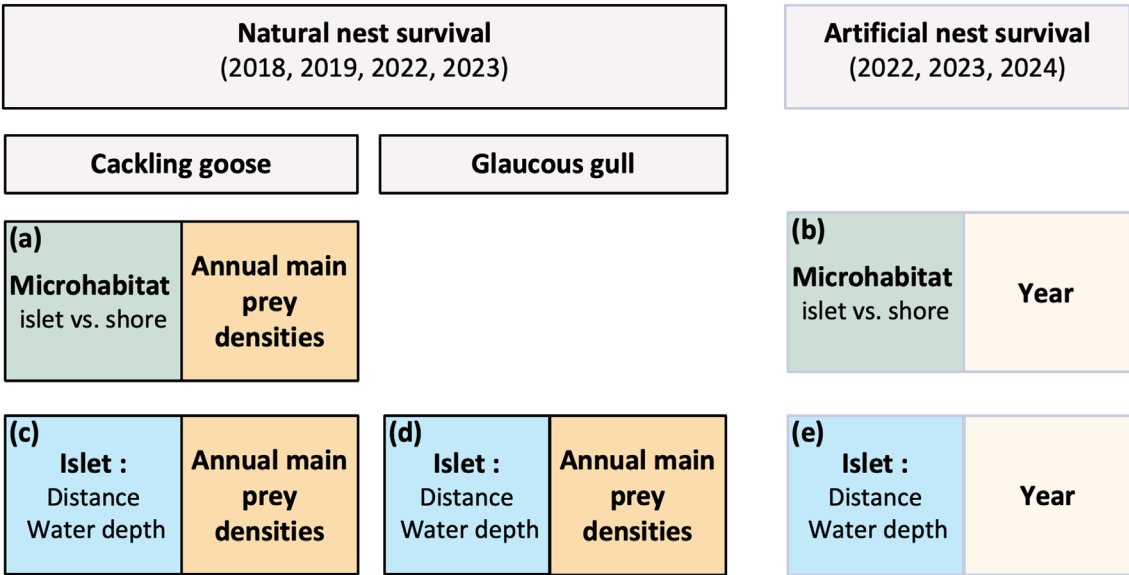


Figure 3. Design for assessing nest survival of natural and artificial nests in relation to nest microhabitat (a)–(b): islet versus shore), or islet characteristics (c)–(e): distance to shore and water depth), and annual main prey densities (a), (c), (d): lemmings and snow goose nests) or interannual variation (b), (e): year) in Bylot Island, Nunavut, Canada. Microhabitat effect could not be tested for glaucous gulls due to low sample size.

wetlands densities relied solely on systematic nest sampling. Third, we multiplied the annual wetland and mesic areas within the main snow goose nesting area by their respective nest density to estimate the total annual nest count. Finally, we divided this count by the study area size (150 km²) to obtain the annual nest density for the entire study area.

In 2024, since the study site only became accessible in late July, we could not obtain these same estimates of lemming and snow goose nest densities. Lemming trapping was only conducted in July and over smaller grids. For snow geese, a systematic nest search was carried out within a 0.2-km² intensively studied core area at the center of the main snow goose nesting area. This survey is usually conducted annually during goose incubation, but in 2024 it was delayed shortly after the hatching period as the site was inaccessible earlier in the season. For 2024, we inferred snow goose nest density from remaining empty nest cups, providing a minimal estimate. This provided a basis for year-to-year comparison. We were thereby able to distinguish general differences in the availability of main prey between 2022, 2023, and 2024 (see the Supporting information for annual main prey densities), when artificial nest experiments were conducted.

Cackling goose and glaucous gull nest monitoring

We conducted nest monitoring for glaucous gulls and cackling geese annually during the incubation period. We found 94% of nests monitored while systematically searching wetland patches in June and opportunistically discovered the remaining nests throughout the nesting period. We conducted nest searches by teams of 2–3 people equipped with binoculars, walking through known and potential nesting sites throughout the study area. Glaucous gulls do not form colonies in the study area. Their nests are conspicuous on elevated mounds, and individuals often begin mobbing from a considerable distance. Cackling goose nests can be harder to spot as females lay flat on their nests (Fig. 2b), making them more cryptic. However, they can display defensive behaviors and alarm calls when approached. Benefiting from the open landscape to directly spot nests and using parental behavior cues, we are confident that we found nearly all nests.

For each nest found, we recorded its GPS position, identified the species, and noted the microhabitat type (islet or shore). To evaluate the influence of islet characteristics on nest survival, we measured the shortest distance in the field from each islet to the shore (using a calibrated step count or the distance between two stationary, averaged GPS points; ± 2 m) and the maximum depth along this transect (measured with a graduated walking stick; ± 5 cm). We estimated nest hatching dates by floating eggs in water and using egg angle and float height as indicators of egg age (Liebezeit et al. 2007). We checked nests irregularly and opportunistically throughout incubation to record signs of predation. We revisited nests on or shortly after their estimated hatch dates to determine their fate. The exact hatching date was observed for > 30% of nests annually. We deemed a nest successful if at least one egg hatched or, when the final visit occurred close to the estimated hatch date, if the nest remained active

(i.e. contained at least one warm egg) at the end of the monitoring period. After goslings and parents had left the nest, successful hatching could be distinguished from egg predation based on the condition of the eggshell membrane. In successfully hatched eggs, the membrane was detached from the inner shell, whereas in scavenged eggs the membrane often remained partially or fully adhered to intact shell fragments. Partial clutch predation was relatively infrequent in successful nests (estimated at < 15% annually). We classified nests as unsuccessful if they were completely depredated during the monitoring period. We excluded a total of 39 out of 229 monitored nests from analyses because they were either: found depredated on the first visit (0.9%, $n = 2$), visited only once (6.1%, $n = 14$), abandoned by parents (0.9%, $n = 2$), had an uncertain fate (3.1%, $n = 7$), lacked a microhabitat identification (3.1%, $n = 7$), or had to be excluded for other reasons (e.g. predation by an avian predator due to the observer) (3.1%, $n = 7$).

