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ORIGINAL PAPER

Spatial variation in predator communities, predation risk, and shorebird daily nest survival near a sub-Arctic human settlement

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Abstract

In the Arctic, nest predation risk is higher at lower latitudes, and some shorebirds (Charadriidae) nesting at the southernmost limits of their ranges near Churchill, Manitoba tend to experience lower nest success than those at other Arctic sites. This study investigates whether proximity to human settlement affects predator abundance, predation risk, and shorebird daily nest survival near Churchill by measuring these variables at varying distances from town during two nesting seasons. Active fox dens decreased in number close to town; however, there was no clear trend in avian predator abundance in relation to town. Predation risk on artificial nests decreased as distances from active fox dens and Parasitic Jaeger (*Stercorarius parasiticus*) nests increased, decreased with proximity to town, and decreased with a camera present. Shorebird daily nest survival tended to be lower near jaeger nests and there was some support for a positive effect of camera presence and proximity to town. Overall, these results suggest that shorebird nest survival in the sub-Arctic can be heavily impacted by proximity to nests of avian predators, but that shorebirds may benefit from proximity to town likely due to reduced fox denning activity.

Keywords Anthropogenic · Artificial nest · Camera trap · Nest predator · Nest survival · Predation risk · Shorebird

Introduction

The Arctic is known for its relatively simple terrestrial ecosystems in which there is a low diversity of predator, prey, and plant species (Gaston 1996). The trophic interactions within such systems have been of great interest in recent decades, and for some regions we now have a relatively good understanding of the direct and indirect interactions among predators and their primary as well as "alternative" and "incidental" prey (e.g., McKinnon et al. 2013; Flemming et al. 2019). However, not all northern ecosystems exist in pristine wilderness areas free of human influence. Indeed, there are some Arctic and sub-Arctic human settlements with populations in the tens of thousands. Our study is an attempt to take account of the spatial anthropogenic effects on an extensively studied trophic system near a sub-Arctic town in Canada.

In Arctic- and sub-Arctic-nesting birds, egg predation is consistently found to be the leading cause of nest failure (Skeel 1983; McKinnon et al. 2010a; Smith and Wilson 2010; Laidlaw et al. 2020). Nest predation risk, defined here as the likelihood that eggs in an uncovered, undefended ground nest will be taken by a predator during incubation, has been shown to decline with increasing latitude in the Arctic (McKinnon et al. 2010a); therefore, shorebirds nesting in the low Arctic may be exposed to a relatively higher risk of predation than those nesting farther north (but see Kubelka et al. 2018, 2019; Bulla et al. 2019). Although increased predation risk does not always directly translate into higher rates of nest predation (McKinnon et al. 2010b), shorebirds nesting at the southernmost extents of their ranges near Churchill, Manitoba are known to suffer unusually high rates of nest predation (Jehl 1971; Ballantyne and Nol 2011). Near Churchill, breeding Red-necked Phalaropes (*Phalaropus lobatus*) and Semipalmated Sandpipers (*Calidris pusilla*) have become scarce, but the cause of these declines is unknown (Smith et al. 2006; Jehl 2007). However, a diversity of shorebird species still nests in this apparently risky sub-Arctic habitat and continues to

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successfully produce offspring (Nol et al. 2010; McKinnon et al. 2013; Senner et al. 2016).

Many factors influence rates of nest predation among Arctic-nesting shorebirds. For example, longer incubation breaks and periods of egg exposure result in higher nest predation risk, which may mean greater risk for uniparentally incubating species (Smith et al. 2012; Meyer et al. 2020a). Biparentally incubating species tend to experience higher nest success over time within a breeding season as their nest defense behavior intensifies, as compared with uniparentally incubating species, which appear to rely more on crypticity in avoiding nest predation (Smith and Wilson 2010). In the high Arctic, predation risk on shorebird nests can be influenced indirectly by cycling microtine rodent populations; when microtine rodent populations decrease, predation risk on shorebird nests can increase due to reduced food availability for their shared predator, the Arctic fox (McKinnon et al. 2014). However, in the sub-Arctic, where microtine rodent population cycles are of lower amplitude (Roth unpubl. data), this relationship is less clear (Weiser et al. 2018).

For nearly a century, naturalists in some parts of the Arctic and sub-Arctic have noted considerable and rapid changes in the distributions and numbers of nest predator species, which have been driven by substantial ecological change (Marsh 1938; MacPherson 1964; Jehl 2004; Post et al. 2009; Elmhagen et al. 2017). Red foxes (*Vulpes vulpes*) are establishing populations farther north throughout many areas of the Arctic, displacing Arctic foxes (*Vulpes lagopus*) and changing predator–prey dynamics (Marsh 1938; MacPherson 1964; Post et al. 2009; Gallant et al. 2020). The abundance of Common Ravens (*Corvus corax*) at high latitudes is increasing, and numbers (according to Christmas Bird Counts) in the Churchill area, for example, have increased roughly sixfold since the 1960s alone (Jehl 2004). A large and still increasing number of breeding Herring Gulls (*Larus argentatus smithsonianus*) has also been observed near Churchill from the 1990s onward (Jehl 2004). The underlying causes of these changes are multifactorial but are driven at least in part by climate change and anthropogenic alteration of habitat and food availability (Post et al. 2009; Stickney et al. 2014; Elmhagen et al. 2017).

Human food subsidies may be the best explanation for the expansion of red foxes into the Arctic (Elmhagen et al. 2017; Gallant et al. 2020). The presence of human infrastructure and garbage in the North can influence the diet, activity, and/or increase the density of opportunistically scavenging predators, including red and Arctic foxes as well as gulls and jaegers (NRC 2003; Liebezeit et al. 2009; Julien et al. 2014). These shifts in predator distribution and density can in turn increase rates of nest predation on, and decrease nest success of, ground-nesting passerines (Liebezeit et al. 2009) and potentially shorebirds (NRC 2003; Liebezeit et al. 2009) in areas closer to human infrastructure and settlement. However, very few studies have explored this human–predator–prey relationship and the potential effects of human settlement on nest predators and shorebird nest survival in the North (but see Bentzen et al. 2017).

The main goal of this study was to examine spatial variation in predation risk and daily nest survival of shorebirds in the vicinity of a human settlement. The specific objectives of our research were to quantify spatial variation in (1) nest predator communities, (2) predation risk using artificial nest experiments, and (3) daily nest survival rates for 7 biparental shorebird species in the vicinity of Churchill, Manitoba. We hypothesized that the composition of predator communities would be influenced by proximity to human settlements. More specifically, we predicted that nest predators would be more abundant in areas closer to human settlement due to the potentially attractive effect of anthropogenic sources of food and predator nesting/denning sites. We also hypothesized that the expected increases in predator abundance near town would have deleterious effects on daily nest survival of shorebirds via an increase in predation risk near town. More specifically, we predicted that (1) the risk of predation would increase as distance from predator nests or dens decreased and (2) daily nest survival of shorebird nests would decrease as distance to predator nests or dens decreased.

Materials and methods

Study site and system

The study was conducted near Churchill, Manitoba, which is situated on the northeastern coast of Manitoba within the sub-Arctic region, where the mouth of the Churchill River flows into western Hudson Bay (58.768410° N, 94.164963° W; Fig. 1). The Churchill area is a transition zone between tundra in the north and spruce-tamarack boreal forest in the south but has been experiencing northward encroachment of woody plants in the last several decades, presumably due to climate change (Ballantyne and Nol 2015). The area offers high-quality breeding habitat (wet; prey dense; open landscape) at the southernmost parts of many shorebird species' breeding ranges (Skeel 1983). Churchill covers an area of 53 km^2 and contains a population of approximately 900 people in about 400 dwellings (Statistics Canada 2017). A domestic airport as well as several businesses, seasonally occupied dwellings, unoccupied ex-industrial and ex-military buildings, and a waste transfer station can also be found within the town boundaries. Outside the town boundaries is a dump that seldom receives waste (i.e., once every 3–4 years) and is electrically fenced.

