Direct and indirect effects of nest predation risk on Arctic breeding shorebirds: Does availability of alternative prey contribute to nest mortality?

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ABSTRACT

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Direct and indirect effects of nest predation risk on Arctic Shorebirds: Does availability of alternative prey contribute to nest mortality?

Arctic breeding shorebirds are often considered alternate or secondary prey to avian and terrestrial predators that primarily feed on cyclic populations of rodents. Predation risk can strongly influence habitat selection; however, there is limited understanding of how nest placement by shorebirds and subsequent risk of nest predation are affected by spatiotemporal patterns involving the indirect effects of alternate prey on predator activity. I examined nest fates of Whimbrel (*Numenius phaeopus*) and Dunlin (*Calidris alpina*) at the southernmost edge of their breeding ranges at Polar Bear Provincial Park, Ontario, using field surveys including direct observations, camera monitors and thermal probes. I used resource selection functions (RSFs) to compare used and available habitat features near shorebird nests. I assessed whether shorebird nest predation was affected by spatial patterns in avian predator activity, habitat, and small mammal alternate prey and annual variation in cyclic small mammal abundance. RSFs confirmed strong habitat selection for graminoid fen habitats with avoidance of tundra heath, presumably to avoid terrestrial predators that may use them as travel corridors. Shorebird nest predation was not affected by the spatial variation in avian predator activity. However, Dunlin nest predation risk was affected by spatial variation in small mammal abundance. Further, the effect was strongest in years consistent with peaks in the small mammal population cycle. These findings highlight the important effects of spatiotemporal variation of alternate prey densities on Arctic-Subarctic food webs, providing insights on the complex relationships affecting shorebird nest success.

Keywords: Shorebird, Whimbrel, Dunlin, nest predation, alternate prey, apparent competition, predator prey, Empirical Bayesian kriging, space use, trophic interactions, resource selection functions

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1: INTRODUCTION

To understand predator-prey interactions, identifying vulnerabilities to mortality and the nature of predation risk can elucidate mechanisms affecting declines of both predators and prey (Brown 1999). The perceived predation risk of a landscape to prey is shaped by encounters with predators (i.e., perceived predation risk) and direct mortality (e.g., failed reproduction; Laundré et al. 2001). Antipredator responses including selection of habitats that provide adequate cover can be altered by perceived predation risk. Predation risk can impede access to resources and the trade-offs made by individuals between predator avoidance and resource acquisition can affect individual fitness and population-level dynamics (Gaillard et al. 2010).

The trade-off between antipredator behaviour and resource acquisition by prey may be observed through both direct and indirect interactions between species. Specifically, the presence of predators may elicit antagonistic responses in prey species including habitat-specific avoidance of predators or elevated rates of antipredator behaviours including vigilance (Brown 1999). Predation risk may force species to rely on lower quality resources. However, when body condition is compromised or resources are limited, individuals may trade safety to obtain the necessary resources where predation risk is high (Brown et al. 1999). Indirect factors that also contribute to predator-prey interactions can be more nuanced, potentially elevating predation risk of multiple species with common predators (Holt 1977; McKinnon et al. 2013; Holt and Bonsall 2017). The indirect effects of habitat characteristics or the presence of alternative prey may also contribute to predation risk because these alternative prey species may act as attractants for predators (Holt and Bonsall 2017; Kittle et al. 2017). These multi-species interactions have implications for predation risk of prey species (Krebs et al. 2014) because the relationship between predators and alternative prey may not be detectable by prey species.

Elevation of predation risk in systems that contain multiple predators and prey species has profound effects on species interactions when ecosystems are subject to destabilization. Changing landscapes result in interactions between resident species and novel migrants where new species can benefit from altered habitats and destabilize residents through predation and competition (Crooks and Soulé 1999; Gauthier et al. 2005; Prugh et al. 2009; Elmhagen et al. 2017). Populations of Arctic and sub-arctic species at their southern range limit may be particularly vulnerable to changes in community composition. For example, northward range expansion of Red Fox (*Vulpes vulpes*) may negatively effect the ecologically similar resident Arctic Fox (*Vulpes lagopus*) at their southern range extent and cause downstream trophic implications for their shared prey (Gallant et al. 2020). Disruptions to ecosystem regimes can be more influential on Arctic species near their southern range limits than at high latitudes because southern ranges will be first to experience range-shifting effects of new inhabitants, shifts in habitat composition and heterogeneity due to climate change (Ballantyne and Nol 2015; Flemming et al. 2019a, 2019b; Hope et al. 2019; Holmes et al. 2020).

Most shorebird species that breed in North America have experienced steep declines in recent decades (Smith et al. 2023). Causes of observed population declines are often difficult to determine and may involve constraints faced at different stages of the annual cycle (Piersma 2007; McKinnon et al. 2010; Galbraith et al. 2014; Piersma et al. 2016). One potential limiting factor for Arctic shorebird populations may be the stresses imposed by nest predation and other sources of mortality during the breeding season (Kubelka et al. 2018; Machín et al. 2019). Little is understood about the population dynamics at the southern range limits of North American Arctic breeding shorebirds, specifically responses to nest predators. Shorebirds have diverse antipredator nesting strategies including biparental investment, vigilance, and crypsis (Bulla et al. 2016) that can affect nesting habitat selection. For example, Whimbrel (*Numenius phaeopus*) select open nest habitat to maintain vigilance to enact active nest defense, providing protection to their nests and to the nests of sympatric species (Larsen and Moldsvor 1992). Dunlin (*Calidris alpina*) also maintain nests within broadly open habitats but rely on concealment of vegetation over their nests, to minimize nest predation (Holmes et al. 2020). In contrast to Whimbrel, Dunlin avoid neighbouring conspecific and sympatric nests and do not appear to gain benefits from the antipredator strategies of nearby nests (Cunningham et al. 2016). These examples describe possible effects of predation risk that may modulate behaviours at nests and space use according to species-specific nesting strategies including vigilance, habitat avoidance and foraging frequency, outside of predator presence.

The abundance or distribution of alternate prey of shared predators may impose an indirect source of predation risk for nesting shorebirds. The alternate prey hypothesis posits that a decline in preferred prey results in predators directing greater search efforts to alternative prey (Angelstam et al. 1984), reflected in changes to predator functional response. Small mammals are preferred prey for Arctic fox, Red Fox and birds of prey including Northern Harrier (*Circus hudsonius*) and Rough-legged Hawks (*Buteo lagopus*). Small mammals also exhibit high inter annual fluctuations in abundance, often in 2-4 year cycles that greatly affect their availability as prey (Krebs et al. 1995; Therrien et al. 2014; Ims et al. 2017). As a result, predators of small mammals may target alternative prey including eggs of, and/or incubating adults of snow geese (*Chen caerulescens*) and shorebirds during years of low mammal densities (McKinnon et al. 2013; Flemming et al. 2019a). In contrast to the alternate prey hypothesis, predator-mediated apparent competition may occur when prey species share common predators and the abundance of one prey species elevates predation risk to another when found near each other, characterized by the numerical response of predators to prey (Holt 1977; Holt and Bonsall 2017). Indeed, shorebird nest predation can be elevated according to the spatial association with high goose densities and are incidental to goose predation, as shorebirds do not appear to be the primary focus of predation efforts (McKinnon et al. 2013; Lamarre et al. 2017; Flemming et al. 2019a). Understanding how predator effort and prey choice changes with variation in prey community structure (involving functional and numerical responses by predators) may help in elucidating the nature of predation risk for multiple prey species with common predators.

Habitat factors that contribute to predation risk and nest mortality are described by only a few studies in the Arctic within a multispecies predator-prey framework, and have not been studied in more southern sub-arctic regions (Laidlaw et al. 2020). Additionally, many studies lack habitat data of sufficient resolution to accurately map fine-scale variation in land cover features relevant to habitat selection; for example, wetlands may appear as homogenous features in a broad-scale land cover classification but may contain numerous microsite features relevant to shorebird and small mammal habitat. This lack of detail may extend to presence of alternate prey as well. Indeed, previous studies have typically been limited to coarse characterization of high and low variation in abundance of small mammals among years and may not necessarily describe the spatial variation in small mammals (McKinnon et al. 2013; Flemming et al. 2019a; Machín et al. 2019). In a landscape context, shorebirds may incur greater predation when nesting in close proximity to alternate prey, such as highly abundant goose colonies (Lamarre et al. 2017). However, there is no analysis that I am aware of that describes spatially-explicit density-dependent relationships linking variation in small mammal abundance to shorebird nest placement and the subsequent influence on nest predation risk. Little is known about the spatial relationship between small mammals and shorebirds or whether shorebird nests can be incidental prey for predators in search of small mammals. Consequently, presence of predators and alternate prey can be evaluated as landscape features similar to other habitat variables including vegetation cover, as they relate to habitat selection, reproductive success and risk of mortality.

I characterized the predator species, nest predation rates, and factors affecting nest site selection and nest predation risk for the sub-Arctic shorebird community that breeds near the southern coast of Hudson Bay. My objectives were to: 1) characterize patterns in predation risk through evaluating how predation probability varies according to shorebird species, year effects which encompass different stages in the local small mammal cycle, and predator species, 2) determine whether shorebird nest predation was affected by spatial variation in avian predator activity and the indirect effects of spatial variation in small mammal alternate prey within years, and 3) characterize vegetation cover selection patterns for shorebird nest sites and test for an interaction effect between vegetation cover and predation risk to shorebird nests. I used field observations collected during the 2018-2021 breeding seasons for nesting shorebirds, including Whimbrel, Dunlin, Hudsonian Godwit (*Limosa haemastica*), and Least Sandpiper (*Calidris* *minutilla*). I used high resolution remotely sensed land cover information to characterize fine scale vegetation features, and field surveys to characterize spatial variation in predation risk associated with avian predator activity and relative abundance of small mammals as alternate prey.

I compared three competing hypotheses on factors affecting shorebird nest predation: a) shorebird predation risk is driven by the spatial relationship with predator and alternate prey near nest sites; b) nest predation risk is driven by vegetation cover effects near the nest; and c) nest predation risk is driven by the additive or interacting effects of predators, alternate prey, and landform conditions. I predicted that probability of nest predation will be negatively associated with alternative prey abundance but will not be significantly related to variation in local vegetation class due to the strong nest site preferences of arctic shorebirds. Presumably, shorebirds have incorporated predation risk into their patterns of habitat selection through the process of natural selection (Nguyen et al. 2013) when selecting nest habitat and may rely on antipredator strategies other than vegetation feature avoidance. However, shorebirds may not necessarily have the capability to respond to indirect sources of predation risk including apparent competition caused by co-occurrence with small mammals. I predicted that shorebird nest predation risk would be elevated in years with lower small mammal abundance across the study area, consistent with the alternate prey hypothesis. However, when examined at finer spatial extents within years, shorebird nest predation may be higher in the immediate vicinity when they co-occur with small mammals and are incidental prey to predators that are in search of small mammals, consistent with apparent competition.

2: METHODS

Study area

This study was conducted at the Burntpoint Creek Research Station, Polar Bear Provincial Park (LAT: 55.24173 °N, LONG: 84.31814 °W) along the Hudson Bay shoreline of northern Ontario. The research station is situated within the Canadian Sub-Arctic in the Hudson Bay Lowlands ecozone (Crins et al. 2009). Poorly drained fens dominate the study area. The coastal portion of the study area is dominated by tidal flats, gravel beach ridges, and salt marshes. Within a few kilometres of the coast, shrub rich fen transitions to open graminoid fen (Hu et al. 2024). Wetlands are intersected by inland ancient beach ridges composed of tundra heath vegetation and increasing numbers of trees inland from the coast of Hudson Bay. Small ponds and lakes are interspersed throughout the area.

Landcover description and remote sensing

I characterized vegetation and other land cover composition using an existing land cover classification developed for the study area using IKONOS multispectral imagery (MAXAR Technologies Inc.) for 18 July 2001, and a 4 m x 4 m raster classification product. Fifteen land cover types were identified including water, mudflats, sand/gravel, tundra heath, tall shrubs, low shrubs, wet graminoid fen, graminoid fen, shrubby graminoid fen, intertidal marsh, lichen woodland, conifer swamp, old burn, peat plateaus and non-land features including cloud cover.

Shorebird nest surveys

There were existing historical data one the nesting ecology of locally breeding shorebirds from field surveys conducted at the site between the years of 2013-2019, Global positioning system (GPS) locations (Figure 2 and 4) were recorded for all nest locations, and nests were marked and monitored to determine success or failure. Shorebird nests were found by searching in “high intensity” search plots or through happenstance by walking through breeding habitat outside these plots. Nests were found by monitoring birds that exhibited defensive behaviours, including alarm calling and distraction flight displays, and by searching where breeding birds emerged or by watching individuals return to a nest. Four 400 x 400 m plots (Figure 2 and 4) were carefully searched following the Arctic Shorebird Demographic Network protocol (hereafter 'high intensity' plots). These plots were partitioned into eight 50 x 400 m sections and each 50 m section was searched using a line of 6-8 people walking in unison. Nests were located by opportunistic encounter or by watching where birds had flushed from the nest. To mitigate the negative effects of nest visits that might attract predators, adult shorebirds were disturbed from nests for no more than 10 minutes when possible. In addition, If temperatures fell below 3 ° Celsius or it was raining or snowing, all nest searching was postponed until weather conditions improved.