Artificial nest experiments

We conducted artificial nest experiments between 28 June and 13 July, in 2022 and 2023, during the cackling goose and glaucous gull incubation period, and between 21 July and 31 July 2024, shortly after the bird hatching period. We deployed 71 experimental units in 2022, 105 in 2023, and 73 in 2024. Each experimental unit consisted of a triad of artificial nests placed in an equilateral triangle, 20 ± 3 m apart: one artificial nest on an islet and two artificial nests on the nearest shore (see the Supporting information for experimental design). Although we deployed a total of 249 triads (747 nests) over three years, only subsets of the data were retained for analyses (190 or 179 experimental units, see justifications below). We placed artificial nests 20 m apart, a distance at which Arctic fox detection is generally high (Beardsell et al. 2021, Weiss-Blais 2025). To avoid defense of artificial nests by nearby nesting birds, we placed each nest > 10 m from red-throated loon, cackling goose, or snow goose nests (Robertson 1995, Bêty et al. 2001) and > 50 m from glaucous gull nests (Burger and Beer 1975).

For each artificial nest, we formed a small depression in the ground, where we placed two standard chicken eggs on a bed of goose down, and inserted a colored nail in the down to help identify depredated nests. To limit detection by avian predators, we covered nests with lichen (genus *Bryoria* or *Gowardia*), completely concealing the eggs and down. We inserted a goose feather into the lichen cover to secure it over the nest. We handled all nest material using latex gloves to minimize human scent. We measured the distance between the shore and islet (using a calibrated step count or the distance between two stationary, averaged GPS points; ± 2 m), as well as the maximum water depth associated with this transect (using a graduated walking stick; ± 5 cm). We revisited all nests in the triad at 24 ± 3 -h intervals and ended the experiment when at least one of the triad's nests was depredated.

In summer 2022 and 2023, we conducted a parallel experiment using motion-triggered cameras to confirm whether Arctic foxes were responsible for depredating covered artificial

nests. We placed cameras ~ 3 m from 40 single artificial nests deployed in wetland habitats in the study area. Arctic foxes depredated 33 nests and one common raven depredated one, while six were not depredated, thus confirming that Arctic foxes were the main predator of covered artificial nests in our study area.

Although Arctic foxes were the primary predators of artificial nests, avian predators could also prey on them (above). To test our hypothesis that nest survival would be higher for nests less accessible to foxes, we excluded triads in which at least one artificial nest showed evidence of avian predation, identified by eggshell remains near the depredated nest (Hall and Arnold 1962). Eggshell remains were found at 7% of artificial nests (50 of 747 nests), and in most cases, only one nest per triad showed evidence of avian predation. Consequently, we excluded 18% of triads (44 of 249 triads), removing any triad that contained evidence of avian predation from the analysis. We also excluded triads when the revisit interval was too long and predation occurred during that interval or when the experiment was interrupted by the observer before any predation occurred ($n = 15$ triads), resulting in a total sample of 190 experimental units used to compare artificial nest survival between islet and shore nests. At least one artificial nest was depredated in each of these triads, indicating that an active predator, most likely a fox, had approached within ≤ 20 m of each artificial nest. To assess whether nest survival of artificial islet nests varied with islet distance to shore and water depth, we further excluded 11 triads in which neither shore nest was depredated, resulting in a sample of 179 islet nests. This ensured that a predator, likely a fox, had traveled along the shoreline nearest the islet and came within 20 m of the artificial nest located on an islet. When conducted with this sample (i.e. 179 experimental units in which at least one shore nest was depredated), analyses comparing artificial nest survival between islet and shore nests yielded similar results (Supporting information).

Statistical analyses

We tested whether nest survival of cackling goose nests 1) differed between islet and shore nests, and 2) was affected by main prey densities (lemming and snow goose nest densities) (Fig. 3a). We used generalized linear mixed models with a binomial distribution (R package 'lme4' ver. 1.1.30; Bates et al. 2015) and the logistic-exposure method, which accounts for variations in nest monitoring length (i.e. exposure) and does not require assumptions about the timing of nest loss (Shaffer 2004). In this method, exposure is incorporated into the link function to estimate daily nest survival. We considered a nest to have survived (1) if at least one egg hatched or was still being incubated by a parent at the end of the monitoring; otherwise, it was deemed depredated (0). For successful nests, we defined exposure as the number of days from discovery to either the hatch date (observed or estimated) or to the last monitoring date if eggs were still incubating. For depredated nests, we calculated exposure as the number of days from discovery to the midpoint between the last active date and the date it was determined to be depredated, since the exact date of failure was not known. Using midpoints for depredated nests with relatively long intervals

between nest visits increases uncertainty in the estimation of daily survival and may reduce our ability to detect small differences or effects. Our global model included nest microhabitat (islet or shore), lemming density, and snow goose nest density as fixed effects, with the year as a random effect to control for other interannual variations (see the Supporting information for a list of the models tested). We tested the inclusion of nesting zones, identified via cluster analysis (see Duchesne et al. 2021 for detailed methodology), as random effect in the global model to account for potential spatial correlation. These zones had species-specific diameter and could be used annually for nesting. However, including this variable did not affect our results (not shown).

We tested whether artificial nest survival 1) differed between islet and shore nests, and 2) among years (Fig. 3b). Here, for each triad, we randomly removed one shore nest so that each experimental unit contributed one islet and one shore nest to the analysis ($n = 380$ nests). We analyzed this dataset using logistic regression models (logit-link and binomial distribution). We classified an artificial nest as successful (1) when at least one egg remained in the nest, and as depredated (0) otherwise. Our global model included microhabitat (islet or shore), year, and their interaction as fixed effects. Pair identity was included as a random effect to account for the paired experimental design. Interactions between variables were included when sample size provided enough events per variable for reliable model estimation and if the model converged (see the Supporting information for a list of the models tested).