Predator abundance and shorebird nest data were collected within four long-term study plots located at varying

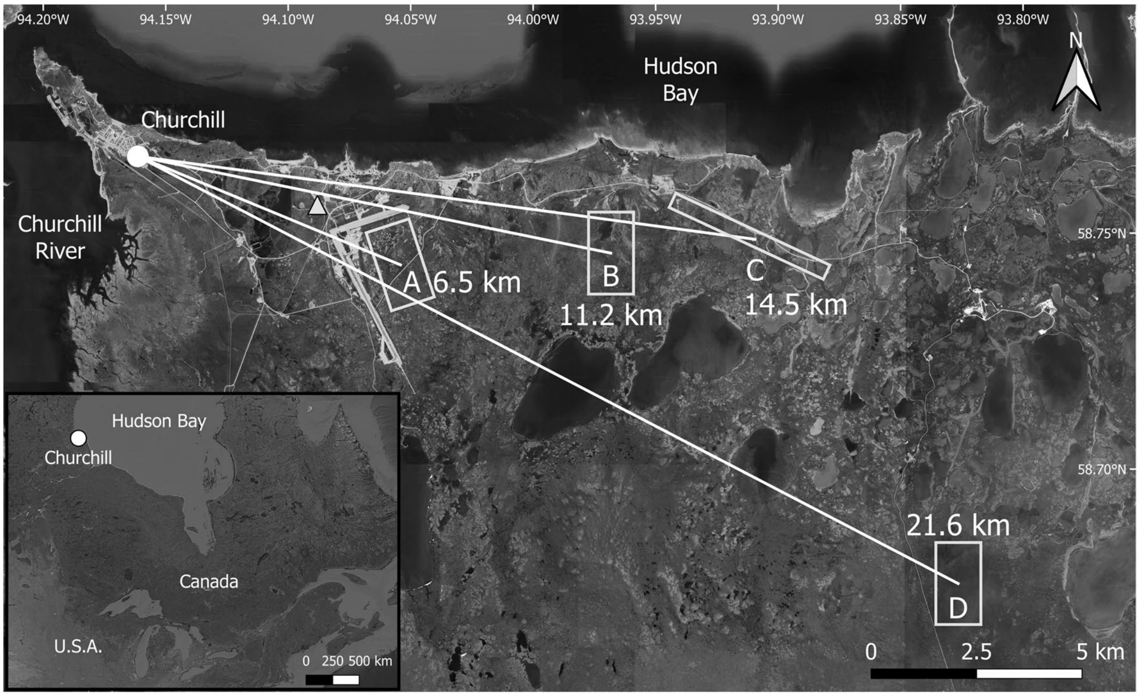

Fig. 1 Location of study plots. Data were collected in four study plots (A–D), located 6.5 to 21.6 km from the town of Churchill. The triangle symbol northwest of plot A indicates the location of the waste transfer station

distances from town (site A: 6.5 km, B: 11.2 km, C: 14.5 km, and D: 21.6 km). Distance from town was measured from plot center to the easternmost building on the edge of town (58.764576° N, -94.159241° W; Fig. 1). Plots were located 1.5–13.0 km apart (Fig. 1) and were chosen due to their high abundance of nesting shorebirds based on long-term monitoring (McKinnon et al. 2013). Three of the plots were 1.0 × 2.0 km (area 2 km^2), but due to topographical limitations, one plot was 4.0 km × 0.5 km (area 2 km^2). Shorebird nesting habitat was similar across the four plots and was characterized primarily by a combination of fen, hummock bog, and lichen heath, interspersed with small ponds. All plots were located within 1.0 km of a road. Plot A was located beside the Churchill airport, but there was no human infrastructure within the plots.

Study species

We investigated spatial variation in nest survival in a community of sub-Arctic-nesting shorebirds, including American Golden-Plover (*Pluvialis dominica*), Whimbrel (*Numenius phaeopus hudsonicus*), Hudsonian Godwit (*Limosa haemastica*), Stilt Sandpiper (*Calidris himantopus*), Dunlin (*Calidris alpina*), Least Sandpiper (*Calidris minutilla*), and Short-billed Dowitcher (*Limnodromus griseus*). All focal species in this study nest between the beginning of June and the first or second week of July, with failed breeders departing in July (Jehl 2004).

Avian predator abundance

The potential shorebird nest predator assemblage in Churchill is known to include Arctic foxes (Roth 2003), red foxes (Skeel 1983), Sandhill Cranes (*Antigone canadensis*; Reynolds 1985), Parasitic Jaegers (hereafter "jaegers," *Stercorarius parasiticus*; Byrkjedal 1989), Herring Gulls (Byrkjedal 1989; Jehl 2004), Northern Harriers (*Circus hudsonius*; Byrkjedal 1989), and Common Ravens (Ballantyne and Nol 2011). We conducted predator surveys concurrently with other field research activities. During each visit to a study plot, one person was the designated predator counter. In 2018, the survey began when the observer arrived at the plot and ended when they departed the plot, and any predator seen in or near the plot (up to approximately 2.0 km from the observer) was recorded along with the time and date of the observation. When possible, repeat observations of the same individual predator were excluded. Due to logistical constraints in 2019, surveys were more opportunistic and only predators visible within approximately 200 m of the observer were counted. Although Herring Gulls were counted in both years, they were excluded from predator abundance analyses because camera trap evidence and anecdotal observations from this study indicate that they make negligible contributions to shorebird nest predation, which is in agreement with previous studies in Churchill and elsewhere (Jehl 1971, 2007; Ballantyne and Nol 2011). Foxes were also initially counted during predator surveys but were excluded from predator abundance analysis post hoc because only one fox was observed. Our predator abundance data thus became an index of avian predator abundance limited to Parasitic Jaegers, Common Ravens, Sandhill Cranes, and raptors.

As an index of avian predator abundance for each survey, we calculated the total avian predators observed during a survey divided by the total hours during that survey. For real shorebird nests, the index of avian predator abundance was calculated by taking the average of all surveys for the plot in which the nest was located, for the year in which the nest was active (mean predators observed hour^{-1}). For artificial nests, the index of avian predator abundance was calculated as the mean number of avian predators observed hour^{-1} during the period (early or late incubation) that the nest was active, in the plot in which the nest was located, in the appropriate year.

Proximity to fox dens, jaeger nests, and town

Red and Arctic fox natal dens were located during surveys conducted in the Churchill area since 1994 and every year since 2010 (described in Roth 2003; McDonald et al. 2017). Dens were surveyed each June and were considered active if at least one burrow was cleared out *and* at least one other indication of fox activity was confirmed (fresh fox scat, fresh prey remains, urine odor, or fox tracks). Summer home range sizes for red and Arctic foxes in the study area average approximately 20 km^2 (Roth unpubl. data), so we included in our analyses only active dens within 40.0 km of town since the home ranges of foxes using these dens could potentially overlap with at least one plot. The distance (km) from each artificial and real nest to the closest active fox den was measured using the straight-line measuring tool ("Ruler") in Google Earth Pro, version 7.3.2.5776. Distances from each active fox den to the easternmost building in town (58.764576° N, -94.159241° W) were also measured to determine the overall distribution of active dens (both red and Arctic foxes combined) within 40.0 km of town.

Locations of jaeger nests were documented during daily shorebird nest searches. The distance from each artificial and real nest to the closest active jaeger nest was measured using the straight-line measuring tool ("Ruler") in Google Earth Pro, version 7.3.2.5776. One jaeger nest was located in or near each of the 4 study plots each year; however, the nest in plot C was never precisely located in 2018, and the nest in plot B was never precisely located in 2019. For these plots in those respective years, missing values were replaced using mean imputation based on distance to jaeger nest data for the other 3 plots in that year.

Distance from town was measured on a per plot rather than a per-nest basis due to (1) a significant negative correlation between distance from nearest active fox den and distance from town, as measured to individual artificial ($r = -0.49$, $p < 0.0001$) and real nests ($r = -0.56$, $p < 0.0001$) and (2) a significant negative correlation between avian predator abundance and distance from town as measured to individual artificial ($r = -0.49$, $p < 0.0001$) and real nests ($r = -0.51$, $p < 0.0001$). Therefore, the distance from town for both real and artificial nests was measured as the distance from the edge of town to the centers of each plot, as described in the study site description.

Predation risk (artificial nests)

One round of deployment and monitoring of artificial nests occurred during "early incubation" (11–25 of June 2018 and 15–26 of June 2019) and one during "late incubation" (2–15 of July 2018 and 2–13 of July 2019). At the beginning of each of these periods, we deployed 25 artificial nests in each of the four 2-km^2 plots, for a total of 100 nests in each of the two rounds of experiments. Four hundred artificial nests were thus deployed and monitored over the course of the two years. If a nest was depredated during the early incubation phase, we moved its location for the late-incubation phase by approximately 10 m. The same nest locations used in the early incubation phase of 2018 were used again in the early incubation phase of 2019.