Data collection: Shorebird nests

Nests of each of my study species consisted of no more than four eggs (Cornell Lab of Ornithology n.d.). Each egg was measured (mm) along the length and width with digital calipers. To estimate the clutch initiation date, eggs were floated in warm water in clear containers with embedded protractors to measure the height above water (mm) and angle of the egg along its width when suspended. Species-specific calculations based on these measures were used to estimate the approximate initiation and hatch dates (Liebezeit et al. 2007). Thermal probes were also placed within nest cups to aid in verifying nest fate and timing (Tinytag Plus2 TGP-4020; Gemini Data Loggers Inc.,West Sussex, U.K.). Thermal probes were composed of two parts: the sensor and wire were attached to the end of a cabob stick (3mm diameter by 150mm length) and were implanted into the centre of the nest cup (Meyer et al. 2021). The end of the probe was positioned where the narrow end of the eggs met when repositioned. The height of the probe was equal to the height of eggs with a focus on ensuring that the probe be high enough to contact the brood patch of incubating adults without disturbance. The recording unit was buried with the organic soil layer approximately 10-20 cm from the nest cup. Thermistors were programmed to record temperature every minute during incubation and the temperature profile was used to differentiate nests that hatched and produced young (slightly declining temperature during the final 36 h of incubation) from nests that were depredated (rapid decrease in temperature within a minute).

Trail cameras were used in 2021 to identify nest predators and other disturbances around shorebird nests. The cameras were placed on wooden stakes with a height 20-30 cm from the ground and 3-5 m from the nest cup (Spy Point Force-Dark n= 22). To avoid interference by sun glare onto camera images, the trail cameras were always positioned towards the North. To ensure sufficient viewing angles of the nest cup, the viewfinder of each unit was used to centre the frame on an observer at the nest cup. The cameras were programmed for continuous sensor activity with instant photo capture upon detection of movement, with two photos taken for each activation of the sensor (using the multishot function). Cameras were equipped with 16 GB SD cards for photo storage. The cameras remained at shorebird nests until either the nest was depredated or until the eggs hatched. After I no longer needed a camera at one nest the camera was collected and redeployed.

After researchers measured eggs and set up cameras, Dunlin nest cups were observed at >20 m distances until adults returned. For Whimbrel, all personnel vacated the immediate vicinity of nests to terminate distress responses in adults (e.g. vocalizations). Researchers revisited nests every 3-4 d to observe if a nest had been depredated. During revisits camera sensitivity and viewing angles were checked and adjusted accordingly to reduce battery depletion and extra photo captures because of vegetation features like blowing graminoids, which could trigger camera sensors. Revisits continued until shorebird nest fates were determined (Table 1). If a nest was found empty 3 days or more prior to the estimated hatch date, the nest was assumed to have failed. Personnel looked for evidence at the nest cup including shell fragments, yolk, embryonic fluid, and signs of predators including scat to further corroborate the identification of nest predator. By contrast, if eggs were found intact but adults were not observed upon approach, researchers evaluated the temperature of the eggs by touch. If found cold, eggs were left in the nest and revisited on the following day and if found cold for two consecutive days, the nest was considered abandoned. During nest visits approaching the estimated hatch date, eggs were evaluated for signs of hatching including pips- small fractures in the shell surface, stars- larger interwoven fragmentation of the shell, and windows- holes in the shell created by hatchlings. If the eggs were in the stages of hatching, revisit frequency was increased to daily to ensure confirmation that nests were successful. Alternatively, within 3 days of the estimation hatch date and/or signs of hatching occurs, revisit frequency was also increased ensuring confirmation of fate. To be evaluated as successful, nests were characterized based on a) hatchlings in or near the nest cup and b) passive monitoring devices including thermal probes and nest cameras. Multiple lines of evidence were used to determine nest fate in addition to thermal probes. Nest fate was also corroborated visually via camera footage. In some cases, a predation event was fully captured on film because the predator was seen entering a nest cup or consuming eggs or hatchings. In some cases, cameras captured an image of a predator passing by the nest, but I did not assume that this predator was responsible for nest loss. Camera traps could also capture nest activity that suggested a successful hatch if adults were seen carrying empty shells from the nest and/or visual confirmation of hatchlings in or near nest cups. In instances where there it was suspected that eggs had hatched but later confirmed via cameras that the nest had been depredated (e.g. predator entering nest cup, seen consuming eggs, or seen consuming chicks), the nest fate was classified as unsuccessful. Shorebird nests with indeterminate fates were excluded in nest site selection and predation risk analyses.

Spatiotemporal variation in small mammal abundance

To characterize temporal variation in small mammal relative abundance, I used counts of small mammal winter nests (SMN) collected within high intensity shorebird plots during 2018-2021 (Figure 1). In our study area SMNs are constructed primarily by Meadow Vole (*Microtus pennslvanicus*) within the subnivean zone where they overwinter and reproduce (Courtin et al. 1991). SMN abundances within shorebird search plots were used to identify the stage of the small mammal population abundance cycle for that year. High and low phases of small mammal abundance (which varied ~40-fold) were differentiated based on whether the abundance within shorebirds search plots was above or below the overall mean from years 2015-2021 (Figure 1).

To characterize spatial variation in small mammal relative abundance, SMN were counted along 500 m transects distributed throughout the study area (n = 30). Each transect was placed based on randomly selected UTM coordinates within the study area margins and were surveyed from 2018-2021 (Figure 2). Researchers walked transects and a single observer recorded all SMN detected and their distances (m) perpendicular to the transect line. SMNs were tallied and then destroyed to ensure that they were not recounted in subsequent years. Additionally, SMNs that were discoloured and or flattened were also excluded. SMN total counts for each transect and the centroid of the transect line were used to estimate the spatially-explicit relative abundance of small mammals across the study area for each year. This spatiotemporal variation in SMN frequency occurrence was used to characterize their distributions during the following spring/summer period of shorebird nesting and at nest locations. Although distributions of small mammals may vary seasonally (Bowers et al. 1996), small mammals including meadow voles have relatively small home ranges (0.3-0.9 ha) and high site fidelity between winter and spring (Jones and Sherman 1983; Bowers et al. 1996). Given that the 500 m transects would roughly encompass the annual home range of a small mammal and transects were 700 m or more apart, we assumed that the spatial maps of relative abundance reflected conditions to which shorebirds were exposed during the nesting period. Furthermore, previous season wintering nest abundance has been shown to reflect observed densities during the following spring in other small mammals (Krebs et al. 2012).

To evaluate whether the SMN abundances from transects were representative of those found within shorebird search plots during the same year, abundance of SMN transects were compared to determine trends in annual abundance (Figure 1). Indeed, SMN indices of shorebird search plots share the same annual patterns as SMN transects (Figure 1 and 2). Therefore, for analysis on small mammal indices in relation to shorebird nest predation risk, I assumed that 2018 and 2019 are years with high and intermediate small mammal abundance respectively and 2021 had low small mammal abundance (Figure 1). No field work was conducted during the 2020 shorebird breeding season.

Spatiotemporal variation in avian predator activity

We measured spatial variation in avian predator activity using incidental observations taken during field surveys. Personnel recorded the time at which they began their daily field work and during which time they recorded all avian potential predators seen or heard. When detected, the estimated distance, number of individuals, species and GPS point of observation were recorded (Figure 4). During nest checks, other field protocols and breaks for food and water; times were noted and designated as times that incidental predators were not being surveyed. This protocol was carried out until at least 200 cumulative hours were specifically dedicated to searching for incidental avian predators. To characterize spatial variation in predation risk, the study area was split into a hexagonal tessellated grid and the sum of incidental avian predator detections were assigned to the corresponding grid cell (Figure 4). The size of the hexagonal grid cells was informed by the mean detection distance among observers. The mean observation distance of avian predators between 2018 and 2021 was 416.0 m (2018 = 476.9 m, 2019 = 445.8 m, 2021 = 325.5 m). For simplicity, each hexagonal grid cell was 400 m along the long diameter. To insure that incidental avian predator detections were representative of predators that depredate shorebird nests, Herring Gull (*Larus argentatus*) were highly abundant in recorded in incidental observations but never observed to attack and consume shorebirds via camera trap analysis were excluded in predator indices , Figure 3, Table 2).

To spatially characterize hexagon cells that were searched but where incidental avian predators were not detected (i.e., apparent absences), I used daily observer tracks from GPS were recorded from personal units every two minutes while researchers walked in the field. These absences were added to the incidental predator detection dataset and assigned to the date of field work.

Predator and alternate prey indices via Empirical Bayesian Kriging (EBK)

Maps describing spatial patterns in relative abundance of predators and small mammals across the study area were created using Empirical Bayesian Kriging (EBK) and the count data associated with the centroids of predator survey hexagons and small mammal transects. Geostatistical interpolation methods use information about the correlation structure between observations in space to create a prediction surface for the property of interest, in my case, relative abundance. EBK has advantages over other interpolation methods in using sub-setting and simulation to facilitate model parameter estimation and its ability to produce accurate predictions of moderately nonstationary data, which may be common for populations distributed in heterogenous habitats (Krivoruchko and Gribov 2019; Esri Inc 2020). An empirical transformation method was used to ensure a Gaussian distribution among abundance samples. Multiple semivariogram models are available for EBK and K-Bessel was chosen following inspection of the visual best fit of the empirical semivariances with the empirical distribution of simulated semivariograms. Other parameter settings included a subset size of 100 for the number of points in each local model, and an overlap factor of 1 among subsets. For my analysis, semivariogram fit did not improve beyond 100 simulations (Appendix IIF1-6). Because semivariogram fit did not improve beyond a smoothing factor of 0.2 across EBKs, I used across interpolation sets (Appendix IIF1-6). I used inspection of cross validation parameters to assess interpolation results. EBK was performed using the Geostatistical Analysis Toolpack in ArcGIS Pro (Esri Inc 2020). I used the prediction surfaces for relative abundances of predators and small mammals in subsequent analysis to assess the effects of alternate prey distribution and predation risk on shorebird nest mortality. I considered the values of these prediction surfaces as indices of predator activity and small mammal availability (Figures 2 and 4). For modelling, predator and small mammal indices were min/max normalized to adhere to the same 0-1 ordinate scaling of the percent vegetation coverage at nests sites.

Predation risk modeling

I tested competing hypothesis on drivers of predation risk on shorebird nests using generalized linear models (GLM) with a binomial response variable for nest depredation (success or failure) and shorebird species, year, vegetation, and indices of small mammals and predators as predictors. Vegetation and the year-specific mean estimates of relative abundances of small mammals and predators created using the EBK interpolation were summarized within 100 m buffers of each nest. A set of competing models were developed using these predictors and compared using Akaike Information Criterion (AICc) to select the most parsimonious model (Table 3). First, I described the effect of nest vegetation on predation risk (Model 1.0, Table 3). To evaluate effects of alternate prey and predators, I included year, species, SMN indices and avian predator indices in a model without vegetation parameters (Model 1.1, Table 3, and Appendix IIIF1). I also constructed a series of sub-models that helped to characterize the effects of nest predation based on biological, ecological and behavioural theory. I excluded shorebird species as a factor in some models under the assumption that incidental predation events occur when predators are not specifically targeting nests but locate nests when searching for other prey as per the alternate prey and apparent competition hypotheses (Model 1.2, Table 4, and Appendix IIIF2). To disentangle the effects of annual trends in small mammal and predator indices from the spatial variation in these features that were mapped using EBK, I included interaction terms between year and both small mammal and avian predator indices (Model 1.3 Table 4, Figure 5). To test whether small mammal and predator indices affect shorebird nest predation risk in addition to vegetation, a model was constructed to include year-index interaction terms and percent vegetation (Model 1.4, Table 5, Figure 6). To test for species-specific effects of predator/alternate prey indices and vegetation, each of the model frameworks (Table 3) were applied to Dunlin (Table 6, Figure 7) and Whimbrel (Table 6, Figure 8) subsets.