We assessed whether nest survival of cackling goose and glaucous gull nests varied with islet distance to shore, water depth, and annual densities of main prey (lemmings and snow goose nests) (Fig. 3c–d). We initially used logistic-exposure models with distance to shore, water depth, lemming density, and snow goose nest density as fixed effects, and year as random effect. However, due to a singular fit with a low number of groups in the random effect term, we re-specified year as a fixed effect. Year was then highly correlated with prey densities and was subsequently removed. Multicollinearity between lemming and snow goose nest densities ($VIF > 5$) led us to run separate models for each variable (VIF values in the Supporting information). Additionally, we removed water depth from cackling goose models due to convergence issues. Consequently, global models for cackling goose included distance to shore and either snow goose nest density or lemming density, whereas global models for glaucous gulls included distance to shore, water depth, and either snow goose density or lemming density (see the Supporting information for a list of all models tested).

We assessed whether nest survival of artificial islet nests varied annually and with islet distance to shore and water depth (Fig. 3e). We performed the analysis using logistic regression models with logit-link, setting distance to shore, water depth, year, and the interaction between either distance and year or water depth and year as fixed effects in the global models (see the Supporting information for a list of all models tested).

When applicable, we tested the inclusion of islet ID as a random effect in the global models for all nest types, since a few

islets were reused across the years. We found that adding this variable did not affect the overall results (not shown) and therefore did not include it in the global models. Given movement constraints on foxes (e.g. jump length and the need to swim in deep water), we suspected potential nonlinear effects of distance to shore and water depth (Corbeil-Robitaille et al. 2024). To investigate this, we applied distance-weighted transformations ($e^{-\alpha/\text{Distance}}$ and $e^{-\alpha/\text{Depth}}$) to Euclidean distance and depth variables for all three nest types (Miguet et al. 2017). Following Carpenter et al. (2010), we tested various α values and used Akaike information criterion corrected for small sample size (AICc) to select the most parsimonious distance-weighted function for each variable, which were then used in the final model selection for each nest type (Supporting information).

Across all analyses, we checked model assumptions, including linear relationship between $\logit(y)$ and each independent variable, multicollinearity, dispersion and checked for the presence of outliers (R packages 'DHARMA' ver. 0.4.6 (Hartig 2022); 'car' ver. 3.1.0 (Fox and Weisberg 2019), and 'blmeco' ver. 1.4 (Korner-Nievergelt et al. 2015)). From global models, we performed model selection by testing various biological meaningful combinations of variables, including the null model. We ranked models using R package 'AICcmodavg' ver. 2.3.1 (Mazerolle 2020). We considered models with $\Delta\text{AICc} \leq 2$ to be competitive (Anderson and Burnham 2002). We visualized results using coefficients from the best-supported model (i.e. the model with the highest weight) and obtained 95% confidence intervals or SEs using bootstrap. We performed all analyses in R ver. 4.2.2 (www.r-project.org).

Results

Effects of refuge use on nest survival

We monitored 132 cackling goose nests in the study area across four breeding seasons (2018, 2019, 2022, and 2023), with 69 nests located on islets and 63 on shore (see yearly

sample size in the Supporting information). Nest survival was best explained by nest microhabitat and annual snow goose nest density. Specifically, we found moderate evidence of higher nest survival rates for nests on islets compared to those on shore, along with strong evidence of increased survival with higher annual snow goose nest density (Table 1, Fig. 4; full model selection in the Supporting information). At snow goose nest densities of 23 and 161 nests km^{-2} (corresponding, respectively, to the lowest and highest densities observed), nest survival rate was estimated to vary from 0.01 to 0.96 on shores and 0.27 to 0.99 on islets, based on a mean exposure of 16 days. In contrast, we found little to no evidence of an effect of annual lemming density, with this variable even excluded from one of the competitive models (Table 1). When excluding data from 2022, the year with the lowest snow goose density, we still observed a moderate effect of nest microhabitat but found little to no evidence of an effect of annual snow goose nest density.

We found moderate evidence of a microhabitat effect on artificial nest survival, with survival rates on islets being 4–13% higher than on the shore, depending on the year. Additionally, we found strong evidence of a year effect, with nest survival rates of 0.19 in 2023 and 0.23 in 2024, compared to 0.06 in 2022, when snow goose nest density was exceptionally low (Table 1, Fig. 4; full model selection in the Supporting information). With a mean exposure of 29 h, the results of the artificial nest experiments thus approximate a daily nest survival rate.

Effects of refuge quality on nest survival

We monitored natural nests located on islets with known physical characteristics (distance to shore and water depth) across four breeding seasons (2018, 2019, 2022, and 2023; see the Supporting information for sample sizes). We monitored 67 cackling goose nests situated at a median distance of 9 m from shore (range: 1–45 m) and separated from the shore by a median maximum water depth of 30 cm (range:

Table 1. Generalized linear model selection of the effects of nest microhabitat (Microhab: islet versus shore) and main prey densities (lemming (Lem) and snow goose nests (SnowG)) on probability of nest survival for cackling goose nests (2018, 2019, 2022, 2023) and artificial nests (2022–2024). Cackling goose models included year as a random effect, whereas artificial nests models included pair identity. Left panel reports null and competitive models ($\Delta\text{AICc} \leq 2$), with number of parameters (K), change in AICc from best-supported model (ΔAICc), and Akaike weights (W). The right panel reports estimated coefficients (β) with their 95% confidence interval (CI) of the model with the smallest AICc. Full model selection is presented in the Supporting information. ^aShore (microhabitat) and Year 2022 (for artificial nests) were used as the reference categories for analyses.