We used the "Path," "Polygon," "Placemark," and "Ruler" functions in Google Earth Pro to plan the placement of artificial nests. All nests were placed at least 150 m apart, resulting in a density of 12.5 nests km^{-2}. To ensure nests would be located at least 150 m from one another, we placed 4 transects, spaced 500 m apart, in each plot running roughly east to west. Then, at 150-m intervals along transects, we placed artificial nests at random distances from the transect line using the RANDBETWEEN function in Excel (from 0 to 500 m). If a nest from one transect line was too close to one from another transect line, another random distance value was generated. In the long plot (4.0×0.5 km), the northern edge of the plot was used as a transect line, and nests were placed at 150-m intervals and at random distances (0–500 m) to the south of the line. Planned nest location coordinates were exported from Google Earth Pro to Garmin BaseCamp software and from there to individual handheld Global Positioning System (GPS) units (Garmin Ltd., Kansas, USA) that were used in the field for deployment and relocation of nests.

We created artificial nest cups by shallowly pressing and twisting one's boot heel into the vegetation and/or soil to make crude circular depressions, roughly 7 cm in diameter. We then pushed a nail with a small piece of fluorescent flagging tape into the center of each nest cup so that the nail head was flush with the bottom of the nest; it was then concealed by the eggs but aided us in relocating the nest when eggs were depredated. Japanese Quail (*Coturnix japonica*) eggs were used in artificial nests because they are similar to shorebird eggs in size, color, and pattern. While wearing sterile nitrile gloves, eggs were rinsed by running them under warm tap water and manually removing any visible excrement; they were then air-dried and 4 eggs were placed in each artificial nest. Each nest received two markers to facilitate relocation: either one placed at 5 m and one at 10 m in line with the nest or one each at 5 m from the nest on opposite sides. Markers consisted of popsicle sticks and natural objects found nearby (sticks, feathers), whichever was close at hand.

In 2018, we visited each artificial nest 5 times following deployment: once every 2 days, over a duration of 10 days, after which any remaining eggs and nest markers were collected. In 2019, artificial nest experiments were shortened to 8 days in duration. Constraints to airport property access unfortunately resulted in missing or delaying checks in plot A: in 2018, the 2-day check was not completed and the 10-day check was completed on the 11th day in the "early" incubation experiment; and in the "late"-incubation experiment the 4-day check could not be completed. In 2019 at plot A, both the 4-day and 6-day checks were not completed in the "early"-incubation experiment, and in the "late"-incubation experiment the 4-day check was not completed. At each visit, we recorded nest status as either (1) nest intact or (2) depredated (at least one egg missing). In conjunction with motion-sensor camera photos from some nests (see below), we determined the dates of nest predation events and identified predators. Five artificial nests were excluded from analyses because their fates could not be determined due to observer error, leaving 395 nests for analyses.

Daily nest survival (real nests)

Shorebird nests were located by 2 or 3 people, walking approximately 25 m apart through appropriate nesting habitat daily (6 to 8 h day^{-1}) to flush adult birds from their nests. Once an adult was flushed, we stopped, moved away if necessary, and watched as the bird returned to its nest. Most nest searching effort was concentrated in early to mid-June, which is the typical nest-building and early laying stage of most shorebirds in the area (Nol et al. 1997; Jehl 2007). To prevent odor contamination of nests, we did not kneel, sit, or place any equipment within 15 m of the nest; nitrile gloves were worn when touching eggs and nests; and no food was consumed in the vicinity of a nest.

When a nest was found, we recorded its location in a handheld GPS unit (Garmin Ltd., Kansas, USA) and placed two markers nearby to facilitate relocation as described above for artificial nests. If the ambient temperature was above freezing, we floated 2–4 of the eggs to determine incubation start date and expected hatch date (Liebezeit et al. 2007). Eggs were placed in a plastic container with pre-drawn compass angles and a millimeter scale and filled with tepid (~21 °C) water. Eggs were then placed back into the nest in their original configuration. We only floated 2 eggs per nest unless the angles at which they floated varied greatly, upon which a third and possibly a fourth egg were floated. Nests were revisited at 4-day intervals and the following data were recorded: date and time; number of eggs in the nest; and clutch status (warm, cold, cracking, pipped, depredated, hatched). When the expected hatch date of a nest was near and/or if eggs were found cracked or pipped, we visited nests more frequently (every 1–2 days) to determine the exact date of hatch. In the event of a nest check where eggs were missing, any signs of nest fate were recorded including presence of chicks, parent behavior, eggshell pieces or fragments, fox urine smell, or dislodged nest material. If the exact date of predation or hatch was unknown, it was assumed to occur mid-way between the two nest checks. Nests were considered successful if at least one egg hatched.

Five out of 9 Dunlin nests in 2018 (none in 2019) were monitored with temperature loggers as part of another study (Meyer et al. 2020a) and resulting nest temperature data were used to confirm dates and times of predation events or hatching for this study.

Nest predator identification

We installed motion-sensor cameras (Reconyx PC900 and Reconyx Hyperfire 2: Holmen, Wisconsin, USA; Moultrie A-25i: Calera, Alabama, USA) at 47 of 200 (24%) artificial nests and 16 of 50 (32%) real shorebird nests in 2018 and at 18 of 200 (9%) artificial nests and 11 of 38 (29%) real shorebird nests in 2019, to identify nest predators. At shorebird nests, all attempts were made to place cameras at every second nest of each species as soon as they were found, and once deployed, the camera remained at the nest until the chicks hatched or the nest failed. At this time, some of the cameras taken from hatched or failed nests were redeployed at active artificial or real nests. Cameras were camouflaged with vegetation and placed 5 m away from the nests on small tripods lying on the ground or, if no dry ground was available, standing ~0.5 m tall. Cameras took a rapid series of 3 (Moultrie cameras) or 5 (Reconyx cameras) photographs each time the built-in Passive InfraRed (PIR) motion sensor was triggered by movement within its field of view. Eggs in real and artificial nests were not conspicuous enough to be seen in camera photos taken at 5 m away, so the installer triggered the camera to take a calibration photo of them pointing to the nest. We checked cameras every 4 days (coordinated with regularly scheduled nest checks described above) and replaced batteries and SD cards during these visits if necessary.

Photographed predator visits were categorized as confirmed predation events, uncertain, or non-predation events.

If a predator was photographed with eggs in its mouth or without eggs in its mouth but with its head in the nest and the nest was then found to be depredated, it was considered a predation event. If a predator was photographed within the vicinity of the nest but without its head in the nest or eggs in its mouth and the nest was then found to be depredated, it was considered a possible but unconfirmed predation event. If a predator was photographed in any position and the nest was then found to be intact or if the predator was only visible at a fair distance from the nest, it was considered a non-predation event.

Statistical analyses

Avian predator abundance

Analyses of avian predator abundance data were conducted for 2018 and 2019 separately, since survey methodologies differed slightly between years. To determine if mean avian predator abundance significantly differed among plots, we conducted a Kruskal–Wallis test in program R 3.5.3 because data were not normally distributed. Proportions of predator species seen in each plot were tested for significant differences using a χ^2 test.

Fox den activity and distance from town

To test whether the number of active fox dens decreased with increased distance from town, we conducted a Spearman's Rank Correlation separately for each year. Bin sizes were set at 5 km, with a total of 8 bins (0–40 km).

Predation risk (artificial nests)

We tested for the effects of nest predators (avian predator abundance, distance from nearest active fox den, distance from nearest jaeger nest), distance from town, and camera presence on predation risk using Cox Proportional Hazards models (Cox 1972) with the *survival* (v.2.44-1.1, Therneau 2015) and *survminer* (v.0.4.6, Kassambara et al. 2019) packages in program R 1.2.1335. Data were stratified by year and by incubation phase ("early" or "late") using the *strata()* function. Assumptions of proportionality of survival and hazards were tested graphically (Hess 1995).

Daily nest survival (real nests)

We tested for correlation among all independent variables (species, camera presence, distance from town, avian predator abundance, distance from nearest jaeger nest, and distance from nearest fox den) using a Pearson correlation test in program R and found no significant correlations. We tested our hypotheses regarding the effects of the above covariates on daily nest survival of shorebirds by constructing 15 a priori nest survival models, including a null model, from combinations of the 5 predictor variables (Table 1). We built competing models and conducted model selection using the Nest Survival function in *RMark* (v.2.2.5, Laake 2019). Due to the differences in methodology between years and the potentially confounding effects of species, all models were stratified (grouped) by year and species. Due to the small sample size of nests, covariate interactions were not tested.