Vegetation cover selection of shorebirds

To characterize nest site selection of nesting shorebirds, I used a logistic regression to predict the probability of space use based on observed nest locations relative to landcover class availability (Manly et al. 2002; McLoughlin et al. 2010). The binomial response variable consisted of 1 = shorebird nest location and 0 = randomly selected coordinates within study area margins that represented available or potential space use. Five random point locations were created for each real nest, which provided a balance in avoiding oversaturation while ensuring good coverage of the study area to represent availability. Whimbrel, Dunlin Least Sandpiper, and Hudsonian Godwit had sufficient sample sizes for monitored nests for inclusion in models of nest site selection. A total of 111 shorebird nests (collected 2018-2021) with known fate were available for the analysis (excluding the one Short-billed Dowitcher nest due to sample size, Table 1). The percentage of each vegetation type within 100 m buffers around shorebird nests and random points was used as explanatory variables in the logistic regressions. 100 m buffers were chosen to adequately meet the nest site margins of both Whimbrel and Dunlin. From field observations, Whimbrel tend to initiate next defence within ~100-200m of next cups. Similarly Dunlin tent to linger near nest cups after disturbance within ~50-75 m. Extraction of land cover information for each polygon was done using the R packages: "terra" and "raster"(Hijmans 2019; Hijmans et al. 2023). Of the 15 land cover types described in the IKONOS classification, I used the following classes for further analysis: graminoid fen, shrubby graminoid fen, tall shrubs, low shrubs and tundra heath. Some land cover types in the original classification were merged based on similarity or evidence of collinearity issues when developing the statistical models (e.g. VIF > 4), including graminoid fen and wet graminoid fen, I assumed that these two land cover types are functionally similar in terms of shorebird nest site selection. Included in the RSFs, were vegetation/land cover types differentiated by: 1) space use potential for shorebird nests including graminoid fen, 2) composite vegetation types that include possible nesting habitat of shorebirds but also composed of other features including shrubby graminoid fen that may affect antipredator behaviours including crypsis and vigilance due to variation in lateral concealment and 3) Other vegetation types that may not directly inform shorebird nest site selection but may help characterize spatial relationships with alternate prey (small mammals) and predators. Lateral concealment is further considered with the inclusion of tall and low shrubby areas and may act as suitable habitat of small mammals. This may be contrasted by tundra heaths that may be considered as individual contributors to shorebird space use (Model 2.0, Table 9) with potential use by terrestrial predators (e.g. fox) as corridors relative to shorebird nest placements. Year was included to account for interannual variability that could not be explained by the time varying variables for small mammal and predator relative abundance. Importantly, inclusion of year also facilitated interpretation of the influence of the year-specific phase of the small mammal population cycle. A peak in the cycle of small mammal abundance was evident for 2018 and declined in subsequent years up to 2021 (Figure 1). To accurately represent this decline in small mammal abundance over the study period, year was considered a continuous variable.

A model was created describing shorebird used and available nest locations and their percentage cover of each vegetation class, year, alternate prey index estimates (EBK), and predator index (EBK) as predictors to determine whether predator and alternate prey indices affect shorebird space use in addition to percent vegetation (Model 2.0, Table 3, Figure 9). A set of sub models were created and compared using AICc model selection that included combinations for vegetation, year effect, predator and alternate prey indexes, and their interaction terms (Table 3). Model 2.1included only vegetation types and Model 2.2 included vegetation and the interactions between year and relative abundance indices for small mammals and predators. To determine if space use of shorebirds was explained by antipredator space-use decisions alone, I tested a model that included only interaction terms for year with predator and alternate prey indices (Model 2.3, Table 3).

3: RESULTS

Shorebird nest monitoring

Between 2018 and 2021, a total of 112 nests of five species with confirmed fate were monitored (Table 1). The number of nests and species varied each year (2018: 31 nests, 4 species; 2019: 33 nests, 2 species, 2021: 48 nests, 5 species). Nests of Whimbrel and Dunlin were the most commonly found (Table 1). Across the study period, 42% of nests failed which varied strongly among years. In 2018, 87% of nests failed, 42% failed in 2019, and 46% failed in 2021. The primary cause of shorebird nest failure was predation which comprised 93% of failed nests (Table 1). We found three abandoned nests (5%) and a single trampled nest (2%, by caribou (*Rangifer tarandus*) (Appendix IF4). The proportion of nests depredated varied among species. Dunlin and Whimbrel had similar mean predation rates: 58% of Dunlin (82% in 2018, 36% in 2019, and 55% in 2021) and 59% of Whimbrel (92% in 2018, 45% in 2019, and 55% in 2021) were depredated. Hudsonian Godwit had the highest predation rate (100% of 3 nests in 2018 and 67% of 5 nests in 2021, mean 83 %) and Least Sandpiper were depredated least among shorebirds (60% of 5 nests in 2018 and 21% of 6 nests in 2021, mean 36%); however, the sample size of nests for both species was very small.

Table 1: Arctic Shorebird nest fates 2018-2021, n = 112

Nest Species	Year	Hatch	Depredated	Abandoned	Trampled	Total
Dunlin	2018	2	9	-	-	11
	2019	7	4	-	-	11
	2021	7	10	1	-	18
Whimbrel	2018	-	11	1	-	12
	2019	11	10	1	-	22
	2021	7	13	-	-	20
Hudsonian Godwit	2018	-	3	-	-	3
	2019	-	-	-	-	-
	2021	1	2	-	-	3
Least Sandpiper	2018	2	3	-	-	5
	2019	-	-	-	-	-
	2021	4	1	-	1	6
Short-Billed Dowitcher	2018	-	-	-	-	-
	2019	-	-	-	-	-
	2021	1	-	-	-	1

* Short billed Dowitchers were excluded from predation and availability models due to low sample size (n=1)

Small mammal sampling

Small mammal wintering nest abundance sampled from four 400 by 400m plots appeared to capture one large fluctuation in abundance characteristic of a population cycle (Figure 1). From 2015 to 2017 small mammal abundances were below the mean plot abundance for their respective year (mean = 16.67 winter nests per plot) (Figure 1) and were therefore considered years with low small mammal abundance. In contrast, small mammal abundance among shorebird search plots was greater than the inter-annual mean in 2018 and 2019 and were therefore considered years with relatively high small mammal abundance (Figure1). The estimates of density of SMNs on shorebird search plots varied from a low of 0.11 SMNs/ha in 2015 (n_{tot} = 7, $mean_{plot}$ = 1.75 +/- 0.479 SE) to a high of 2.67 SMNs/ha (n_{tot} = 171, $mean_{plot}$ = 42.75 +/- 5.218 SE) in 2018.

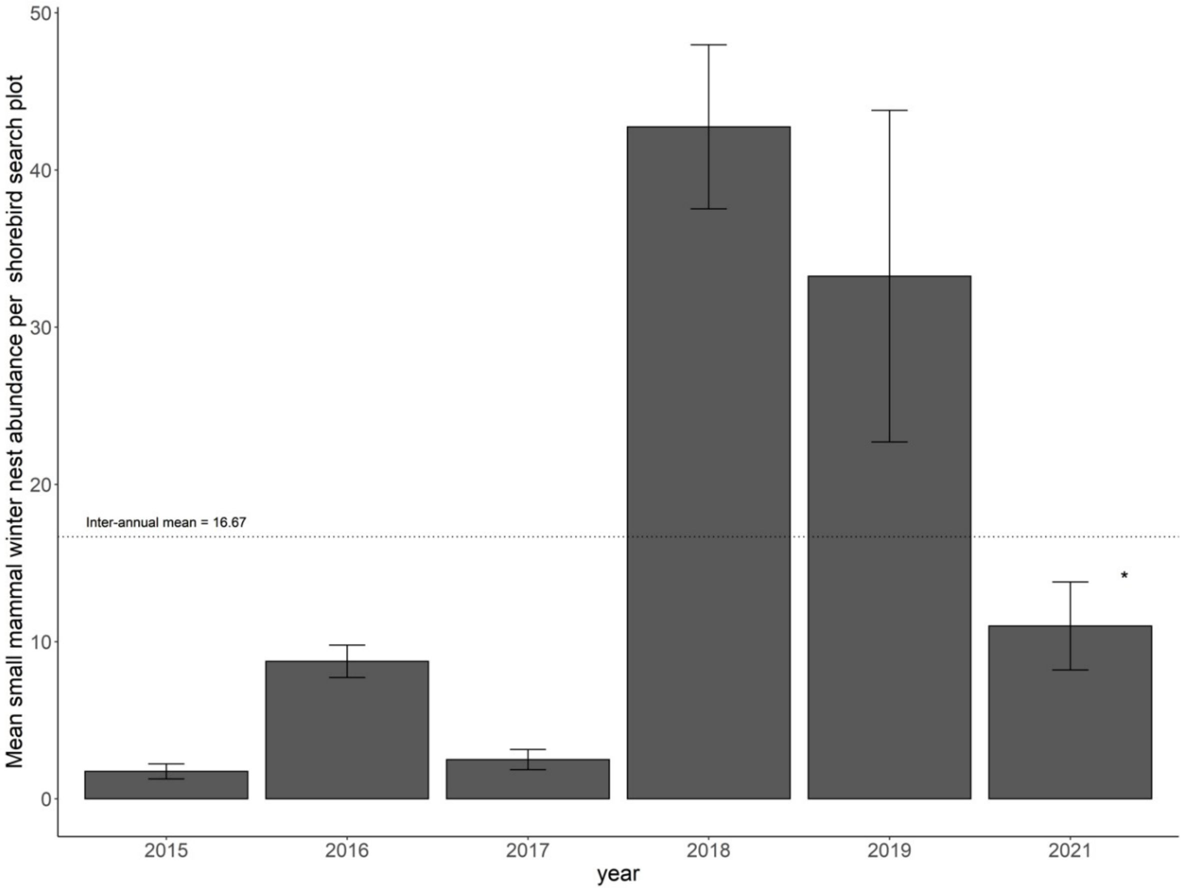

Figure 1: Annual mean small mammal wintering nest abundance averaged among four 400m x 400m shorebird search plots; dotted line represents the mean winter nest abundance per plot, averaged among all years (16.67 nests/plot); error bars indicate SE from the mean. Values above means may be considered years with high small mammal abundance.

Empiricle Baysian Kriging of alternate prey

Across all years, the spatially explicit small mammal index revealed consistently greater relative abundance of small mammals near the northern portion of the study area and lower relative abundance in areas near shorebird nests (Figure 2). Estimated SMN index was consistent with annual trends seen in small mammal abundance estimated using the shorebird plots. Smal mammal relative abundance estimated using shorebird search plots was highest in 2018 and 2019 and lowest in 2021 (Figure 1). Likewise, mean SMN index at shorebird nests were highest in 2018 (mean_{2018} = 3.37+/- SE 0.262), followed by 2019 (mean_{2019} = 3.149 +/- SE 0.257) and lowest in 2021 (mean_{2021} = 2.425+/- SE 0.322). Despite the differences of annual SMN index at shorebird nests, small mammals did not vary much annually when sampled across the study area (mean_{2018} = 3.28+/- SE 0.186, mean_{2019} = 3.64+/- SE 0.159, mean_{2021} = 3.734+/- SE 0.236). Instead, there is a visible difference in the abundance of small mammals detected within transects with more concentrated at the northern end of the study area and less concentrated near shorebird nests. Transects associated with greatest SMN index were consistent across all years but appeared to be more concentrated during the low abundance year of 2021 (median_{2021} = 2.15. max_{2018} = 19.26). By contrast, years with high small mammal abundance had lower maximum indices but more homogeneously spread (median_{2018} = 2.56, max_{2018} = 11.42; median_{2019} = 3.205, max_{2019} = 10.29).

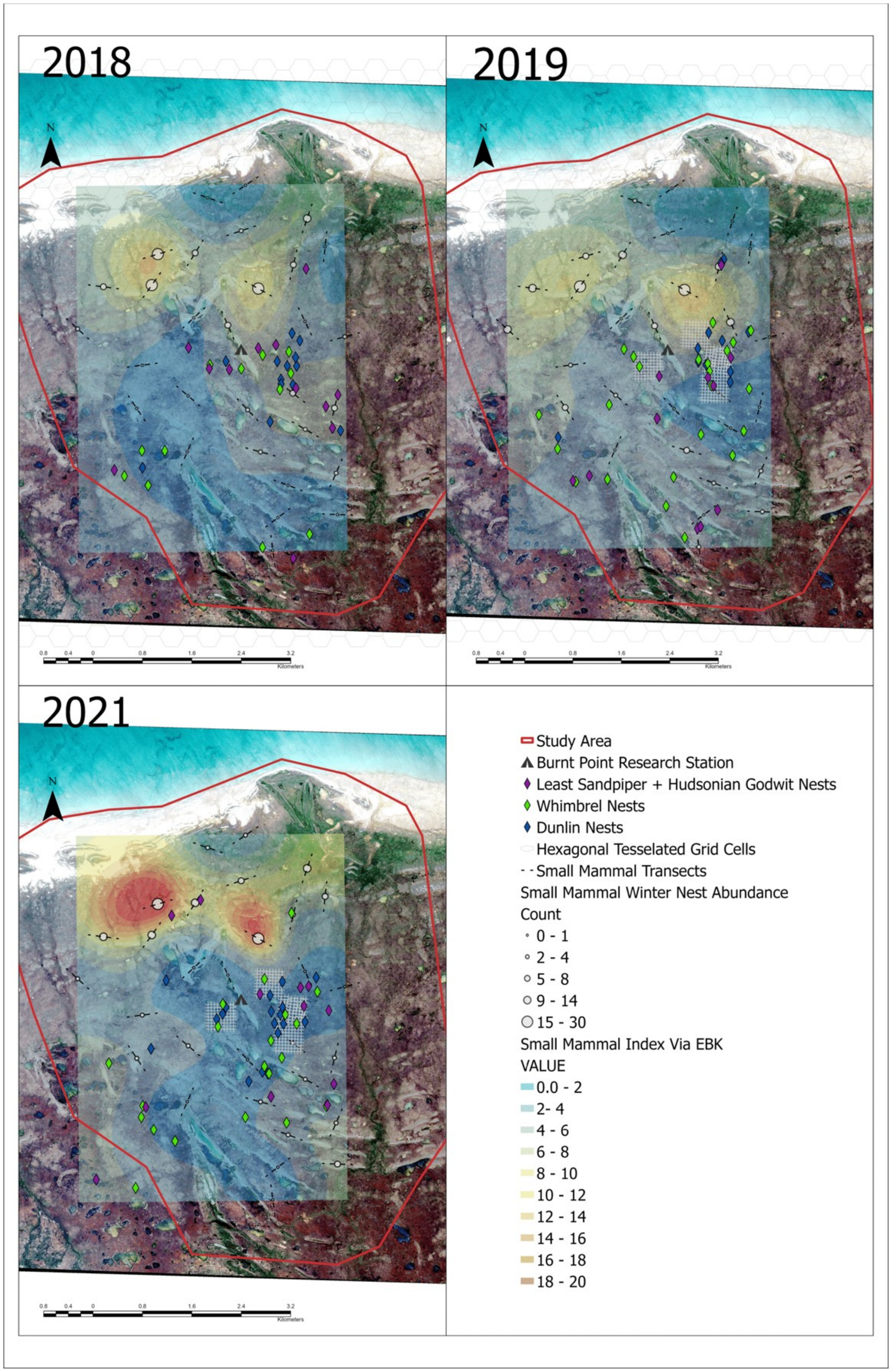

Figure 2: Small mammal nest (SMN) index via empirical Bayesian Kriging (EBK) relative to shorebird nest locations in 2018-2021. Extracted from 500m SMN transects.