Nests	Model selection				First model summary	
	Model fixed effects	K	ΔAICc	W	Variable ^a	β [95%CI]
	Microhab + SnowG	4	0.00	0.56	Int.	0.43 [−1.97; 2.38]
	Microhab + SnowG + Lem	5	1.84	0.22	Microhab _{islet}	1.31 [0.42; 2.52]
	Null	2	10.25	0.00	SnowG	0.03 [0.01; 0.06]
	Microhab + Year	5	0.00	0.77	Int.	−3.10 [−4.57; −2.25]
	Null	2	12.08	0.00	Microhab _{islet}	0.73 [0.19; 1.39]
					Year ₂₀₂₃	1.22 [0.38; 2.14]
					Year ₂₀₂₄	1.46 [0.53; 2.52]

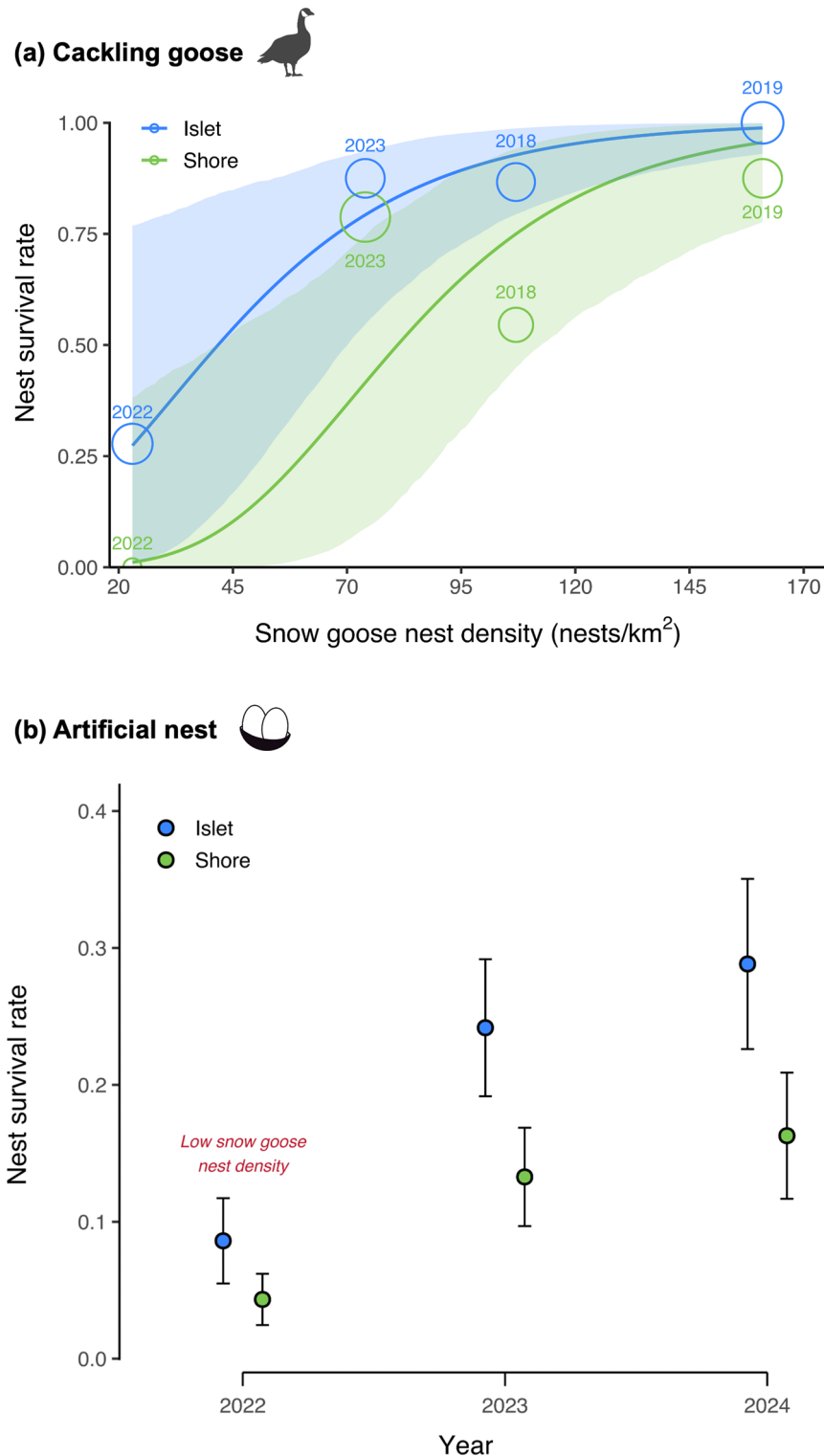


Figure 4. (a) Effect of nest microhabitat (islet versus shore) and annual snow goose nest density on the survival rate of cackling goose nests (2018, 2019, 2022, 2023; $n = 132$). (b) Interannual variation in the survival rate of artificial nests across both microhabitats (2022–2024; $n = 380$). Year 2022 was characterized by exceptionally low snow goose nest density. In both panels, solid lines (a) and dots (b) show mean model predictions over the mean nest monitoring period (16 days in (a); 29 hours in (b)), with 95% confidence intervals (a) and SEs (b). Color denotes nest microhabitat. Open circles sizes are proportional to the number of observed nests contributing to each survival estimate.

3–40+ cm). We also monitored 55 glaucous gull nests located on islets at a median distance of 15 m from shore (range: 1–35 m) and separated from the shore by a median maximum water depth exceeding 40 cm (range: 7–40+ cm).

For natural nests, we found little to no evidence that distance to shore or water depth influenced nest survival in either species, with the latter excluded from competitive models (Table 2, see selection of decay variables and full model selection in the Supporting information). Still, the best-supported model suggested that nests located on islets further from shore presented higher nest survival rates, ranging from 0.75 to 1.00 for cackling goose (at 1 versus 45 m from shore, based on mean exposure of 16 days) and from 0.58 to 0.94 for glaucous gull (at 1 versus 35 m from shore; based on mean exposure of 15 days). However, as confidence intervals overlapped 0 for both species, these ranges should be interpreted with caution due to the limited evidence supporting an effect of distance. Note that water depth analysis was not feasible for cackling goose due to convergence issues, but an examination of raw data showed no strong survival pattern associated with either physical characteristic (Fig. 5). Additionally, survival of nests located on islets was strongly associated with annual snow goose nest density. As snow goose nest density increased from 23 to 161 nests/km², nest survival rates rose from 0.62 to 1.00 for cackling geese and from 0.42 to 0.97 for glaucous gulls. In contrast, lemming density did not appear in any competitive models (Table 2, full model selection in the Supporting information).