The nesting season specific to this study began the earliest date that the first nest was found in both years combined (June 8) and ended the latest date that any nest was checked in both years combined (July 14) and was thus composed of 37 exposure days. Nests were considered successful if at least one egg hatched. We used second-order Akaike's Information Criterion corrected for small sample sizes (AIC_c) to identify the top model. The best-fitting model to describe variation in nest survival was that which had the lowest AIC_c value, but all models within 2 ΔAIC_c from the top

Table 1 Shorebird nest survival hypotheses and models tested

#	Hypothesis	Model
1	Null	Intercept only
2–4	Individual predators	Intercept + Fox distance OR Jaeger distance OR Avian predator abundance
5–7	Individual predators and cameras	Intercept + Camera + Fox distance OR Jaeger distance OR Avian predator abundance
8	All predators	Intercept + Fox distance + Jaeger distance + Avian predator abundance
9	All predators and cameras	Intercept + Camera + Fox distance + Jaeger distance + Avian predator abundance
10	Town	Intercept + Town distance
11–13	Individual predators and town	Intercept + Town distance + Fox distance OR Jaeger distance OR Avian predator abundance
14	All predators and town	Intercept + Town distance + Fox distance + Jaeger distance + Avian predator abundance
15	All predators and town and cameras	Intercept + Camera + Town distance + Fox distance + Jaeger distance + Avian predator abundance

All models were stratified (grouped) by year and by species to account for interannual variation in daily nest survival due to unmeasured components (weather, food availability, alternative prey) and variation in nesting behavior between species model were considered competitive (Burnham and Anderson 2004).

Results

Avian predator abundance

A total of 169 h of survey time yielded 287 observations of avian predators (Parasitic Jaegers, Common Ravens, Sandhill Cranes, and raptors) across the 4 plots in 2018 (average survey duration 2.73 h; minimum 25 h of surveying in each plot) and 165 avian predators were observed during 58 h of observations in 2019 (average survey duration 1.32 h; minimum 13 h of surveying in each plot; Table 2). Common Ravens were most common (39% and 50% of predators observed in 2018 and 2019, respectively), followed by jaegers (30% and 29%) and Sandhill Cranes (24% and 17%). Individuals of 6 other species made up the remaining (7% and 4%) observations (Table 2).

Proportions of avian predator species observed varied among plots in both years (2018: Pearson Chi-square test: $\chi_9 = 57.167$, $p < 0.0001$. 2019: $\chi_9 = 23.432$, $p = 0.0053$, Fig. 2); however, there were no significant differences in mean total avian predator abundance (all species combined) among plots in either year (2018: Kruskal–Wallis test: $H_3 = 6.8155$, $p = 0.0780$; 2019: $H_3 = 6.6948$, $p = 0.0823$). In general, Common Ravens were consistently least abundant far from town (plot D) and more abundant in the other 3 plots, whereas in both years Sandhill Cranes were most common in plots B and D. Jaegers appeared to be relatively uniformly distributed among each of the 4 plots in both years.

Proximity to fox dens, jaeger nests, and town

In 2018, 5 active Arctic fox dens, 9 active red fox dens and 1 active fox den of undetermined species were found within 40.0 km of town. In 2019, 7 active Arctic fox dens, 8 active red fox dens and 2 active fox dens of undetermined species were found within 40.0 km of town. There was no significant difference in average (± SE) distance from town between active Arctic (26.5 ± 6.2 km, $n = 12$) and red fox dens (24.5 ± 10.0 km, $n = 17$; $t_{27} = -0.59$, $p = 0.5574$); therefore, both species were combined for further analyses. The number of active fox dens increased significantly with distance from town in 2018 (Spearman's Rank Correlation: $r_s = 0.85$, $n = 15$, $p = 0.0082$), but not in 2019 ($r_s = 0.47$, $n = 17$, $p = 0.2440$).

The average distance from a real shorebird nest to the nearest active fox den was 3.32 ± 0.28 km ($n = 40$) in 2018 and 2.81 ± 0.20 km ($n = 34$) in 2019. For artificial nests, the average distance from the nearest active fox den was

Table 2 Avian predator counts and average abundances

Species	Plot (distance from Churchill)								Total	
	A (6.5 km)		B (11.2 km)		C (14.5 km)		D (21.6 km)			
	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019
Common Raven[a]	27	32	37	25	37	18	11	8	112	83
Parasitic Jaeger[b]	28	15	28	8	4	13	26	12	86	48
Sandhill Crane[c]	6	9	26	10	9	3	29	6	70	28
Other[d]	4	0	4	1	3	5	8	0	19	6
Total Predators	65	56	95	44	53	39	74	26	287	165
Total Hours	35.02	16.33	48.47	13.67	25.80	15.00	60.13	13.30	169.42	58.30
Mean Pred Hr^{-1}[e]	1.97	3.63	1.87	3.06	2.10	3.00	1.24	2.07	1.74	2.94
SD	0.77	1.26	1.06	1.90	1.73	1.65	0.62	1.33	1.11	1.60

Presented are counts of avian predators observed in each of 4 plots with their associated distances from town, the total hours spent in each plot observing predators, and the calculated mean avian predators observed hour^{-1} in each plot for each year. Note: because some individuals of locally breeding species were likely observed (and counted) many times over the entire season, count totals do not accurately reflect real population sizes

[a] *Corvus corax*

[b] *Stercorarius parasiticus*

[c] *Antigone canadensis*

[d] "Other" predators include Bald Eagle *Haliaeetus leucocephalus* (5 in 2018; 3 in 2019), Merlin *Falco columbarius* (1 in 2018), Northern Harrier *Circus hudsonius* (5 in 2018; 3 in 2019), Peregrine Falcon *Falco peregrinus* (5 in 2018), Rough-legged Hawk *Buteo lagopus* (2 in 2018), and Snowy Owl *Bubo scandiacus* (1 in 2018)

[e] Rather than calculating Mean Pred Hr^{-1} as Total Predators ÷ Total Hours, it is calculated as the Mean Pred Hr^{-1} of all surveys for each plot in each year

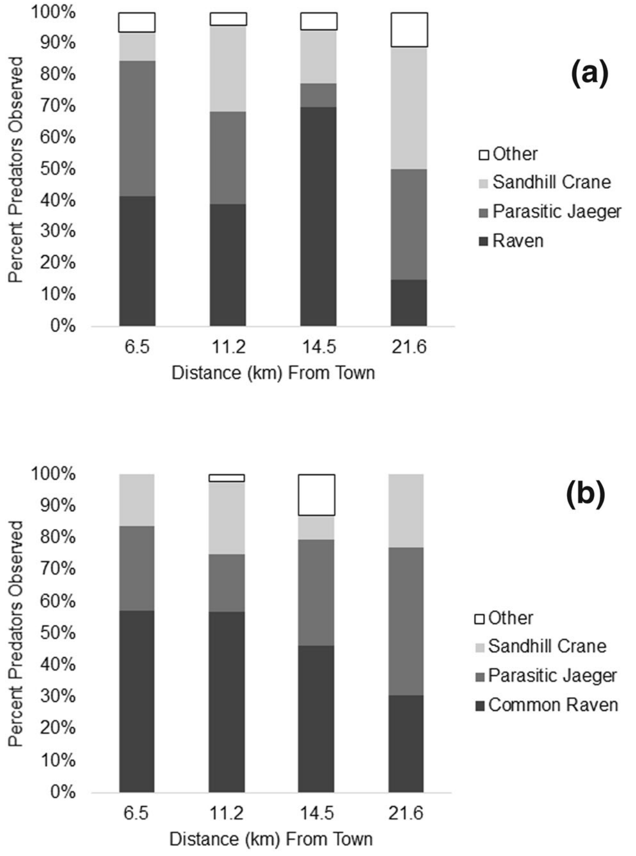

Fig. 2 Proportions of avian predators in study plots. Avian predator species were observed in significantly different proportions in each of the four study plots A (6.5 km from town), B (11.2 km from town), C (14.5 km from town), and D (21.6 km from town) in 2018 (**a**) and 2019 (**b**)

2.86 ± 0.13 km ($n = 197$) in 2018 and 2.87 ± 0.13 km ($n = 198$) in 2019. The average distance from a real shorebird nest to the nearest jaeger nest was 0.67 ± 0.08 km ($n = 40$) in 2018 and 0.70 ± 0.09 km ($n = 34$) in 2019. For artificial nests, the average distance from the nearest jaeger nest was 0.70 ± 0.02 km ($n = 197$) in 2018 and 1.17 ± 0.06 km ($n = 198$) in 2019.