Predator identification from camera observations

Predators captured on nest cameras during 2021 revealed two avian and two terrestrial species. Northern harrier was responsible for most predation events (n = 7) including four Dunlin and three Whimbrel nests, one of which (Whimbrel) was observed by field staff (Table 2). Instances of nest predation on whimbrel by Northern Harrier were characterized by defence by the incubating adults eventually succumbing to harassment by the harrier and leaving the nest site. Two of the nests depredated by harrier occurred within estimated hatch times and harriers were observed feeding on live chicks. We observed a second nest where a Harrier consumed the incubating adult and the eggs (Appendix IF1). A predation event by Northern Harrier on dunlin also involved loss of the incubating adult. A Parasitic Jaeger (*Stercorarius parasiticus*) attacked a Whimbrel nest on two separate occasions (two of four eggs were consumed) (Appendix IF3). The two remaining eggs eventually hatched successfully. This event was the only case of partial predation captured by the nest cameras. The most prominent among terrestrial predators were red fox (n = 6). Red Fox was responsible for the predation of four Whimbrel nests, one Least Sandpiper nest, and one Dunlin nest (Table 2). Predation events by fox were primarily during the night (Between ~ 23:00 and 05:00 local time) and no form of nest defence by incubating adults was documented on camera. A single terrestrial predation event by Black Bear occurred on a Dunlin nest (Table 2). The nest was found depredated and the camera destroyed with identifiable teeth marks in the camera body although the camera failed to capture the event. Seven events identified as predation were not captured by cameras deployed at the nests. Two Whimbrel nests were found by researchers already depredated with adults remaining near the nest site, but the camera failed to trigger. Predators could not be identified for the remaining predation events due to camera malfunction including battery depletion, file corruption and loss of camera function. For nests where cameras malfunctioned, fate was instead determined using evidence found during field investigations and thermal probe data.

Table 2: Shorebird nest predator identification and frequency via camera traps 2021, n = 22.

	Predator Species				
Nest Species	**Northern Harrier**	**Red Fox**	**Black Bear**	**Parasitic Jaeger**	**Unknown**
Dunlin	4	1	1	-	3
Whimbrel	3	4	-	1*	3
Least Sandpiper	-	1	-	-	1

No cameras were deployed on Hudsonian Godwit nests.
*** Indicates cases where partial predation was observed.**

Predator Sampling: Incidental predator observations

Herring Gull consistently ranked as the most commonly observed potential predator across the three years of study (Figure 3A-D) but were not observed to depredate shorebird nests during the 2021 nest-camera monitoring (Table 2). The only avian predators that were observed at high frequency that were also observed to depredate nests in 2021 were Northern Harrier and Parasitic Jaeger. Northern Harrier were the second most observed species in 2018 (0.27 obs/h) (Figure 3A), third in 2019 (0.12 obs/h) (Figure 3B), third in 2021 (0.18 obs/h) (Figure 3C) and second in total observations (0.172 obs/h) (Figure 3D) with no less than 29 observations each year. Parasitic Jaeger were observed in only one partial predation event via 2021 camera trap analysis (Table 2) and were the fourth most common predator in 2018 (0.156 obs/h) (Figure 3A), sixth in 2019 (0.0375 obs/h) (Figure 3B), fifth in 2021(0.0929 obs/h(Figure 3C) and fifth overall (0.0930 obs/obs hrs) (Figure 3D).

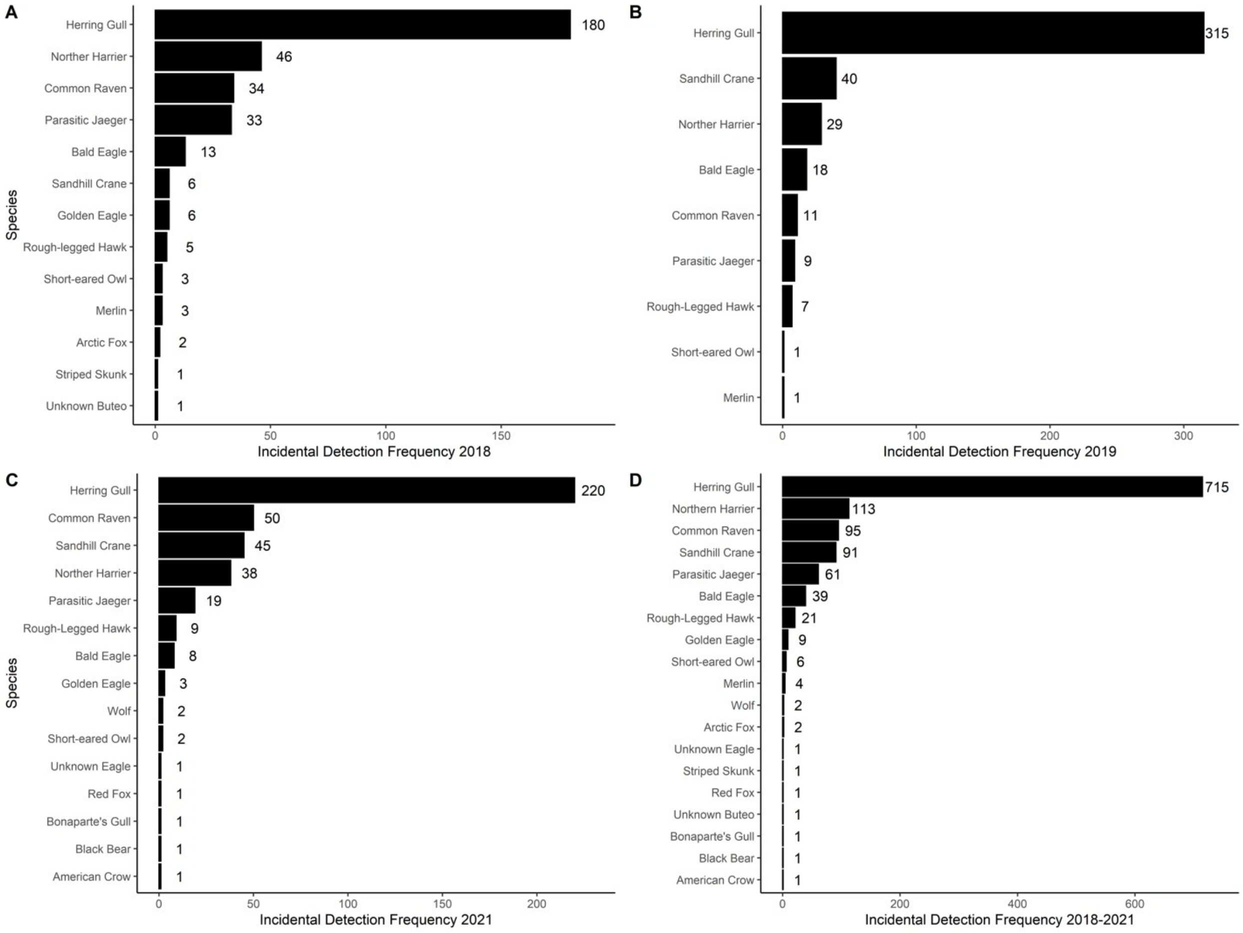

Figure 3: Incidental predator abundances during shorebird surveys A) 2018, B) 2019, C) 2021, D) total 2018-2021. Total hours dedicated to incidental predator observations were: 2018 = 211.7 hrs, 2019 = 239.9 hrs, and 2021 = 204.5 hrs

Empirical Bayesian Kriging: Incidental predator observations

Across all three years, avian predator detections were mainly spatially overlapping shorebird nest placements (Figure 4). The predator detection index appeared to be higher and spanned a greater extent in 2018 and 2019 relative to 2021. The mean avian predator index among pooled shorebird nests was lowest in 2018 (1.78 +/- 0.152 SE) greatest in 2019 (2.32 +/- 0.194 SE), and marginally lower in 2021 (2.06 +/- 0.213 SE) (Figure 4). By contrast, the avian predator index had lower mean across the entire prediction surface compared to values at shorebird nests (mean_{2018} = 0.954+/- SE 0.060, mean_{2019} = 1.409+/- SE 0.081, mean_{2021} = 1.25+/- SE 0.076) (Figure 4).

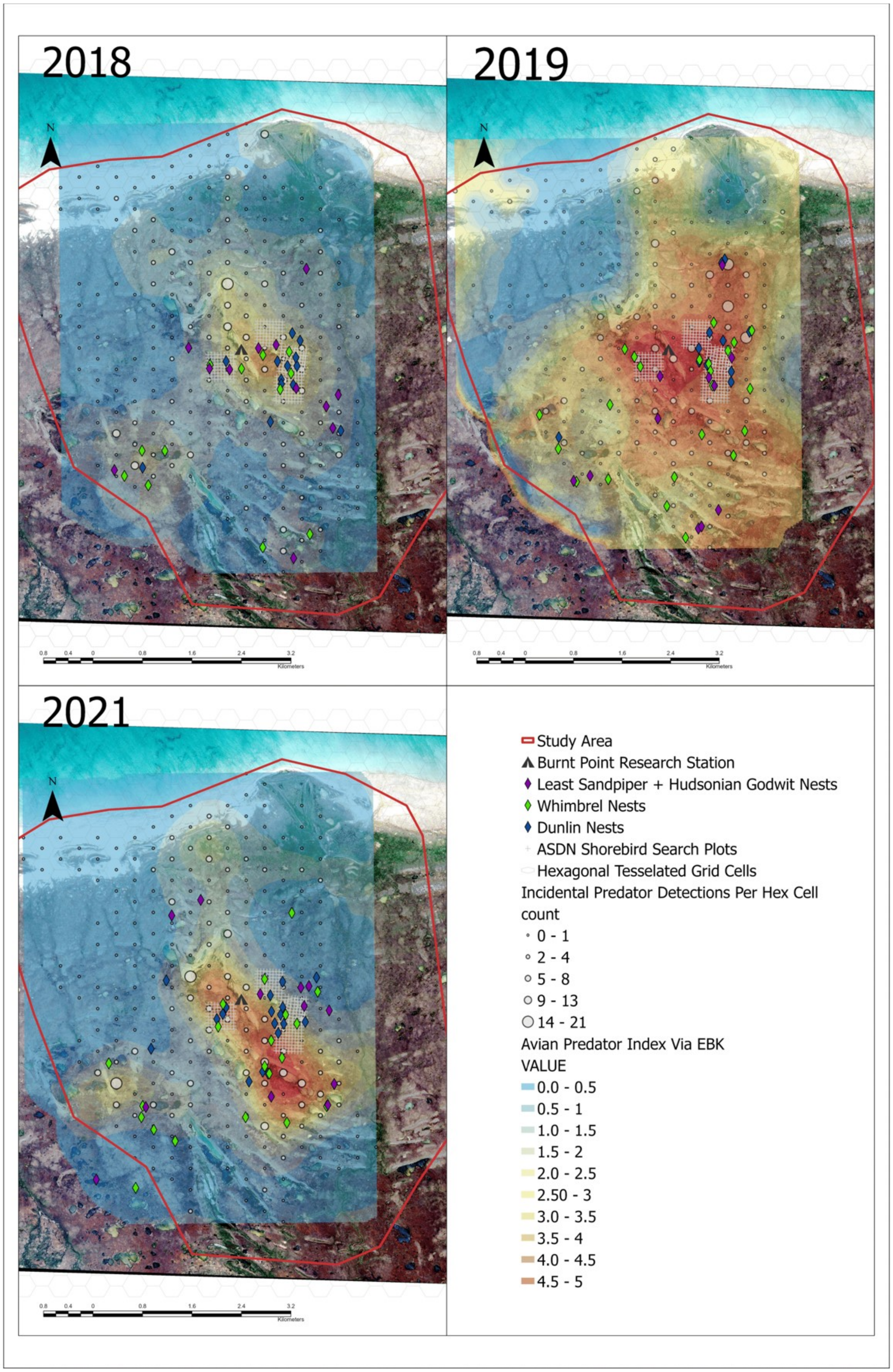

Figure 4: Shorebird nest placements in 2018-2021 relative to avian predator index estimated using empirical Bayesian kriging (EBK). Extracted from incidental observations along hexagonal tessellated grid.