Artificial nests monitored in 2022, 2023, and 2024 to assess whether nest survival varied with islet characteristics

(see the Supporting information for annual sample sizes) were located on islets at a median distance of 7 m from shore (range: 1–20 m) and were separated from the shore by a median maximum water depth of 25 cm (range: 5–40+ cm). Nest survival was best explained by distance to shore and year. Specifically, we found strong evidence for a nonlinear relationship between nest survival and distance to shore, as all competitive models included a distance-weighted function (Table 2). Nest survival on islets was lowest in 2022, characterized by exceptionally low snow goose nest density, and for nests located within a few meters from the shore. Nest survival increased sharply up to about 5 m from the shore, then gradually stabilized (Fig. 6). For nests located 2 and 12 m from shore (representing jumping distance and requiring entry into water, respectively), estimated nest survival rates, over a period of 29 hours, ranged from 0.03 to 0.19 in 2022 and 0.11 and 0.45 in 2023 and 2024. In contrast, there was little to no evidence of an effect of maximum water depth (whether on Euclidean or Decay scale) (see selection of decay variables and full model selection in the Supporting information).

Discussion

Prey refuges can promote species occurrence and coexistence (Léandri-Breton and Bêty 2020, Duchesne et al. 2021). Using multi-year nest monitoring and field experiments, we showed that both natural and artificial nest survival was generally higher for nests located in microhabitats less accessible to the Arctic fox, the main nest predator in the Arctic tundra.

Table 2. Generalized linear model selection of the effects of islet physical characteristics (distance to shore (Dist) and water depth (Depth)), and annual main prey densities (lemming and snow goose nests (SnowG)) or year, on the probability of nest survival for cackling goose nests (2018, 2019, 2022, 2023), glaucous gull nests (2018, 2019, 2022, 2023), and artificial nests (2022–2024). Star «*» indicates that a distance weighted function was used. Left panel reports null and competitive models ($\Delta\text{AICc} \leq 2$), with number of parameters (K), change in AICc from best-supported model (ΔAICc), Akaike weights (W). The right panel reports estimated coefficients (β) with their 95% confidence interval (CI) of the model with the smallest AICc. Full model selection is presented in the Supporting information. ^aYear 2022 was used as the reference category in the artificial nests' models.

Model selection					First model summary	
Nests	Model fixed effects	K	ΔAICc	W	Variable ^a	β [95%CI]
 Cackling goose	Dist*+SnowG	3	0.00	0.48	Int.	0.53 [−1.29; 1.58]
	SnowG	2	0.87	0.31	Dist*	10.45 [−3.36; 48.07]
	Dist+SnowG	3	1.75	0.20	SnowG	0.05 [0.03; 0.08]
	Null	1	42.67	0.00		
 Glaucous gull	Dist+SnowG	3	0.00	0.27	Int.	1.07 [−0.63; 2.41]
	Dist*+SnowG	3	0.45	0.21	Dist	0.07 [−0.01; 0.17]
	SnowG	2	1.62	0.12	SnowG	0.03 [0.01; 0.05]
 Artificial	Null	1	16.84	0.00		
	Dist*+Year	4	0.00	0.26	Int.	−7.23 [−13.12; −3.86]
	Dist*+Depth+Year	5	0.80	0.18	Dist*	6.29 [2.38; 12.84]
	Dist*+Depth*+Year	5	0.80	0.17	Year ₂₀₂₃	1.24 [0.44; 2.41]
	Null	1	10.78	0.00	Year ₂₀₂₄	1.26 [0.27; 2.48]