Predation risk (artificial nests)

Predation risk on artificial nests increased by 7% km^{-1} as distance from town increased (Cox proportional hazards model: $z = 3.79$, $p = 0.0002$, Fig. 3). Predation risk decreased 13% km^{-1} as distance from the nearest fox den increased ($z = -3.79$, $p = 0.0002$, Fig. 4) and by 30% km^{-1} as distance from the nearest jaeger nest increased ($z = -3.84$, $p = 0.0001$, Fig. 5). Camera presence resulted in a decrease in predation risk of 38% ($z = -2.90$, $p = 0.0038$, Fig. 6). The abundance of avian predators did not affect predation risk ($z = 1.91$, $p = 0.0565$).

Daily nest survival (real nests)

In 2018, 50 shorebird nests of 7 species were found in the 4 study plots. In 2019, 38 nests of 5 species were found. Ten nests in 2018 and 4 nests in 2019 had unknown fates and were removed from analyses. Thus, 74 nests of 7 species were used in analysis of nest survival (Table 3).

The model that best described observed variation in daily nest survival included only distance from the nearest jaeger nest (Table 4). Daily nest survival was higher as distance from nearest jaeger nest increased ($\beta = 0.927$, SE $= \pm 0.450$, Fig. 7). The next most competitive model included distance from the nearest jaeger nest and camera presence ($\Delta \text{AIC}_c = 1.241$, Table 4), where survival increased with a camera present ($\beta = 0.319$, SE $= \pm 0.369$). A model including distance from nearest jaeger nest (to each shorebird nest) and distance from town (to the center of each plot) was also competitive, where nest survival decreased with increasing distance from town ($\Delta \text{AIC}_c = 1.832$, $\beta = -0.011$, SE $= \pm 0.369$, Table 4).

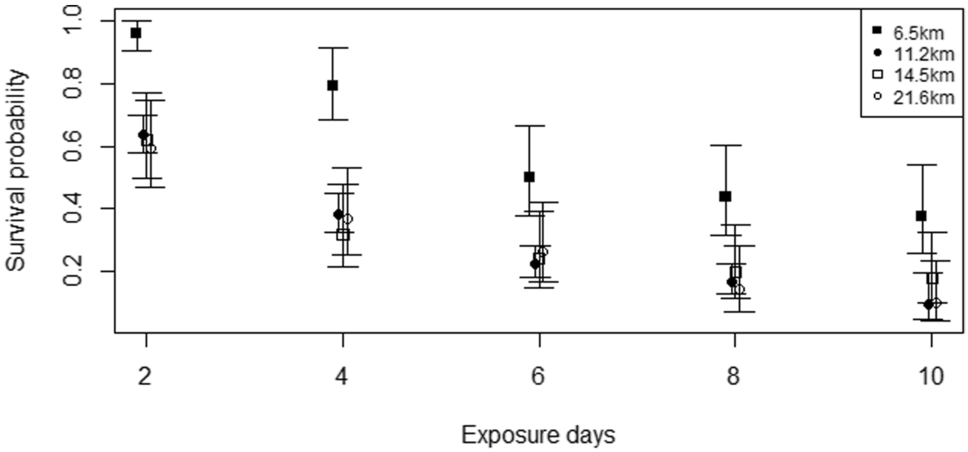

Fig. 3 Artificial nest survival with distance from town. Survival estimates of artificial nests in each of the four study plots A (6.5 km from town), B (11.2 km from town), C (14.5 km from town), and D (21.6 km from town). Data are from both "early" and "late" phases of incubation and for both 2018 and 2019 ($n = 395$ nests, approximately 100 nests per plot in total)

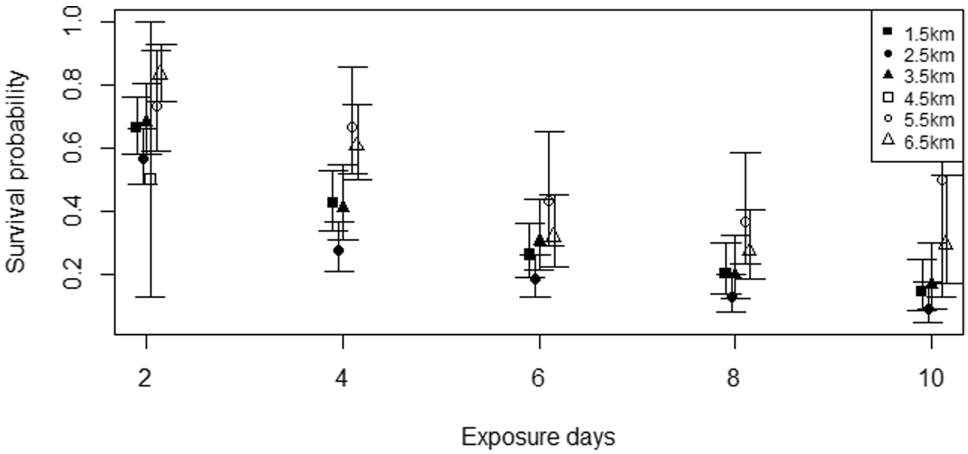

Fig. 4 Artificial nest survival with distance from fox dens. Survival estimates of artificial nests at various distances from the nearest active fox den (*Vulpes lagopus* and *V. vulpes* combined), monitored over a 10-day period. Data are from both "early" and "late" phases of incubation and for both 2018 and 2019 ($n = 395$ nests). Each point represents a group of nests that are located *n-1* to *n* km from the nearest active fox den

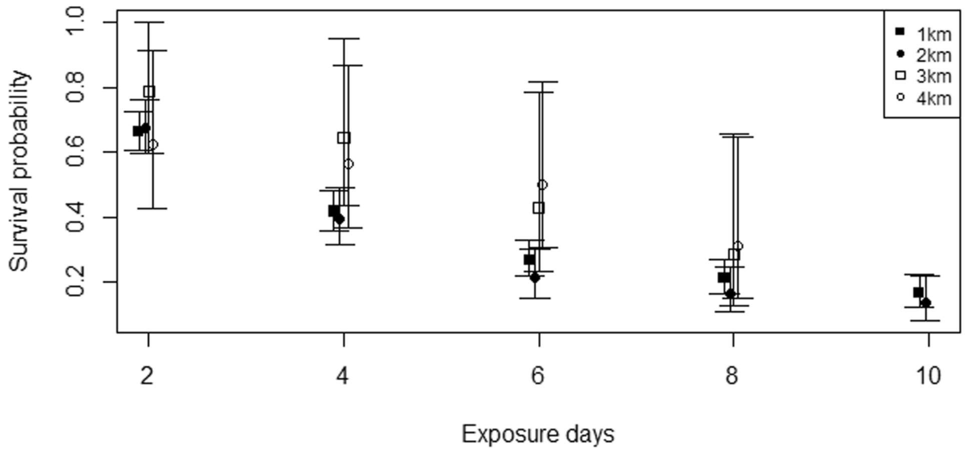

Fig. 5 Artificial nest survival with distance from jaeger nests. Survival estimates of artificial nests at various distances from the nearest Parasitic Jaeger (*Stercorarius parasiticus*) nest, monitored over a 10-day period. Data are from both "early" and "late" phases of incubation and for both 2018 and 2019 ($n = 395$ nests). Each point represents a group of nests that are located *n-1* to *n* km from the nearest jaeger nest

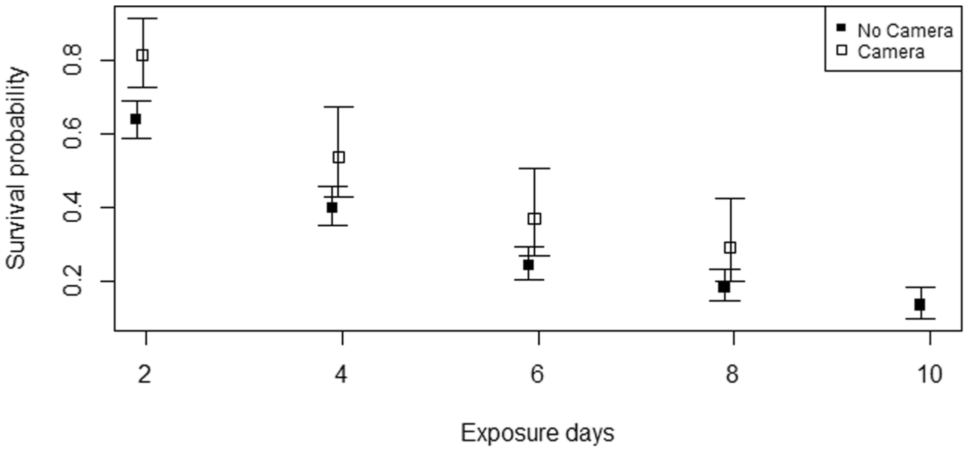

Fig. 6 Artificial nest survival with and without cameras. Survival estimates of artificial nests with and without cameras present, monitored over a 10-day period. Data are from both 'early' and 'late' phases of incubation and for both 2018 and 2019 ($n = 395$ nests)