Effects of alternate prey, predators, shorebird species and nest site on shorebird predation risk

The best supported models with Δ AICc < 2 included a vegetation-only model, a model with vegetation plus interaction terms for year x alternate prey and year x predators, and a model with only these interaction terms (Table 3). Among the habitat parameters, graminoid fen and shrubby graminoid fen showed marginally significant effects on predation risk (Table 5). Predation risk was positively related to the amount of graminoid fen, which is consistent with the strong habitat selection of nest sites (slope = 0.154, intercept = 0.459) (Figure 6A), and negatively related to the percent shrubby graminoid fen (slope = -0.400, intercept = 0.619) (Figure 6A, Figure 9). Other vegetation types evaluated showed no significant relationship with predation probability (Table 6). As an independent variable, year did not have a significant effect on predation probability (Table 6). However, both small mammal and predator indices and their interaction terms (year) had marginally significant effects on probability of predation (Table 5). The pattern of risk of the interaction between year and indices alone (model 1.3) followed a similar annual pattern with to the model considering vegetation class in addition to indices with interaction (Model 1.4) with 2018 displaying the greatest instances of predation probability explained by the interaction term but did not seem to increase as SMN index increased with a relatively isometric relationship ($\text{slope}_{2018} = 0.082$, $\text{intercept}_{2018} = 0.6720$); while 2019 produced a positive risk relationship with the small mammal index ($\text{slope}_{2019} = 0.641$, intercept = 0.440). By contrast, 2021 produced lowest instances of predation probability with a negative relationship with predation risk and the small mammal index ($\text{slope}_{2021} = -0.626$, $\text{intercept}_{2021} = 0.608$) (Figure 6B). Relative to predator index there appears to exhibit the opposite annual pattern with SMN indices. Probability of nest predation was negatively associated with the predator index in 2018 and 2019, whereas, the relationship was slightly positive or an isometric relationship in 2021 ($\text{slope}_{2018} = -2.79$, $\text{slope}_{2019} = -5.67$, $\text{slope}_{2021} = 0.0714$).

Table 3: Model comparisons (AICc) of effects by multivariate combination on shorebird predation probability and nest site selection (RSF)

Model	Model Variables	K	AICc	Δ AICc	AIC Wt	LL
Predation probability						
1.0	Vegetation	6	150.82	0.00	0.34	-69.41
1.4	Vegetation+ SMN Index*Year + Predator Index*Year	11	151.10	0.28	0.29	-64.55
1.3	SMN Index*Year + Predator Index*Year	6	151.46	0.64	0.24	-69.73
1.2	SMN Index + Predator Index + Year	4	153.35	2.53	0.10	-72.67
1.1	SMN Index + Predator Index + Year + Nest Species	7	155.50	6.68	0.03	-70.75
Shorebird nest site selection (RSF)						
2.0	Vegetation + SMN Index + Predator Index +Year	9	466.22	0	0.73	-224.11
2.2	Vegetation + SMN Index*Year + Predator Index*Year	11	468.22	2.00	0.27	-223.11
2.1	Vegetation	6	484.12	17.90	0.00	-236.06
2.3	SMN index*Year + Predator index*Year	9	533.97	67.74	0.00	-255.885

The interaction between small mammal nest index and year revealed a relationship between the probabilities of predation on shorebird nests that appears dependent on the stage of small mammal cycling (Figure 5A). There was a marginally significant interaction between year and small mammal index on shorebird nest predation risk (p = 0.0574) (Table 4). In 2018, a high abundance year for small mammals (Figure 1, Figure 5A), there was a positive relationship between small mammal index near nests and predation probability on shorebird nests with the highest mean predation probability ($mean_{2018}$ = 0.732 +/- 0.016 SE, slope = 0.271, intercept = 0.674) (Figure 7A). By contrast, 2019 had lower predation probability than 2018 but had similar patterns. As small mammal abundances and indices begin decline in 2019 (Figure 1, Figure 5A), there was also a positive relationship between SMN index on predation probability ($mean_{2019}$ = 0.574 +/- 0.026 SE, slope = 0.391, intercept = 0.497) (Figure 5A). In 2021 however, a relatively low small mammal abundance year (Figure 1, Figure 5A), showed the lowest nest predation probability ($mean_{2021}$ = 0.518 +/- 0.15 SE) and a negative relationship with SMN index (slope = -0.604, intercept = 0.604) (Figure 16a). Unlike the small mammal index, predation probability explained by the interaction between year and the avian predator index did not reveal a significant relationship (p = 0.893) (Table 4). However, plotting the separate slopes for each year as a function of the spatial relationship between each nest and the predator index suggested a possible negative effect of avian predator indices on nest predation in 2018 and 2019 but no apparent relationship in 2021 (Figure 5B).

Table 4: Shorebird nest predation variables estimating risk of nest predation from 2018 -2021 via GLM. Year and predator/alternate prey indices are evaluated as interaction effects.

Shorebird nest predation			
Predictors	**Estimate**	**Statistic**	**p**
(Intercept)	4.422 x 10^2	-0.671	0.573
Year	-0.214	-0.562	0.574
Predator Index	-1.815 x 10^-2	0.893	0.123
Small Mammal Nest Index	5.871 x 10^3	1.900	**0.057**
Predator Index : Year	1.190	1.540	0.123
Small Mammal Nest Index : Year	-2.90	-1.900	**0.057**
Observations	111		
R^2 McFadden's	0.0695		

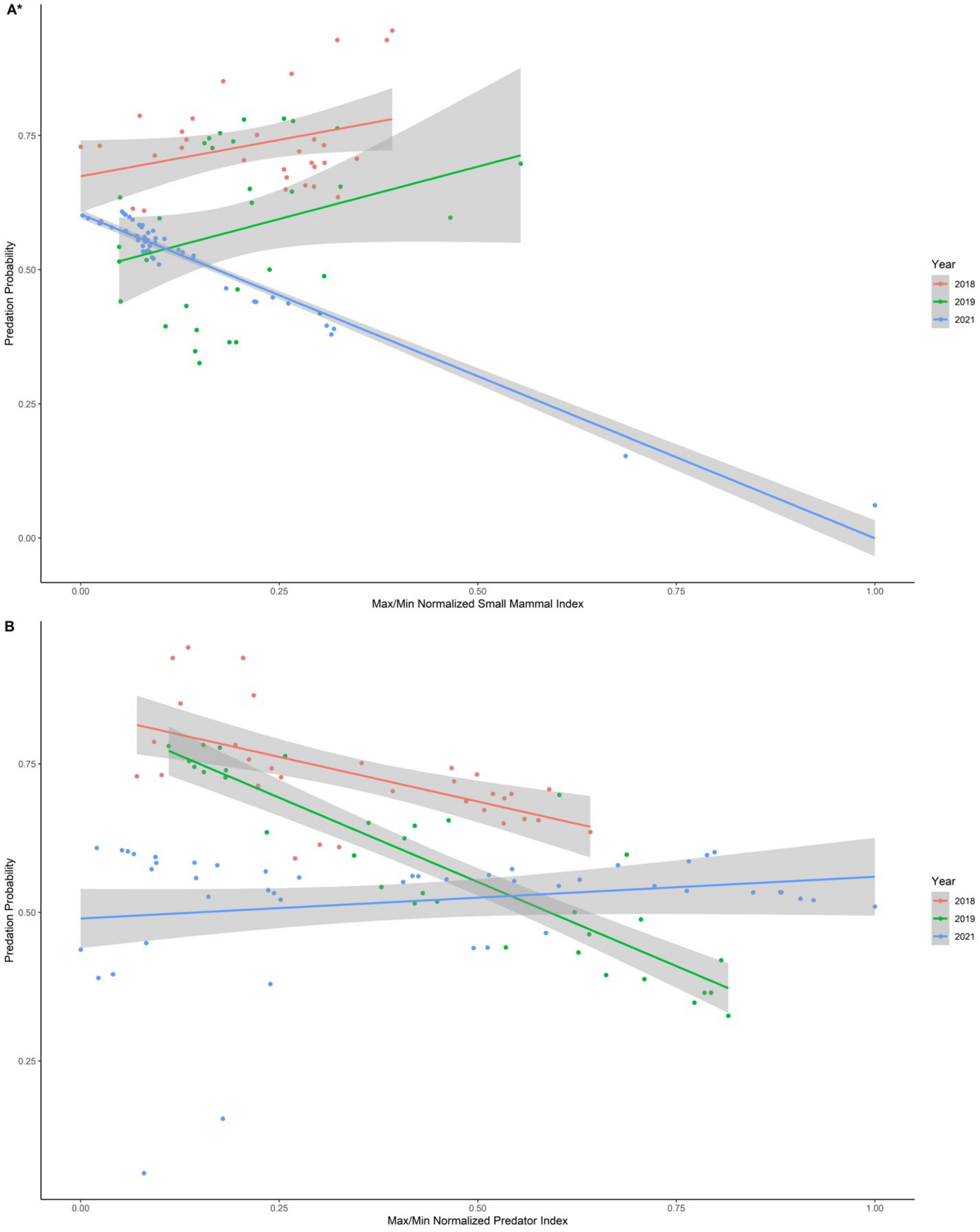

Figure 5: Interaction effect between year and A) small mammal nest and B) predator indices. Coloured lines indicate regression predicted by GLM +/- 95% confidence (grey) (*indicates significance).

Table 5: Shorebird nest predation due to vegetation cover and predator/alternate prey indices effects estimating risk of nest predation from 2018 -2021 via GLM. Year and indices estimates are evaluated as interaction effects

Shorebird nest predation			
Predictors	**Estimate**	**Statistic**	**p**
(Intercept)	3.532 x 10^2	0.384	0.701
Year	-0.169	-0.371	0.710
Predator Index	-3.019 x 10^3	-1.80	**0.0752**
Small Mammal Nest Index	7.926 x 10^3	1.744	**0.0810**
Predator Index : Year	1.494	1.778	**0.0753**
Small Mammal Nest Index : Year	-3.924	-1.744	**0.0811**
Tundra Heath	-1.177 x 10^1	-1.431	0.152
Tall Shrubs	2.284 x 10^1	0.652	0.514
Low Shrubs	-7.90 x 10^1	-0.955	0.340
Graminoid Fen	-1.041 x 10^1	-1.821	**0.0687**
Shrubby Graminoid Fen	-1.158 x 10^1-	-2.038	**0.0415**
Observations	111		
R^2 McFadden's	0.139		

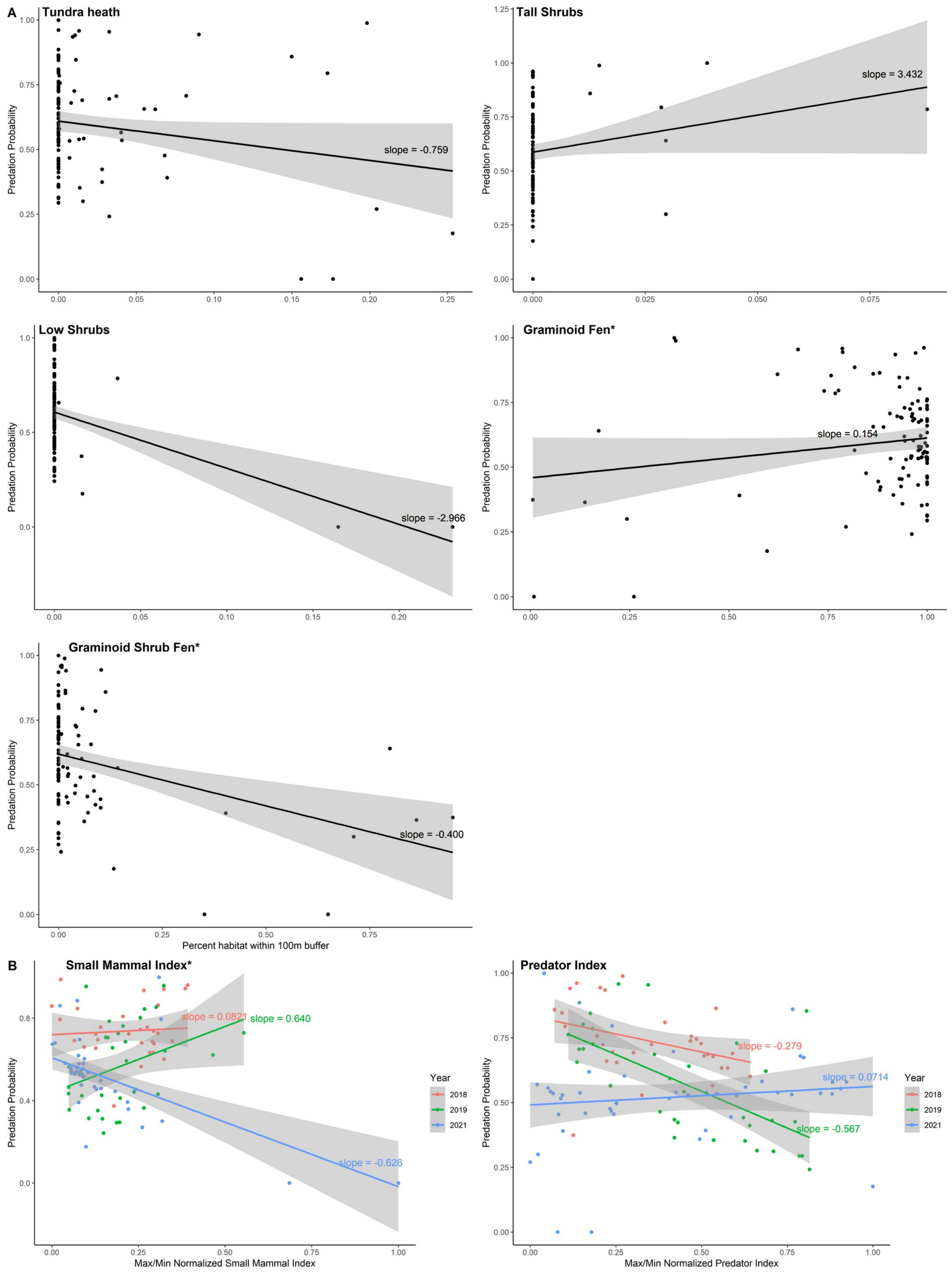

Figure 6: Nest predation risk of shorebirds explained by (A) percent vegetation cover and (B) year-index interaction effects within 100m buffers. Black line indicates regression predicted by GLM +/- 95% confidence (grey) (* indicates a significant model at p = 0.05).