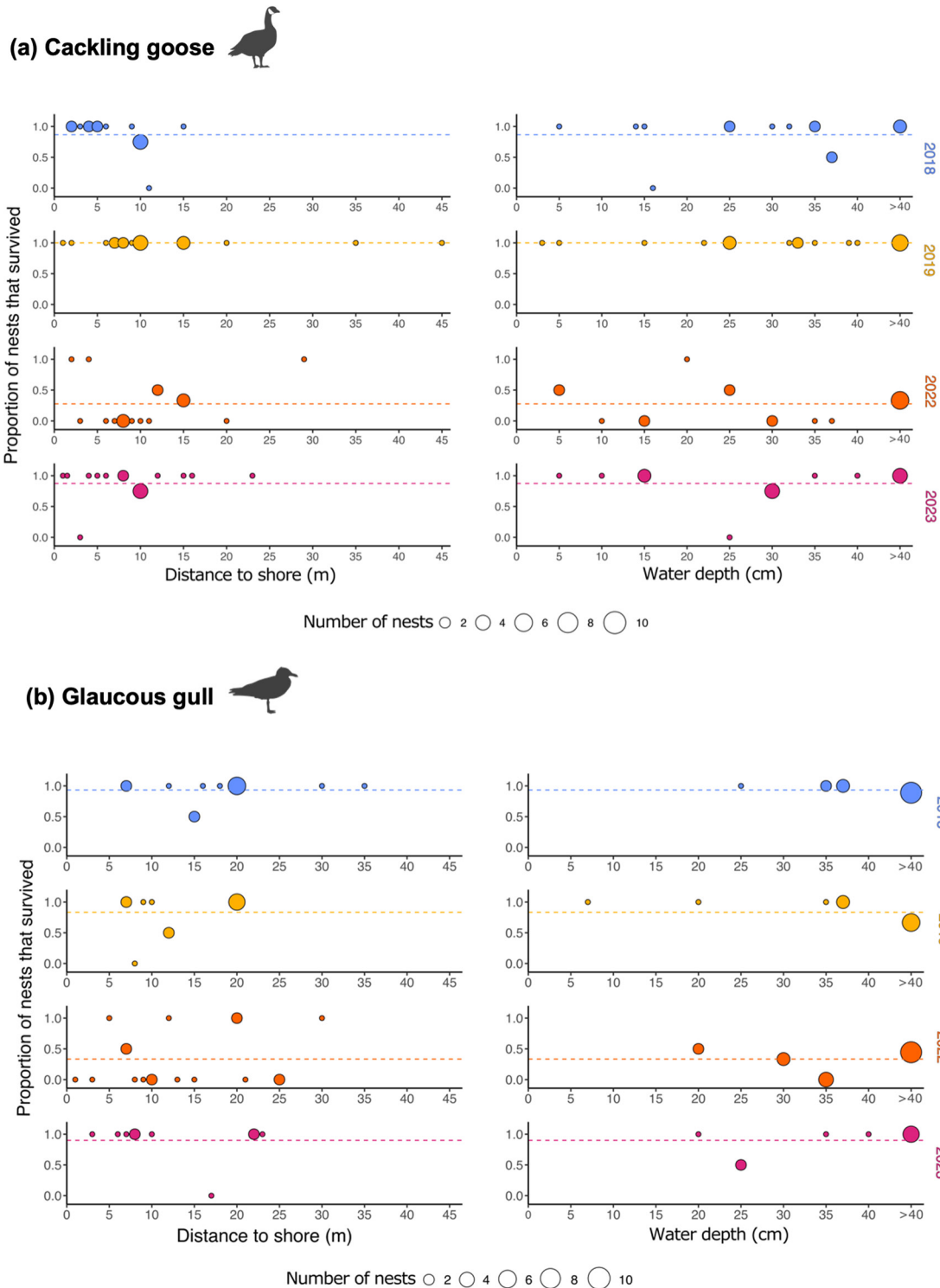


Figure 5. Proportion of nests that survived the monitoring interval for (a) cackling geese ($n=67$) and (b) glaucous gulls ($n=55$), on islets differing in distance from shore and water depth, shown by year (2018, 2019, 2022, and 2023). Points represent observed data, with size proportional to sample size. Dashed lines indicate the yearly mean observed nest survival.

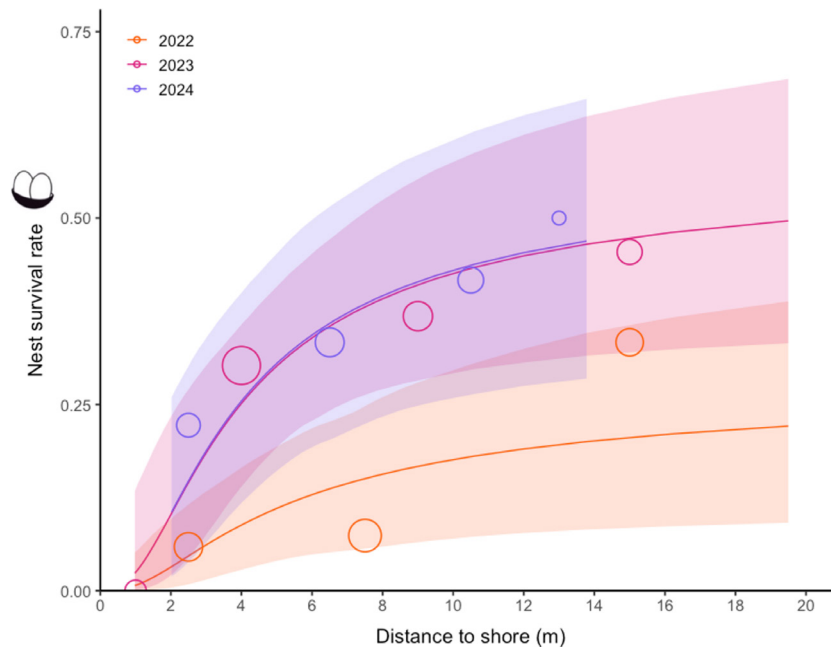


Figure 6. Interannual variation in the effect of distance to shore on nest survival rate of artificial nests located on islets (2022–2024). Circles represent observed data, with size proportional to the number of observations ($n = 179$ nests). The full lines show the mean model prediction over the mean nest monitoring period (29 h), with 95% confidence intervals.

As predicted (P1), survival was higher on islets than on shore. Among nests located on islets, survival was generally higher for those located at a greater distance from the shore. However, there was little evidence of a distance effect for cackling geese and glaucous gulls, both of which rarely nested on islets near the shore (Corbeil-Robitaille et al. 2024). No effect of water depth was detected for any nest types. Together, these results provide only partial support for P2. Though the use of islets reduced predation risk, our results also support the hypothesis that prey densities in the landscape can positively affect the survival of nests located on these partial refuges. This conclusion is mainly based on a single year characterized by exceptionally low density of one key prey species (snow goose nest density in 2022). Despite only two years of overlapping monitoring, the consistency of annual variation between natural and artificial nest survival suggests that Arctic foxes are more likely to target prey in less accessible microhabitats when energy intake is low (Beardsell et al. 2026). As nest survival on islets within or near the main snow goose nesting area appeared to be influenced primarily by snow goose nest density and less by summer lemming density, our results partially support P3. Overall, our study highlights the importance of considering both the physical landscape and prey densities to fully assess prey refuge quality and predator–prey interaction strengths (Fig. 7).

Pond and lake islets as partial refuges from Arctic fox nest predation

As predicted, nest survival was higher on islets than on pond and lake shores for both natural and artificial nests. Since Arctic foxes were the primary predators of artificial nests,

our findings indicate that even small waterbodies (mean waterbody size of 0.008 km²; Corbeil-Robitaille et al. 2024) can hinder access to islets for these mammalian predators (Gauthier et al. 2015). The alignment between islet selection by birds (Bergman and Derksen 1977, Eberl 1993) and reduced nest predation risk supports an adaptive predator avoidance strategy, which could be particularly crucial to improve reproductive success in areas of high fox density (Clermont et al. 2021, Duchesne et al. 2021). Indeed, this strategy likely targets mammalian predators, as islets do not offer protection from avian predators.