Nest predator identification

Of 41 confirmed predation events recorded at artificial nests by camera traps in both years, 24 (59%) were by jaegers, 7 (17%) by Arctic foxes, 4 (10%) by Common Ravens, 3 (7%) by Herring Gulls, 2 (5%) by red foxes, and 1 (2%) by a Northern Harrier (Table 5). There was no clear pattern of confirmed artificial nest predators in relation to distance from town for avian or mammalian predators (Table 5). Jaegers were photographed predating artificial nests in all but one plot (C), whereas Common Ravens were photographed predating nests in plots C and D. Herring Gulls, like red foxes, were detected as artificial nest predators in the two plots closest to town (A, B), while

Table 3 Shorebird nests by plot and year

Species	Plot (distance from Churchill)								Total	
	A (6.5 km)		B (11.2 km)		C (14.5 km)		D (21.5 km)			
	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019
American Golden-Plover[a]	2	1	1	1	2	0	0	1	5	3
Whimbrel[b]	3	3	7	6	0	0	6	11	16	20
Hudsonian Godwit[c]	1	0	2	0	0	0	0	4	3	4
Stilt Sandpiper[d]	0	0	0	0	0	0	1	0	1	0
Dunlin[e]	1	0	1	0	1	1	4	4	7	5
Least Sandpiper[f]	2	0	0	0	0	0	1	0	3	0
Short-billed Dowitcher[g]	1	0	1	1	0	0	3	1	5	2
Total	10	4	12	8	3	1	15	21	40	34

Presented are the numbers of nests of each shorebird species in each of 4 study plots used in nest survival analyses from 2018 and 2019. Counts are arranged by species and plot, with each plot's distance from the town of Churchill given in brackets ($n = 74$ nests)

[a] *Pluvialis dominica*

[b] *Numenius phaeopus*

[c] *Limosa haemastica*

[d] *Calidris himantopus*

[e] *Calidris alpina*

[f] *Calidris minutilla*

[g] *Limnodromus griseus*

Table 4 Model selection results

	Hypothesis	df	AICc	ΔAICc
1	Intercept only	1	207.15	3.32
2	Intercept + Fox distance	2	208.51	4.68
3	Intercept + Jaeger distance	2	203.83	0
4	Intercept + Avian pred. abund	2	207.42	3.58
5	Intercept + Camera + Fox distance	3	208.64	4.81
6	Intercept + Camera + Jaeger distance	3	205.07	1.24
7	Intercept + Camera + Avian pred. abund	3	207.08	3.25
8	Intercept + Fox distance + Jaeger distance + Avian pred. abund	4	206.48	2.65
9	Intercept + Camera + Fox distance + Jaeger distance + Avian pred. abund	5	207.03	3.2
10	Intercept + Town distance	2	208.88	5.04
11	Intercept + Town distance + Fox distance	3	210.52	6.68
12	Intercept + Town distance + Jaeger distance	3	205.67	1.83
13	Intercept + Town distance + Avian pred. abund	3	209.44	5.10
14	Intercept + Town distance + Fox distance + Jaeger distance + Avian pred. abund	5	208.50	4.66
15	Intercept + Camera + Town distance + Fox distance + Jaeger distance + Avian pred. abund	6	208.92	5.09

Competitive models (those with $\Delta AIC_c < 2$) included "Intercept + Jaeger distance," "Intercept + Camera + Jaeger distance," and "Intercept + Town distance + Jaeger distance". All models were stratified (grouped) by year and species to account for interannual variation in daily nest survival due to unmeasured components (weather, food availability, alternative prey) and variation in nesting behaviour between species

Arctic foxes were only photographed taking artificial nests in plot C (Table 5).

All 11 of the photographed and confirmed predation events at real shorebird nests occurred in 2018. Four (36%) were by Arctic foxes, 3 (27%) by red foxes, 3 (27%) by jaegers, and 1 (9%) by a Northern Harrier (Table 6). Jaegers were photographed predating real shorebird nests only in the plot farthest from town (D), red foxes only in the two plots closest to town (A, B), and Arctic foxes only in plots B and D (Table 6). Of the 11 shorebird nests outfitted with cameras in 2019, 8 were successful, 1 was still intact at the end of the field season, and for 2 the fate could

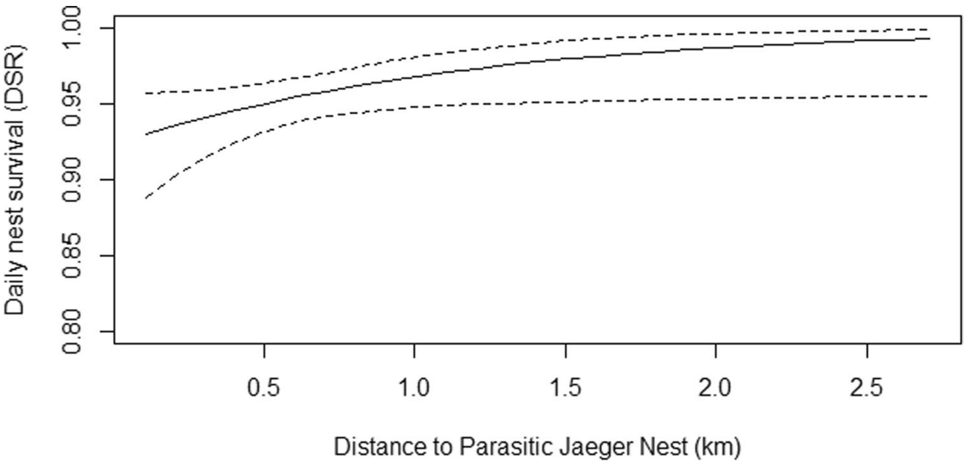

Fig. 7 Shorebird nest survival with distance from jaeger nests. Daily survival rate (DSR) of shorebird nests (all species combined) near Churchill tends to increase as distance from the nearest Parasitic Jaeger (*Stercorarius parasiticus*) nest increases. Solid line is estimated DSR with dashed lines representing 95% confidence intervals

Table 5 Confirmed artificial nest predators

Predator	Plot (distance from Churchill)								Total	
	A (6.5 km)		B (11.2 km)		C (14.5 km)		D (21.6 km)			
	2018	2019	2018	2019	2018	2019	2018	2019	2018	2019
Parasitic Jaeger[a]	0	1	8	2	0	0	11	2	19	5
Arctic fox[b]	0	0	0	0	7	0	0	0	7	0
Common Raven[c]	0	0	0	1	1	2	0	0	1	3
Herring Gull[d]	2	0	1	0	0	0	0	0	3	0
Red fox[e]	1	0	1	0	0	0	0	0	2	0
Northern Harrier[f]	0	0	0	0	1	0	0	0	1	0

Presented are counts of artificial nest predators in each of 4 study plots with their associated distances from the town of Churchill, as confirmed by camera traps, in each year

[a] *Stercorarius parasiticus*

[b] *Vulpes lagopus*

[c] *Corvus corax*

[d] *Larus argentatus smithsonianus*

[e] *Vulpes vulpes*

[f] *Circus hudsonius*

Table 6 Confirmed real shorebird nest predators

Predator	Plot (distance from Churchill)				Total
	A (6.5 km)	B (11.2 km)	C (14.5 km)	D (21.6 km)	
Arctic Fox[a]	0	2	0	2	4
Parasitic Jaeger[b]	0	0	0	3	3
Red Fox[c]	1	2	0	0	3
Northern Harrier[d]	0	1	0	0	1

Presented are counts of shorebird nest predators in each of 4 study plots with their associated distances from the town of Churchill, as confirmed by camera traps. All occurred in 2018

[a] *Vulpes lagopus*

[b] *Stercorarius parasiticus*

[c] *Vulpes vulpes*

[d] *Circus hudsonius*

not be determined with confidence and no predators were photographed.

Discussion

Human presence can influence the activity and/or density of nest predators and thus indirectly affect prey species (Liebezeit et al. 2009). In our study, we hypothesized that the composition of predator communities would be influenced by proximity to the town of Churchill, Manitoba. Our prediction that nest predators would be more abundant in areas closer to town was not supported by our data. Indeed, despite differences in avian predator abundance among plots, there was no clear pattern of change in avian predator communities in proximity to town based on both avian predator surveys and confirmation of nest predators using cameras at artificial and real nests. For the two confirmed mammalian predators, the red and Arctic fox, our results were opposite to those predicted as the number of active fox dens decreased in proximity to town and foxes were photographed predating nests in all plots.