Species-specific effects of predation on Dunlin and Whimbrel

Predator indices did not significantly influence predation risk in either Whimbrel or Dunlin (p>0.05) (Table 6, Figure 7B Figure 8B). Small mammal index, however, significantly influenced predation probability in Dunlin but not in Whimbrel. Predation probability in Dunlin had a significant and highly positive relationship with small mammal index in 2018 ($slope_{2018}$ = 1.367), an intermediately positive relationship in 2019 ($slope_{2019}$ = 0.501), and a highly negative relationship in 2021($slope_{2021}$ = -0.904) (Table 8, Figure 7A). Mirroring the temporal trends in predation probability, relative abundance of mall mammal near Dunlin nests in 2018 ($mean_{2018}$ = 3.9, $Range_{2018}$ = 1.6 - 4.8) and 2019($mean_{2019}$ = 3.7, $Range_{2019}$ = 1.2 - 6.6) far exceed that of 2021($mean_{2021}$ = 1.6, $Range_{2021}$ = 0.7 - 3.7) (Figure 7A).

Table 6: GLM summaries for the effects indices of small mammals/predators, and their interaction with year, on Dunlin and Whimbrel nest predation.

Dunlin nest predation

Predictors	Estimate	Statistic	p
(Intercept)	-3.238 x 10^3	-1.450	0.147
Year	1.60	1.451	0.147
Predator Index	7.364 x 10^2	0.241	0.809
Small Mammal Nest Index	1.101 x 10^4	2.200	**0.028**
Predator Index : Year	-0.366	-0.242	0.809
Small Mammal Nest Index : Year	-5.006	-2.200	**0.028**
Observations	40		
R^2 McFadden's	0.147		

Whimbrel nest predation

Predictors	Estimate	Statistic	p
(Intercept)	1.213 x10^3	-1.032	0.302
Year	-.0600	-1.032	0.302
Predator Index	-3.504 x10^3	-1.596	0.110
Small Mammal Nest Index	1.387 x 10^3	0.455	0.649
Predator Index : Year	1.734	1.596	0.110
Small Mammal Nest Index : Year	-0.686	-0.455	0.649
Observations	54		
R^2 McFadden's	0.0341		

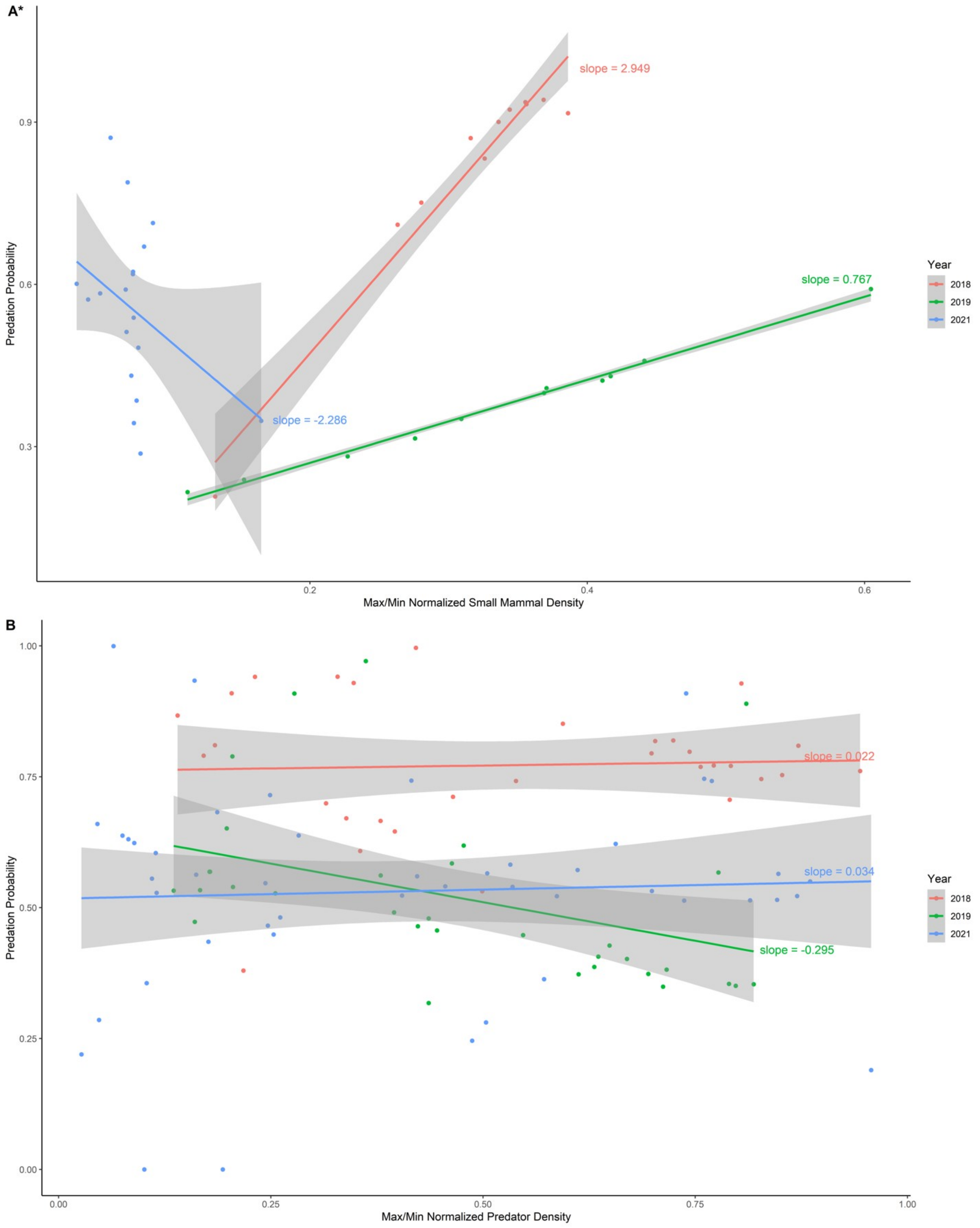

Figure 7: Dunlin nest predation risk explained by the interaction effect between year and: A) small mammal and B) predator indices. Coloured lines indicate regression predicted by GLM +/- 95% confidence (grey) (*indicates significance).

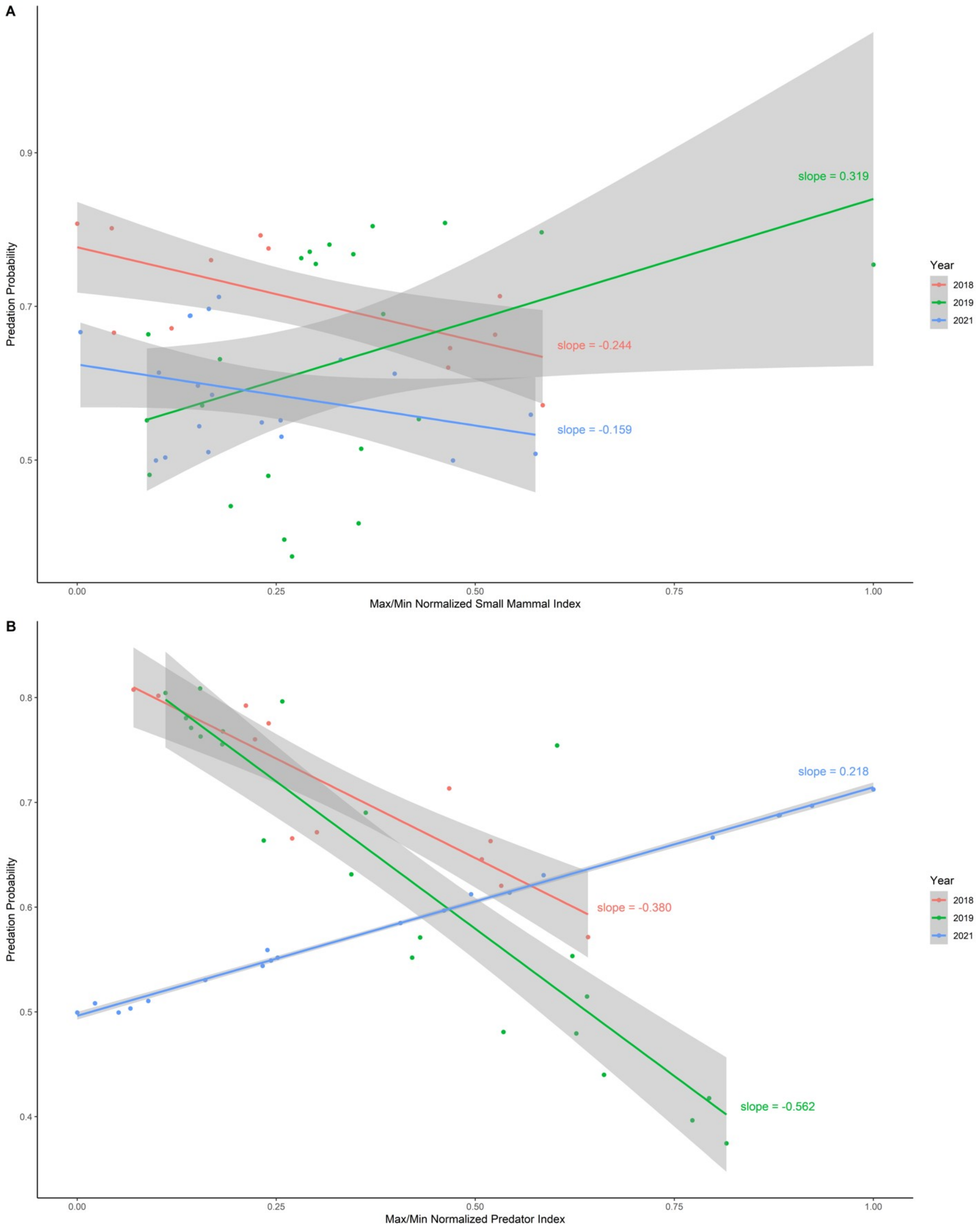

Figure 8: Whimbrel nest predation risk explained by the interaction effect between year and: A) small mammal and B) predator indices. Coloured lines indicate regression predicted by GLM +/- 95% confidence (grey) (*indicates significance).

Effects of vegetation, predator and alternate prey indices on shorebird nest site selection

The most parsimonious model of shorebird nest site selection included terms for vegetation type, predators, SMNs and temporal effects (Table 3). Shorebird nest site selection has a significant positive relationship with percent cover of graminoid fen (beta = 2.760, 95% CI [0.813, 4.705], p = 1.190 x 10^-3), and with predator index (beta = 2.300, 95% CI [1.370, 3.230], p = 1.26 x 10^-6). However, contextually, predator indices cannot be interpreted as selected for nor avoided. Rather, logistic regression reveals a spatial relationship whereby shorebird nest placements coincide with higher values of predator index (Figure 9). Shorebirds used tundra heath for their nests less than their availability, displaying a negative association with high significance (beta = -6.834, 95% CI [-11.592, -2.075], p = 4.879 x 10^-3) (Figure 9). The remaining land cover types, shrubby graminoid fen, low shrubs and tall shrubs did not significantly influence nest selection (p>0.05) (Figure 9). Additionally, SMN indices did not significantly influence shorebird nest placements (p>0.05) (Figure 9).