These findings likely reflect physical and behavioral constraints on Arctic foxes, which could reduce both the frequency and success of attacks on islets. Reaching islets may involve higher short-term costs, such as time involvement leading to missed foraging opportunities and increased energy expenditure from swimming (Alexander 2002), thermoregulation in cold water (Prestrud 1992), and cleaning or drying fur. Foxes may also avoid attacking nests on islets due to the higher risks of injury from harassing birds (e.g. to eye, skull, and limbs), as limited movement in water may make it more difficult to anticipate and evade attacks (Mukherjee and Heithaus 2013, Shepard et al. 2013). Foxes, which typically rely on swift, agile charges to capture larger prey (Samelius and Alisauskas 2001), may find their mobility hindered in water. This reduced speed can make it more challenging to evade bird parental defense and may also provide incubating birds with additional time to return to their nests if they were temporarily away, such as during an incubation recess. These factors likely contribute to fox hesitation to enter water, rendering islets into partial refuges for nesting birds.

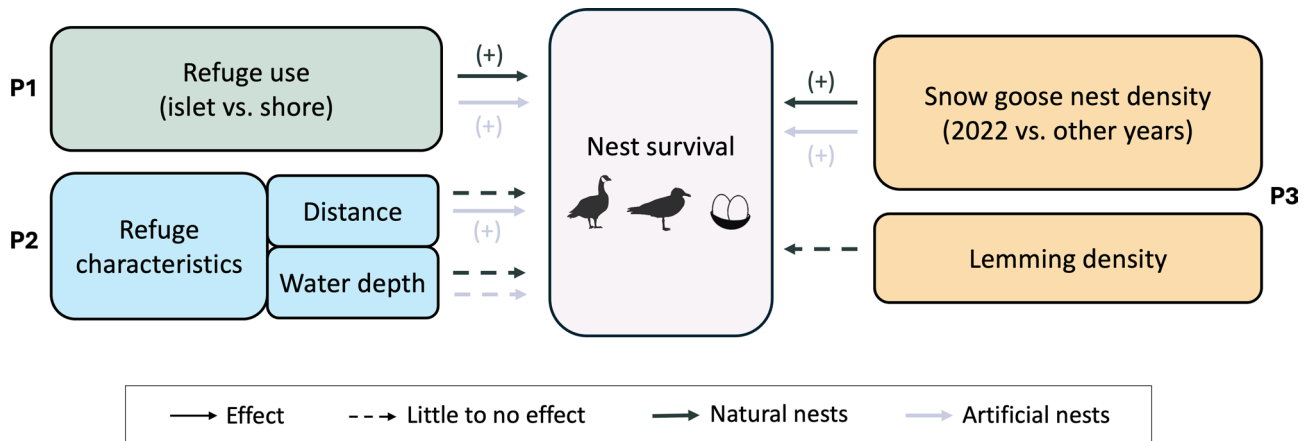


Figure 7. Schematic representation showing differences in the strength of evidence (solid versus dashed lines) for biotic and abiotic drivers affecting natural (black) and artificial (grey) nest survival on pond and lake islets located within or near the main snow goose nesting area on Bylot Island, Nunavut, Canada. Predictions are shown alongside the drivers (Introduction).

Despite higher nest survival on islets, a significant number of cackling geese nested on pond and lake shores, even though most islets (> 80%) remained unoccupied. One possible explanation is that late spring snow and ice cover reduced the availability of suitable nesting sites. During late spring break-up, some islets can be surrounded by an ice sheet at the beginning of the incubation period. However, cackling geese and glaucous gulls were rarely encountered nesting on islets surrounded by ice. This may result from risky conditions, as islets early in the season cannot be considered as refuges: a thick ice sheet may facilitate access for terrestrial predators, while later in the season, broken ice blocks could increase the risk of breeding failure due to shifting ice (Haynes et al. 2014). As cackling goose numbers have grown exponentially on Bylot Island since 1996 (Moisan et al. 2025), more individuals may be forced to nest outside islet refuges due to intra-specific competition and limited availability of suitable nesting sites.

Subtle influence of islet physical characteristics on nest survival

The protective quality of islets against nest predation can vary with their physical characteristics. Nests on islets farther from shore generally exhibited higher survival rates, a pattern consistent with previous studies on island refuges (Strang 1976, Eberl 1993, Albrecht et al. 2006). In contrast, nests on islets close to shore faced greater predation risk from Arctic foxes, especially those within a single jump reach, up to 4 m (Bahr 1989). Beyond this distance, fox mobility is hindered by the presence of water, and the fitness costs of attacking a nest, particularly the risk of injury, may level off with increasing distance. While model selection identified distance to shore as a relevant predictor, its effect was little for natural nests but pronounced for artificial nests. This likely reflects the distribution of natural nests: over 70% of cackling goose nests and over 90% of glaucous gull nests were located more than 5 m from shore. In contrast, artificial nest experiments indicate that the primary shift in predation risk occurs within

the first 5 m (Fig. 6). Consequently, because natural nests were mostly located beyond the 0–5 m zone where predation risk changes most sharply, our ability to detect this effect was likely reduced.

Alternatively, the limited effect of distance to shore observed for natural nests could result from the short islet-to-shore distances in the study area (maximum recorded distance: 54 m). For example, Eberl (1993) found that red-throated loons which nest on islands > 100 m from shore were spared from fox predation, while those located < 20 m faced heavy losses. Similarly, Robertson (1995) reported that foxes avoided islands > 50 m from shore. The selection of islets farther from shore by cackling geese and glaucous gulls observed on Bylot Island (Corbeil-Robitaille et al. 2024) may still reflect an adaptive response to nest predation risk. However, under high predation pressure, this strategy may be less effective in the relatively small waterbodies of our study area compared to larger lake systems.