Our prediction that the risk of predation would increase with decreasing distance from predator nests and dens was supported by the data. Predation risk was higher near active fox dens and jaeger nests. However, contrary to our predictions, predation risk was lower closer to town. Finally, our prediction that daily nest survival of shorebird nests would decrease in close proximity to predator nests and dens was only partially supported. Daily nest survival did decrease in proximity to jaeger nests, but we found no support for a relationship with distance from fox dens. We found some support for higher daily nest survival closer to town (competing model), but this effect appears to be driven by the high daily nest survival in the plot closest to town (plot A). Overall, results from our study indicate that proximity to human settlement may affect shorebird—nest–predator relationships for mammalian predators, but not necessarily for avian predators; shorebird nests experience lower risk and higher survival near settlement where there are also fewer fox dens, at least in the sub-Arctic trophic system near Churchill, Manitoba.

Predator abundance

Common Ravens, jaegers, and Sandhill Cranes were the most abundant potential avian nest predators across all study plots, which concurs with previous studies conducted in Churchill (Skeel 1983; Byrkjedal 1989; Ballantyne and Nol 2011) and other sub-Arctic sites (Smith et al. 2007a). Avian predator abundance was expected to be higher closer to town because of the potential attractive effect of anthropogenic food sources, such as pets, garbage, roadkill, and hunting- or fishing-related offal, as well as artificial nesting sites (NRC 2003; Liebezeit et al. 2009; Selås et al. 2010; Julien et al. 2014). In our study, the variation in average number of avian predators observed in the 4 plots exhibited a tendency toward higher abundances near town in both years, but the relationship was non-significant. In 2019, Common Ravens formed a larger proportion of the predator community closer to town and appeared to account for some of the apparent increase in avian predator abundance there. These results are coherent with previous observations of ravens nesting on towers and large industrial buildings, which are more plentiful near town. Jaegers, on the other hand, were sighted in relatively even proportions across the 4 plots, and only 1 jaeger nest was found within each plot each year. This relatively uniform distribution is supported by anecdotal observations that suggest Parasitic Jaegers do not use human-subsidized food or nesting sites in the Churchill area.

On Alaska's North Slope, human infrastructure related to oil, gas, and other activities has attracted predators such as bears, foxes, ravens and gulls in higher densities due to the availability of supplemental food and artificial denning/nesting sites associated with buildings (NRC 2003; Weiser and Powell 2010, 2011), which has generally caused decreases in nest success of local breeding birds, sometimes to the point of mortality being higher than recruitment (NRC 2003). Churchill offers artificial nesting sites for Common Ravens as well as supplemental food for all scavenger species in the form of garbage at the unfenced and completely wildlife-accessible waste transfer station just north of the airport (Fig. 1). This is in addition to the scavenging of curbside waste by ravens and availability of hunted animal carcasses discarded near town (even though they are supposed to be disposed of at the transfer station). Thus, we had expected the same attracting effect of human infrastructure and anthropogenic food sources to occur with avian predators in the vicinity of Churchill, but our avian predator survey results and confirmed predator data from camera monitoring do not provide strong evidence for this effect. One potential caveat in the characterization of avian predator communities in our study is the limited number of study plots ($n = 4$); therefore, the lack of pattern detected must be interpreted with caution.

The frequency of active fox dens increased with distance from town, but this trend was only significant in one of 2 years. This relationship is also opposite what we expected based on the potential availability of food subsidies near town (NRC 2003). Indeed, foxes have been observed scavenging in the Churchill waste transfer station near plot A; anecdotal observations suggest plenty of hunting-related offal is discarded near town; and some residents in town intentionally feed foxes. Red foxes are also willing to den and hunt near human settlement (Selås et al. 2010; Stickney et al. 2014), especially in open landscapes (Alexandre et al. 2020), and Arctic foxes can habituate to humans (Larm et al. 2020). However, in Churchill specifically, there may be fewer fox dens and less fox activity near town due to hunting and trapping of foxes in winter and/or avoidance by foxes of loud aircraft traffic and air cannons at the local airport (next to plot A). Arctic fox den use in Norway was not correlated with distance to human infrastructure (Frafjord 2003) but at one site, den use and reproductive success were higher with fewer cabins and roads nearby (Selås et al. 2010), indicating a potential benefit to foxes of denning farther from human infrastructure. In Alaska, Arctic foxes can commonly be found denning and hunting in highly anthropogenically disturbed areas if fox harvesting is absent (NRC 2003). Therefore, we suspect that hunting and aircraft activity in the immediate vicinity of Churchill may be the primary drivers of reduced fox denning there.

With no clear trend in avian predator abundance in relation to town and evidence of reduced fox denning activity in proximity to town, our data indicate that overall predator abundance is not higher near town. It is uncertain exactly which human–predator interactions are most influential to predator distributions near Churchill; therefore, study of the variation in predator abundance and its drivers here as well as in proximity to other northern settlements should be pursued further.

Predation risk (artificial nests)

Predation risk, as measured by artificial nests, increased by 7% km^{-1} as distance from town increased, which is opposite to our prediction of higher predation risk near town. The results appear to be driven primarily by the reduced predation risk in plot A, which is closest to town. Given that active fox dens increased in frequency with distance from town (significant only in 2018), lower predation by foxes in plot A could explain this unexpected result. However, these results should be interpreted with caution given our limited number of study plots ($n=4$) at varying distances from town. That a significant trend in predation risk with relation to distance from human infrastructure was found near Churchill is surprising, given the lack of such a relationship found near infrastructure in Prudhoe Bay, Alaska (Bentzen et al. 2017). This may be because the predator assemblages and distributions there are presumably different from Churchill; for example, in addition to Parasitic Jaegers, Prudhoe Bay also hosts Long-tailed (*Stercorarius longicaudus*) and Pomarine (*Stercorarius pomarinus*) jaegers (Bentzen et al. 2017); and foxes there are generally more abundant near infrastructure (Liebezeit et al. 2009).

Predation risk was reduced by 13% for each additional kilometer away from an active fox den (red and Arctic foxes combined). Similarly, in the high Arctic, predation risk increased as fox density increased (McKinnon et al. 2014). Both Arctic and red foxes are thought to hunt primarily using olfactory cues (Smith et al. 2012), but as opportunistic omnivores they use any cues available to find prey such as small mammals, birds, birds' eggs, insects, and carrion (Chesemore 1968; Bahr 1989; Elmhagen et al. 2000) and may simply stumble upon prey incidentally (McKinnon et al. 2014). It is perhaps not surprising that the rate of change of nest predation risk with distance from the nearest active fox den (− 13% km^{-1}) is smaller in magnitude than that for the nearest Parasitic Jaeger nest (− 30% km^{-1}), considering the home range size of foxes in this area averages 20 km^2 (Roth unpubl. data), while jaegers may restrict their hunting to core areas around the nest as small as 1 km^2 (Andersson and Götmark 1980). Our observations support this: during our time spent surveying avian predators, the jaeger pair breeding in each plot was almost always present within the plot (area of 2 km^2). In addition, artificial nests were located closer on average to jaeger nests (0.7 km in 2018, 1.2 km in 2019) than they were to fox dens (approximately 2.9 km in both years). Thus, it is possible that a simple explanation for the sharper decrease in predation risk over distance relative to jaeger nests compared to fox dens is borne out of a difference in home range size, whereby jaegers concentrate their search for prey into a smaller area around their nests than do foxes around their dens.

Jaegers are opportunistic carnivores that prey on lemmings (*Lemmus* and *Dicrostonyx* spp.), birds, and birds' eggs; the latter two items sometimes constitute the largest proportion of their diet (MacInnes 1962; Bêty et al. 2002; Wiley and Lee 2020). Jaegers are visually oriented avian predators that often cruise low to the ground (1–3 m) in search of prey and can learn to preferentially search areas where encountering nests is more likely (Wiley and Lee 2020). At a high-Arctic site, Long-tailed and Parasitic Jaegers were responsible for the majority of artificial shorebird nest losses (Bêty et al. 2002; McKinnon and Bêty 2009). Although artificial nests are small and well camouflaged, the absence of an incubating parent means they are likely a relatively easy target for such a low-flying avian predator (Meyer et al. 2020b), which may also help explain the steep decrease in predation risk of 30% with each additional kilometer away from a jaeger nest observed in our study.