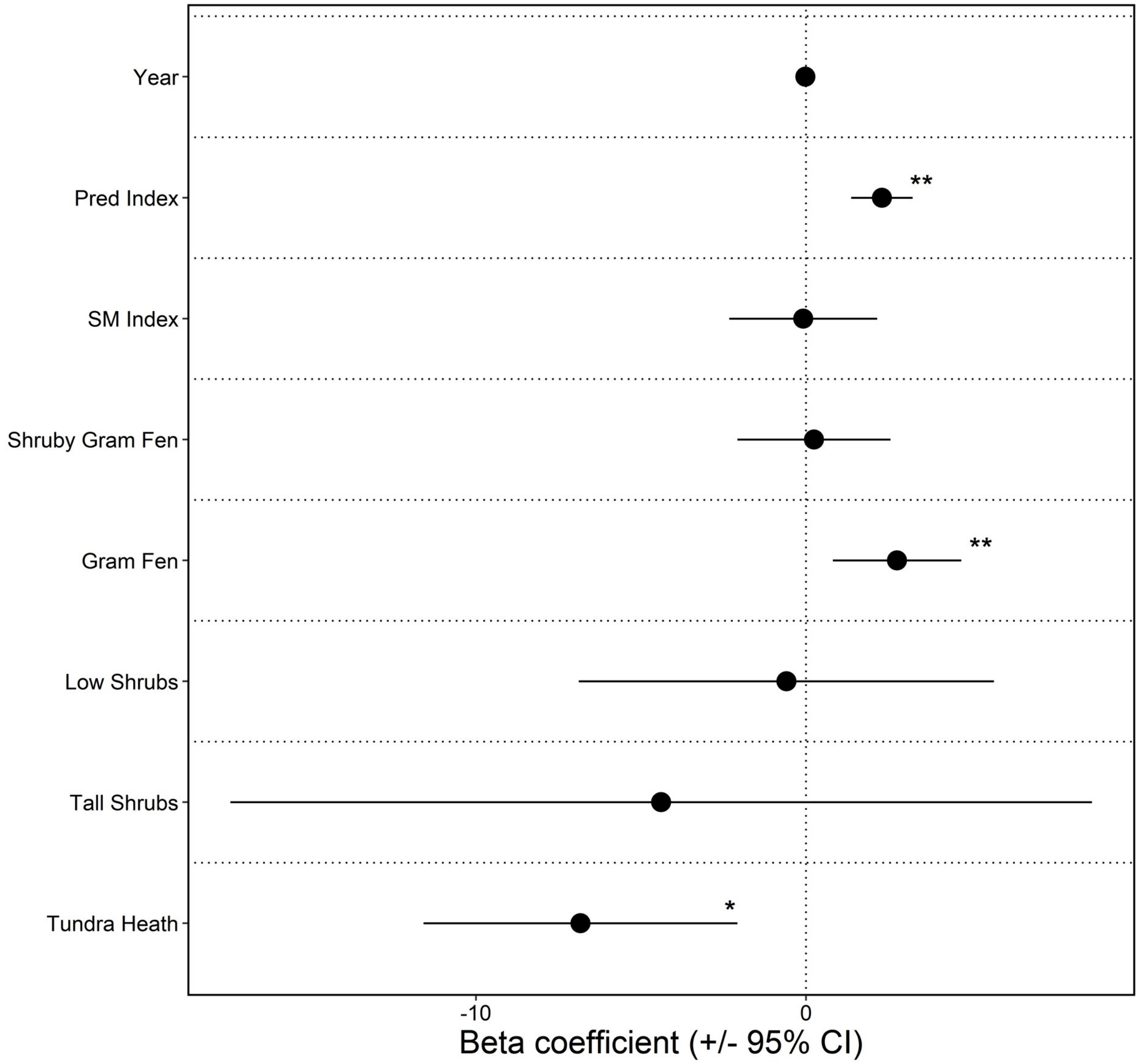

Figure 9: Explanatory variable beta coefficients +/- 95% confidence intervals that influence nest selection (placement) of shorebirds 2018-2021. Vertical dotted line indicates a coefficient of 0 meaning no selection (where >0 is selection and <0 is avoidance) (*indicates significance).

4: DISCUSSION

Through overlaying spatially explicit indices of small mammals on the locations of nesting shorebirds in a sub-arctic landscape, I have revealed elevated shorebird predation risk when small mammal relative abundance was high. This suggests that apparent competition between small mammals and shorebirds for sub-arctic habitats can elevate predation risk- where breeding shorebirds may be incidental prey when attracted by presence of small mammals. I also show that the strength of these associations between shorebird predation risk and the distribution of small mammals may be species-specific. Dunlin appeared more vulnerable to higher predation risk when they co-occurred with small mammals than Whimbrel (Figure 7 and 8). I also showed annual variation in the distributions of small mammal alternate prey that corresponded to different phases of the small mammal reproductive cycle. As these differences in distribution of small mammals were associated with annual differences in patterns of nest loss in shorebirds, this implies that the risk landscape for shorebirds co-varies with the reproductive cycles of small mammals. Within the southernmost breeding range of these two focal shorebird species, I used camera monitoring to reveal a predator community that is dissimilar to higher latitude sites within shorebird breeding ranges.

What is the nature of the multi-prey/multi-predator relationship?

The spatial relationship between predation of shorebird nests and small mammal prey availability was not consistent with conventional interpretations of the alternate prey hypothesis and counter to my predictions. Other studies focusing on the relationship of shorebird nest predation risk and alternate prey availability reported a general reduction of predation risk in shorebirds when small mammals were more available (McKinnon et al. 2014; Lamarre et al. 2017; Weiser et al. 2018; Flemming et al. 2019c). However, when both shorebird nests and indices of small mammals were spatially explicit such as my analysis, alternate prey indices were positively related to the probability of predation. Therefore, the observed elevation in predation risk of shorebirds is more consistent with the apparent competition hypothesis as a seemingly numerical response to shifts in prey community distribution. This relationship persisted despite the consistent spatial separation of the areas of greatest abundance of small mammals with the areas of nesting shorebird habitat. The spatial separation is presumably attributed to differences in habitat preferences between shorebirds and small mammals because Meadow Voles, the main small mammal in the study area, prefer xeric habitats with more vegetation cover than shorebirds (Lin and Batzli 2001, 2004). Despite spatial separation, small mammals were more evenly distributed across the study area in years of high relative abundance. This more even distribution meant that there was increased overlap with shorebird nest sites in years of high small mammal abundance and may be explained by small mammal migration due to resource limiting factors (Lin and Batzli 2004; Morris 2020). By contrast, during years of lower small mammal abundance, there was less overlap between shorebird nest sites with relatively lower small mammal indices at shorebird nest sites and this lower decrease in overlap coincided with lower shorebird predation rates. Such annual variation in the distribution of small mammals has not been previously described and provides valuable insights as to how these distributions may reflect the space use of predators. Indeed, such patterns of the distribution small mammal availability may explain predator activity patterns observed among predators (Brown 2022, Beardsell 2023, Delude de Broin 2023). Because small mammals are an important food source in the sub-high arctic (Ims and Fuglei 2005), greater understanding of the variation in spatial availability will improve understanding of the subarctic/arctic food web, specifically the spatial relationships of species with shared predators.

The increased predation risk on shorebird nests when small mammal abundance was high, suggests that the cyclical shifts in small mammal abundance may have a previously unreported negative effect on shorebird nest success when they co-occur with alternate prey with patterns consistent with predator mediated apparent competition. The difference in my results compared to those of other study systems may be due to the different suite of predators in our study area and that high abundance of small mammals may not alleviate predation risk on shorebirds at this sub-arctic location. While several other studies conducted at higher latitude sites have shown that shorebirds benefit through high nest success when lemming populations are high (McKinnon et al. 2014; Lamarre et al. 2017; Weiser et al. 2018;

Flemming et al. 2019a), terrestrial predators like arctic fox and red fox can continue to capture prey past the stage where they are satiated because they cache and hoard food (Beardsell 2021). Shorebird predation risk increases with proximity to (Arctic) fox dens and decreases with low small mammal abundance at shorebird nests due to their respective differences in predator activity (Brown 2022). However, all shorebird nests in my study area were within 5 km of known (Red) fox dens, suggesting that variation in small mammal abundance (both spatially and annually) was more influential to shorebird predation risk than fox activity or proximity to dens.

While the abundance of small mammals reflected the spatial variation in nest predation on shorebirds, across years, the pattern of overall predation was more complicated. Despite the year with the highest rates of nest predation (2018) coincided with the highest small mammal availability to predators at shorebird nest sites, the year with the lowest small mammal availability (2021) had intermediate levels of nest predation when compared to a year with intermediate small mammal availability (2019, Figure 1, Figure 2). Thus, other contributing factors may include differences in risk according to annual differences in predator composition and space use. Additionally, this study does not accurately capture the functional response in predator prey selection and population dynamics in lieu of depletion of primary food sources which may vary greatly (Gilg et al. 2006, 2009). Despite these caveats to my analysis, I demonstrate that predators may still consume incidental prey including shorebirds even when primary prey like small mammals are abundant. Therefore, evaluating the spatial relationship between multiple prey species is a key component to understanding the contributors to predation risk in declining species within the home ranges of their shared predators and predator space use decisions.

Species specific patterns in shorebird nest predation risk

Differences in nest defence strategies between Whimbrel and Dunlin may affect predation risk. Dunlin may be more vulnerable to increases to predation risk when SMN indices are high. Indeed, species-specific differences related to the risk associated with shifts in alternate prey and predators reveal some species are more vulnerable to these shifts than others, consistent with my prediction (Smith et al.

2007). From camera traps, Whimbrel were observed to repel numerous avian predation attempts through chasing and calling (Larsen and Moldsvor 1992). By contrast, Dunlin perform no such antipredator behaviours and flee from nests when approached by predators and/or researchers in the field. Such fleeing behaviour was observed during both nest searches and via cameras captures. Therefore, I suggest that Whimbrel may mitigate the increase in predation risk by avian predators and species that rely primarily on crypsis including Dunlin are especially vulnerable to shifts in alternate prey availability. This supports the prediction that factors that affect nest predation risk including alternate prey availability vary among shorebird species (Holt and Bonsall 2017). This was further supported in my study when comparing the better fit of the relationship between small mammal abundance and predation probability for Dunlin than Whimbrel (Figures 7 and 8).

The lateral concealment provided by graminoids for nesting Dunlin may have some protection against detection by terrestrial predators. This concealment was demonstrated by camera traps. From camera footage, Red Fox appearing on nest cameras did not necessarily result in predation, unlike Northern Harrier. Indeed, camera trap footage reveals that Northern Harrier were the cause of more Dunlin nest failures than Red Fox during the time of deployment. This suggests that Dunlin may be specifically vulnerable to avian predators including Northern Harrier relative to terrestrial predators including Arctic and Red Fox presumably because lateral concealment is less effective against detection by avian predators. This vulnerability to avian predators especially when co-occurring with small mammals may be key in elucidating contributors to Dunlin decline (Weiser 2020).

By contrast, Whimbrel experienced predation from both Harrier and Red Fox from camera trap footage. On occasion, Whimbrel were capable of deterring predation attempts by avian predators but appeared to be unable to defend against terrestrial predators including Red Fox. Additionally, Whimbrel nests and eggs are large and incubating adults are conspicuous. Camera footage revealed that adult Whimbrel at the nests perform regular scans of their surroundings presumably to detect possible threats. These scans were detected on cameras as erect postures and head saccades. When potential predators approached, Whimbrel left the nest cup to fly out to intercept. On occasion, conflict between avian predators and Whimbrel occurred at the nest cup, interactions which were captured by cameras. My camera observations suggest that Whimbrel often flew to attempt to intercept avian predators, but when foxes were observed, Whimbrel leave the nest cup and did not engage foxes in defence resulting in predation of the nest. These differences in responses are presumably linked to the relative threats to the adult Whimbrel (Giroux 2016).

Characterizing predators of shorebird nests and their spatial relationship

The biogeographical context of my study reveals novel species interactions where species at the southern extent of their breeding range are intersecting with the northern range extent of more southern predators. This emergent predator prey community structure is integral in understanding the march of destabilization - especially throughout sub-arctic ecozones. My camera traps captured both expected an unexpected shorebird nest predators. Red Fox emerged as a primary terrestrial nest predator (Appendix IF2). The avian predator community differed from other arctic-breeding shorebird ranges. I found that Northern Harrier represent a major source of nest predation risk for both Dunlin and Whimbrel. Northern Harrier has not previously been identified as a significant shorebird nest predator under the alternative prey hypothesis (Angelstam et al. 1984), whereas, at higher Arctic locations, Snowy Owl (*Bubo scandiacus*) is the main avian predator documented to shift from small mammals to bird predation in the absence of sufficient small mammal prey (Bêty et al. 2001). Confirmed predation by harriers on shorebird nests has been observed on Semipalmated Sandpiper (*Calidris pusilla*) in the Alaskan archipelago (Liebezeit and Zack 2008) but to my knowledge, they have not been observed as a major predator of Whimbrel and Dunlin nests. Parasitic Jaeger and various species of gull are common nest predators of shorebirds at higher latitudes. However, I observed predation by Jaeger only once by camera traps and gulls were not observed to depredate any shorebird nest. Conversely, Liebezeit and Zack (2008) reported that Northern Harrier represented few instances of shorebird nest predation in the arctic. These findings provide insight on the potential shift of the predator structure of arctic shorebirds that nest at lower latitudes. Burntpoint marks the southernmost point of both Dunlin and Whimbrel where both Northern Harriers and Red Fox overlap the ranges of these shorebird species. This study serves as an indication of how shorebird predation risk may be altered as new predators continue to migrate further into higher latitude shorebird breeding ranges (Prugh et al. 2009).