Apparent discrepancies between the results from natural and artificial nests regarding the effect of distance may also arise from a higher detection probability of natural nests by foxes. Indeed, foxes rely mainly on olfactory cues to detect covered artificial nests, while natural nests also provide visual cues (e.g. from parental activity; Martin et al. 2000). Furthermore, odor-mediated detection varies with chemical composition (e.g. presence of down and incubating adult) and fluid dynamics (e.g. wind direction and strength) (Finelli et al. 2000). Odor cues from artificial nests on islets located farther from shore may dissipate more effectively, reducing detection and increasing nest survival. In contrast, natural nests may emit stronger cues, aiding detection by foxes even at greater distances. Strong distance effect in artificial nests could therefore arise from slightly lower detection and attack probabilities. However, the very limited number of natural nests found near the shore, and the resulting limited statistical power at short distances, most likely explains discrepancies in the effect of distance and suggests that birds avoid nesting on riskier islets located close to shore.

Water depth surrounding islets appeared less influential than distance to shore in determining islet protective quality, with little to no effect on natural and artificial nest survival. This contrasts with previous studies showing that greater water levels can reduce terrestrial predator access (Zoellick et al. 2004, Albrecht et al. 2006, Schmidt et al. 2023). This difference could be explained by limitations in the water depth variable used, which may not have accurately captured variation relevant to predator access. Other measurements, such as mean water depth along paths or intra-seasonal water depth variations, might better capture fox accessibility. However, the latter was irrelevant for artificial nests, as each experiment lasted a maximum of four days. Moreover, the composition of bottom sediments in small waterbodies could also influence predation risk. In shallow waterbodies presenting deep mud layers, foxes may face significant movement constraints, such as suction-induced drag (Liu et al. 2023), potentially exceeding the challenges of swimming. The joint effect of water and substrate barriers could therefore reduce fox efficacy and efficiency in depredating nests on islets, while increasing their vulnerability to bird counterattacks. Thus, water depth alone might be insufficient to predict fox accessibility.

This study focused on clutch predation risk but overlooked the potential threats to incubating adults. Unlike most avian predators, foxes pose a significant risk of injury or death to adults of both species. Cackling geese, for instance, exhibit short flushing distances (Kellett and Alisauskas 2011) and glaucous gulls leave one adult alone on the nest during alternating incubating and feeding shifts (Bustnes et al. 2001), making both species vulnerable to fox attacks. Islets farther from shore may enhance adult survival by reducing predator speed when approaching the nest and by providing earlier predator detection and more reaction time for incubating birds. Thus, selection for islet characteristics may not only be driven by short-term reproductive success but also by the need to support long-term adult survival, which may be even more critical. For example, pink-footed geese *Anser brachyrhynchus* in Svalbard show higher nesting success in slope habitats but still select cliff habitats, likely to enhance adult survival. Fox-killed geese are often found in slope habitats but never in cliffs (Anderson et al. 2015). Similarly, in 2022, we observed a fox decapitate a female cackling goose incubating on a nest situated on a peninsula accessible to foxes, an observation that underscores the vulnerability of adults. Observational data on interactions between defensive nesting birds and offensive foxes would enhance our ability to model and quantify the strength of species interactions (Beardsell et al. 2026). Moreover, including incubating adult survival in future studies could reveal more complex drivers of nest site selection and population viability in natural communities (Rivers et al. 2025).

Main prey availability as an indirect key factor in allospecific nest survival

Nest survival rates on islets and on pond and lake shores varied annually in both natural and artificial nests. While factors such as the physiological condition of incubating adults

(Skinner et al. 1998) and their behavior (e.g. frequency and length of incubating recesses) may affect nest survival (Anderson et al. 2015), our experiments indicate that variation in predation pressure was a key driver of these interannual differences. Our conclusions are reinforced by the consistent patterns observed in natural and artificial nests, with survival of artificial nests being solely influenced by predation risk. Overall, our results strongly support the hypothesis that the protective quality of islets as prey refuges is modulated by predator foraging behavior, which appears closely tied to fluctuations in prey availability.

Predation pressure in prey partial refuges was closely linked to prey availability in our study area, with snow goose nest densities playing a dominant role. The summer of 2022 provided a rare opportunity of exceptionally low snow goose nest density in the study area (Supporting information), coupled with low lemming density. This prey scarcity coincided with significantly lower nest survival rates on islets compared to other years. In periods of low prey abundance, foxes may experience a much lower energy acquisition rate, prompting increased foraging efforts (Beardsell et al. 2026). For instance, foxes are typically more active and travel longer daily distances when lemming densities are low (Beardsell et al. 2022). Such elevated activity could result in a greater time spent foraging in wetlands, increasing the likelihood of encountering and detecting nests on islets. Additionally, foxes may exhibit a greater willingness to take risks (Brown and Kotler 2004, Berger-Tal et al. 2009, Beardsell et al. 2026). Experiments with captive red foxes *Vulpes vulpes* have shown that hungry individuals spent more time foraging in riskier patches compared to when they were in better condition (Berger-Tal et al. 2009). Such behavioral changes, driven by energetic constraints, could explain an increased risk-taking behavior by foxes, even towards nests located in partial refuges such as islets.

We found strong evidence that snow goose nest densities in the landscape affected nest predation on islets, but little to no evidence that lemming densities did. The relatively low lemming densities throughout the study period, combined with the limited number of monitoring years and statistical constraints (i.e. multicollinearity inducing separate prey models), may have reduced our ability to detect lemming effects. However, our findings align with prior observations of poor nest survival on islets during periods of prey scarcity. Although our study did not include a control site away from the main snow goose nesting area, previous studies suggest that large snow goose colonies can buffer the effects of lemming fluctuations on predator–prey dynamics (Iles et al. 2013, Flemming et al. 2019). Fox reproduction on Bylot Island is strongly tied to lemming availability (Giroux et al. 2012), yet when lemmings are scarce, some foxes with access to snow goose eggs can reproduce (Giroux et al. 2012). Remarkably, 2022 was the only year in the past two decades of monitoring with no fox reproduction recorded across the entire ~ 600-km² study site of Bylot Island (Berteaux unpubl.), emphasizing the critical role of goose colonies in mitigating food shortage when lemming densities are low. This potential

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