Camera presence resulted in a decrease of predation risk in our study, which agrees with results from some camera studies involving real and artificial nests (Herranz et al. 2002; Bentzen et al. 2017) but is contrary to the neutral results of others (Liebezeit and Zack 2008; MacDonald and Bolton 2008; McKinnon and Bêty 2009; Richardson et al. 2009). When cameras are conspicuous, their presence may increase predation risk if predators can make associations between the presence of a camera and an active nest (Cantar and Montgomerie 1985). The same conspicuous camera could decrease predation risk via predator avoidance (i.e., neophobia; Richardson et al. 2009). Alternatively, that we sometimes removed cameras from failed nests and redeployed them at active nests relatively later in the experiment may have biased results toward reduced predation risk with a camera present (discussed in Richardson et al. 2009; Bentzen et al. 2017), although we doubt that such a bias could account for the large (38%) effect of camera presence that we observed. As such, although our cameras were camouflaged as best as possible in the field, given the terrain and lack of woody vegetation it appears as though they acted as deterrents to potential predators. Although cameras can be useful tools in helping to identify predators at artificial and real nests, responses to human objects by predators likely vary by species and location according to the adaptation of those species to geographic variation in human factors (e.g., fur trapping; garbage as food subsidies). This is reflected in the range of effects from positive to neutral to negative that is introduced into nest survival studies when using cameras (discussed above) and suggests that interpretation of camera-related nest survival data should be conducted through a lens of local human–predator interactions at each study site independently.

Daily nest survival (real nests)

Based on the top model, daily survival rate of shorebird nests increased with increasing distance from the nearest jaeger nest. These results concur with only one sub-Arctic study demonstrating the importance of jaegers in models explaining variation in shorebird nest survival (Flemming et al. 2019). Indeed, very few Arctic studies on shorebird nest survival have identified jaegers as important real nest predators (McKinnon and Bêty 2009) and/or important predictors of nest survival (McKinnon et al. 2014). This lack of literature documenting the effects of jaegers could be due to site-specific differences, since Churchill is one of the lowest sub-Arctic sites used to study shorebirds. It could otherwise be explained by the lack of camera evidence supporting jaegers as important nest predators. In our study, we were somewhat surprised that nest survival was best explained by distance to jaeger nests, given that jaegers were confirmed predators at only 3 of 11 shorebird nests. The discrepancy between daily nest survival results and camera results could, however, be easily explained if jaegers display neophobia and/or avoidance behaviors toward the nest cameras as described above (Richardson et al. 2009). Although, a larger sample size of photographed predation events might be necessary to draw any reliable conclusions about the true proportion of nests depredated by jaegers.

Arctic and red foxes were responsible for 4 and 3 of 11 (64%) photographed predation events, respectively, at real shorebird nests but distance from the nearest active fox den was not identified as an important variable explaining daily nest survival. Arctic foxes have often been considered unimportant predators of shorebird nests in Churchill (Byrkjedal 1989) or ignored as potential nest predators there altogether (Jehl 1973; Skeel 1983; Ballantyne and Nol 2011, 2015), even though Arctic foxes have been observed depredating shorebird eggs near Churchill in years of both high and low lemming abundance (Bahr 1989) and they are dominant shorebird nest predators elsewhere (Liebezeit and Zack 2008). Indeed, a review of shorebird nest camera monitoring studies in mostly temperate Europe revealed that roughly 61% of nest predation events were by foxes (MacDonald and Bolton 2008). Interestingly, some of those same studies showing high fox predation on camera, tested for and found no effect on shorebird nest survival of proximity to fox dens (MacDonald and Bolton 2008), which is similar to the results of our study. Effects of fox density and proximity to fox dens on shorebird nest survival have been documented in several studies in the low and high Arctic (Smith et al. 2007b; Liebezeit and Zack 2008; McKinnon and Bêty 2009; McKinnon et al. 2014). Our camera trap results confirm the importance of shorebird nest predation by foxes near Churchill, but it is unclear why our nest survival models incorporating distance from nearest active fox den do not reflect this importance. The discrepancy between nest survival results and camera results for foxes cannot be explained by the potential for foxes to make an association between the presence of a camera and that of an active nest, because one of the competitive models indicated that the presence of cameras increased, rather than decreased, survival. The discrepancy could be explained if foxes were actually distracted enough by the cameras to miss the nest (McKinnon and Bêty 2009), but we did not document this phenomenon. It may be that shorebirds actively avoid nesting near fox dens, given that dens are often prominent on the landscape and characterized by raised mounds or ridges with visibly distinct and relatively lush plant communities (Garrott et al. 1983). Clearly, further study is needed to better elucidate and quantify the spatial effects of fox predation on shorebird nests in Churchill and, indeed, elsewhere in the sub-Arctic.

One competitive model included a positive effect of distance from jaeger nests, with a positive additive effect of camera presence ($\Delta AIC_c = 1.24$). The positive effect of cameras on daily nest survival aligns perfectly with the predation risk results. Predation risk decreased in the presence of cameras, thus increasing nest survival. As discussed above, positive effects of camera traps have been found in other studies on real nests (Thompson et al. 1999; Herranz et al. 2002; Richardson et al. 2009). Camera presence may affect risk of predation by mammalian and avian predators differently; in one study, magpies avoided conspicuous cameras (Herranz et al. 2002), while in another, Arctic foxes approached and scent-marked cameras (although this did not result in higher predation; McKinnon and Bêty 2009). During our study, Arctic and red foxes, jaegers, and Herring Gulls were all photographed approaching cameras at real nests despite our best attempts at concealment. In future studies, where sample sizes permit, interactive effects of camera presence and predator type should be considered.

A second competitive model included the same positive effect of distance from the nearest jaeger nest, with a negative additive effect of distance from town ($\Delta AIC_c = 1.83$). Again, the negative effect of distance from town on daily nest survival aligns perfectly with the predation risk results. Predation risk was lower closer to town, thus increasing nest survival in proximity to town. Given that distance from the nearest jaeger nest was clearly an important variable explaining variation in daily nest survival of shorebirds (i.e., found in all competitive models), the effect of proximity to town is surprising given that jaegers did not show any trends in abundance in relation to town and we know that one pair of jaegers was consistently nesting in each plot in both years of study. The effect of proximity to town was also surprising given that no effect was found for real shorebird nests near oil field infrastructure on the Arctic Coastal Plain (Liebezeit et al. 2009). As noted above, however, predator assemblages and distributions differ between northern Alaska and Churchill; and with only 4 study plots, the effect we found of distance from town must be interpreted with caution.

Conclusion

Our study documents evidence for effects of proximity to both mammalian and avian predator breeding sites on shorebird nest predation risk and survival rate in the sub-Arctic. Further, we found that although predation risk and nest survival were both significantly affected by proximity to Parasitic Jaeger nests, a smaller effect of proximity to active fox dens on predation risk appeared to be, at least in part, mediated by proximity to human settlement by way of there being fewer fox dens near town (in 1 year of the study). In fact, shorebirds nesting in the study plot closest to town experienced the highest daily nest survival out of all four plots, a strong enough trend to make competitive a model that included both jaeger nest proximity and town proximity. Camera trap monitoring revealed that red and Arctic foxes predated more real nests than did jaegers, while artificial nests were much more heavily predated by jaegers; a result that possibly reflects the efficacy of nest defense and/or camouflage against avian predators at real nests. The high predation of real nests by foxes that we observed from camera traps was also counter to the long-standing belief that foxes were insignificant nest predators in the Churchill area. Taken together, our results indicate that humans may have a larger predator-mediated influence on ground nest predation risk and shorebird nest survival than previously anticipated, which is what we predicted given the relatively simple trophic systems of the sub-Arctic and Arctic. What we did not predict was the directionality of influence, whereby closer proximity to the town of Churchill may have a sort of sheltering effect on shorebird nests; however, this directionality is likely to change on a per-settlement basis according to the different relationships that exist between humans and nest predators in each place. In sum, future studies investigating the effects of predator and alternative prey populations on shorebird nest survival in Arctic and sub-Arctic regions should not ignore the potential for direct or indirect anthropogenic effects on predator–prey interactions.

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Author contributions TMB and LM conceived the ideas and formulated hypotheses and designed the field protocols and methods. TMB analyzed the data and wrote the first version of the manuscript. TMB and VO collected the field data. JR contributed essential data and feedback on the paper. All authors reviewed the final versions of the manuscript.

Data availability Data are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors confirm that there are no competing interests associated with the manuscript.

Ethical approval All protocols were conducted in compliance with regulations of the Canadian Council on Animal Care and approved by the York University Animal Care Committee (2016-10W R1, 2019-8W R3).

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