Although areas of high avian predator activity heavily coincided with nest sites, the abundance of avian predators did not significantly influence nest predation. This suggests that avian predator presence alone may not sufficiently indicate predation risk in shorebirds despite the strong co-occurrence with nests. The annual variation in predator indices suggests that predator space use varies temporally. This is corroborated by shifts in home ranges of terrestrial predators in the sub/arctic according to prey availability but such shifts are not well understood for avian predators including Northern Harrier, especially within the low latitude extreme of shorebird breeding ranges (Prugh et al. 2009; Sokolov et al. 2016). Therefore, predator functional responses including search effort in addition to prey detection may be important in spatially disentangling predator presence and predation risk. Although predator observation coverage was well distributed across the study area, and documented areas with and without predator detection, there may have been unknown bias introduced in search effort relative to where observers spent most time in the study area performing other field activities. Due to the nature of data collection, multiple protocols were simultaneously conducted including nest checks, artificial nest placements, and small mammal sampling. Future studies of this nature will benefit from more targeted predator surveys that ensure consistent and spatially dispersed search effort across the area of inference. Further analysis focused on top-down effects on prey species risk should assess the spatial relationships of the predator community in addition to multi-prey distributions. Indeed, my study demonstrates the importance of evaluating not only risk associated with multi-prey distributions, but also that specific prey vulnerability may be attributed to specific predator traits. By including direct predator observations, space use of predators— i.e. their home ranges and effective number of predator present and the multi-predator-muti-prey spatial relationship outlined by my study, may be better understood.

Patterns in shorebird nest site selection

Nesting habitat did not apparently alter predation risk. However, the strong preference for fen vegetation types may explain the lack of associated variation in predation risk, contrary to my predictions. This suggests that, instead of vegetation characteristics that may compromise nest success, there may be more underlying variability within fen habitat that may affect predation risk. Despite the marginal association with graminoid fen habitats, I interpret this as an artifact of nest site selection of shorebirds. Because most nests were within graminoid fens, all predation events are therefore also associated with fen type land cover as nest site selection is a prerequisite to nest fate. This also affected AICc model selection. The interaction of predator/alternate prey indices with temporal effects in addition to vegetation type (model 1.4) was the top model for predicting predation probability. However, this model as well as vegetation exclusive effects (model 1.0) is skewed by habitat selection of shorebirds for graminoid fen. Indeed, the delta AICc between models containing habitat effects are all competitive (AICc <2) and therefore may be interpreted as equal in explanatory value (Arnold 2010). Because this study is incapable of disentangling microhabitat conditions within graminoid fens where nests are placed but also subsequently depredated, the interaction between predator/alternate prey effects (Model 1.3) is more relevant to the direct and indirect predator-prey effects at play. However, habitat preference in nest placements independent of predation may reveal antipredator decisions made by nesting shorebirds (Smith et al. 2007). Habitats suitable for nests and predation risk varies by both the nesting strategies and habitat preferences of shorebird species with responses to habitat shifts that may have far reaching implications on community structures. For example, Whimbrel face declines in preferred nesting habitat as open, graminoid and moss rich habitats transition into shrubland resulting in lower nest densities in southern-most breeding ranges (Ballantyne and Nol 2015). The significant negative association of shorebird placements with tundra heaths suggests antipredator avoidance of such habitat that may be associated with predators. Shorebirds may avoid placing nests in closer proximity to dry upland conditions because they may facilitate easier movement by terrestrial predators compared to fen with abundant surface water that may impede predator movements (Frey and Conover 2006). These patterns in nest site selection of shorebirds provides valuable insights on the potential space use of predators and the antipredator habitat structure and space use decisions of nesting shorebirds that may influence predation risk.

Conclusions

This study illustrates possible negative effects of alternate small mammal prey on shorebird nest success. Specifically, breeding arctic shorebirds including Dunlin appear to be particularly vulnerable to nest predation risk near areas of relatively high small mammal abundance suggesting that apparent competition effects may influence predators to incidentally depredate shorebird nests while focused on capturing small mammals. This result is counter to results from other studies evaluating the multi-prey interaction with small mammal cycles and shorebirds. However, spatial co-occurrence at nest sites was not considered by previous studies. My study also reveals that variability in small mammal distribution according to their reproductive cycling and abundance, affects the severity of predation risk on shorebirds by apparent competition (indirect) effects at nest sites. This has previously unconsidered implications on factors that may influence shorebird decline according to the spatial relationship between prey species. Conversely, predator presence, as indicated by my predator indices, was not found to influence predation risk in shorebirds. However, antipredator behaviours including nesting strategy may be responsible for mitigating this risk associated spatial relationship. The profile of shorebird nest predators using camera traps reveal Red Fox and Northern Harrier as potentially major predators within the southernmost breeding ranges of Whimbrel and Dunlin. This provides potentially valuable insights on how predator expansion into higher latitude ecosystems may affect resident species of the sub-high Arctic. Lastly, despite a lack of effect of vegetation on predation risk, negative associations of land cover types that facilitate predator movements suggest antipredator space use decisions made by nesting shorebirds to alleviate predation risk.

5: SUMMARY AND CONCLUSIONS

My research is the first to spatially characterize the effects of heterogeneity in alternate prey availability on nest predation risk in two arctic shorebirds, Whimbrel and Dunlin within the southern extreme of their breeding range. I found that instances of predation increased according to spatial and temporal effects related to small mammal abundance. This suggests that shared predators of small mammals and shorebirds may incidentally depredate shorebird nests when in search of small mammals, which is a primary food source within Subarctic and Arctic regions. This finding was consistent with predator mediated apparent competition - where predators may gain access to alternate prey while in search of primary prey species. I found that Dunlin may be particularly vulnerable to shifts in predation risk due to small mammal abundance near nest sites because the strength in response of predation probability varied according to small mammal abundance. By contrast, the variation in small mammal abundance did not appear to significantly affect predation in Whimbrel. My study also revealed the importance of Red Fox and Northern Harrier as predators of Arctic breeding shorebirds at their southern extend of breeding range, which have not previously been identified as important nest predators in Arctic regions. The observations in my study provides insights on the biogeographical interactions between predator and prey communities at the intersection of latitudinal extremes of species range. My findings can inform management strategies through the insights of potential novel species interactions within the Canadian Subarctic as community structures continue to shift.

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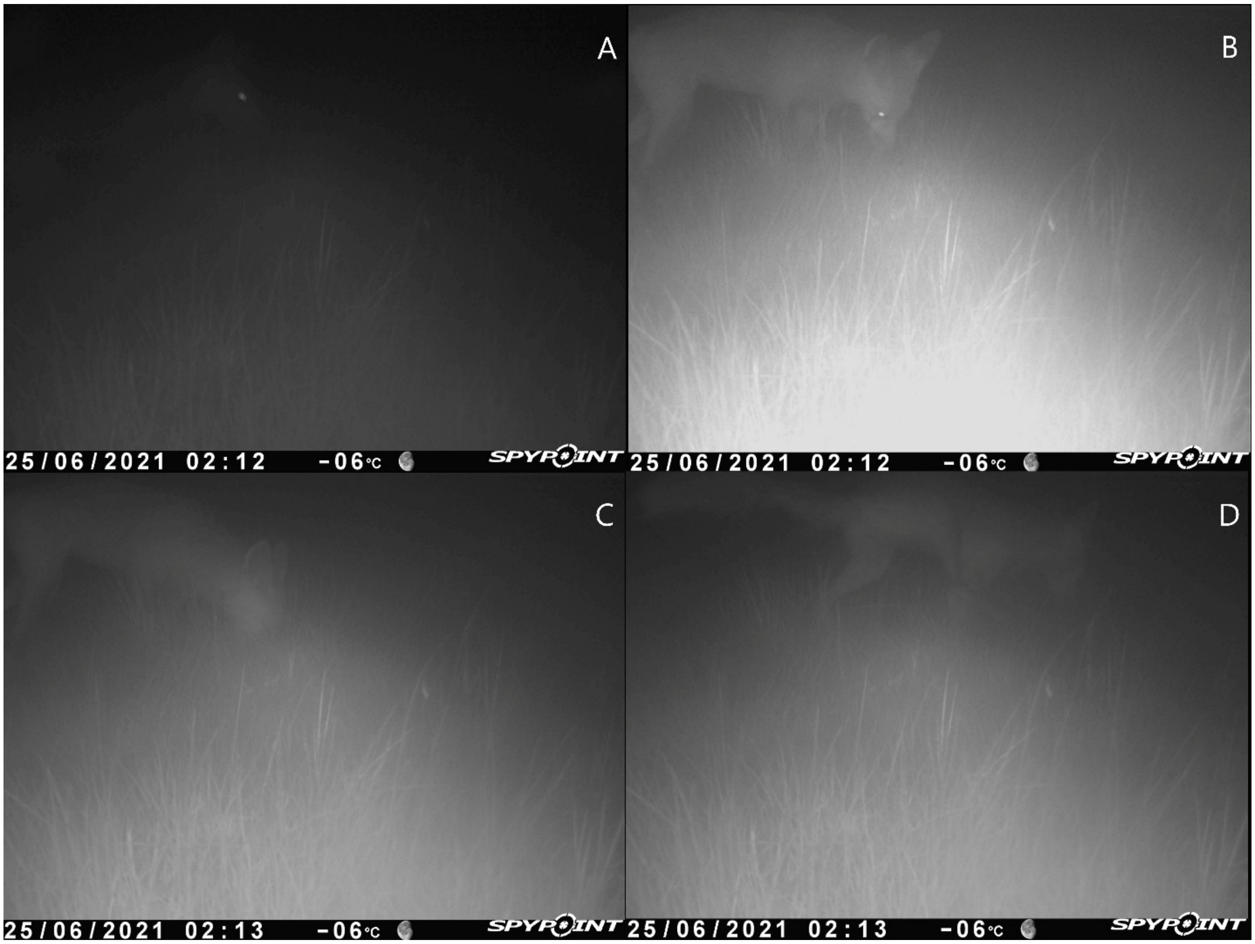
APPENDIX I: Shorebird nest Photos

Appendix IF1 Predation event captured by shorebird SPYPOINT ™ nest camera on a Dunlin nest. N. Harrier attacks Dunlin nest (A-B) and carries away the incubating adult Dunlin (C-B). All eggs were destroyed during the predation event and was confirmed through subsequent nest revisit.

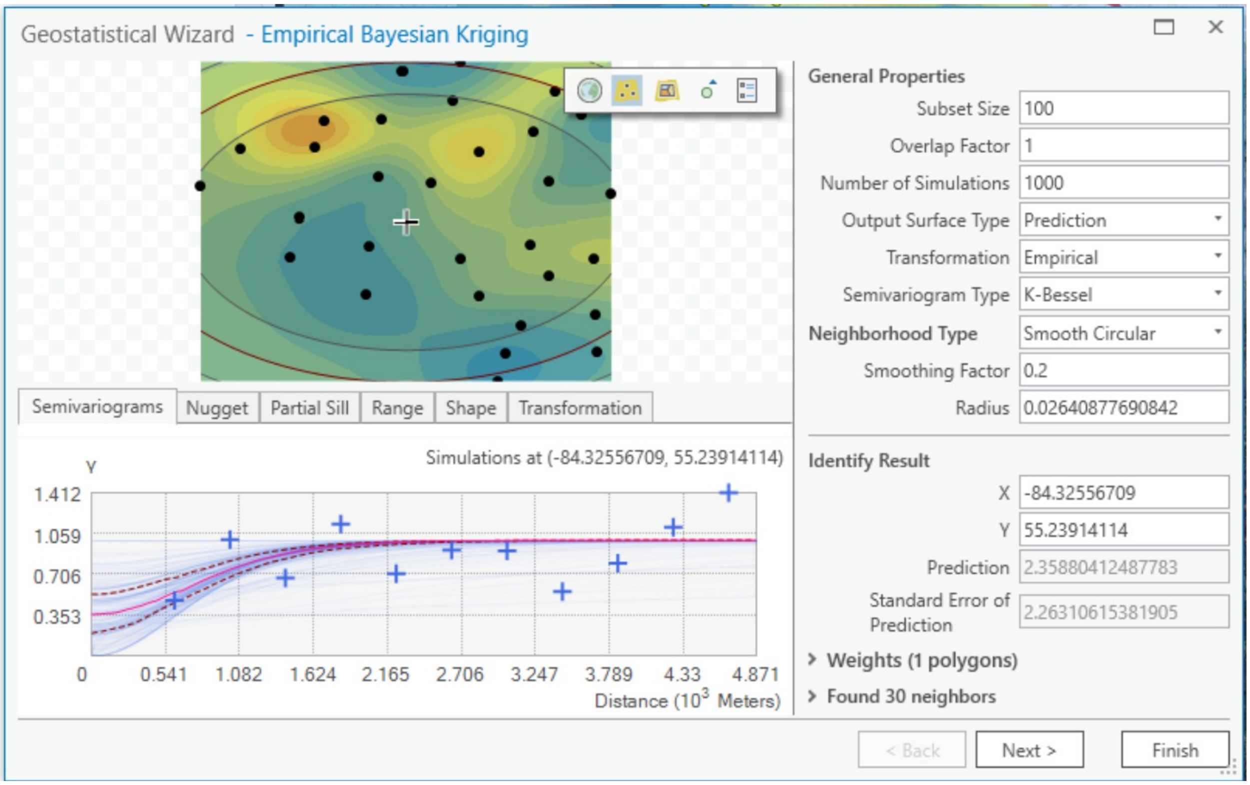


Appendix IF2 Predation event captured by shorebird SPYPOINT ™ nest camera on a Dunlin nest. R Fox can be seen triggering the night vision sensor (A-B) and proceed to depredate a Dunlin nest (C-D)

Appendix IF3 Predation event captured by shorebird SPYPOINT ™ nest camera resulting in partial predation of Whimbrel nest. Parasitic Jaeger can be seen attacking a Whimbrel nest and successfully capture one egg after being deterred by the incubating adult Whimbrel (A). A second attempt was made approximately three days later (B) where the Jaeger was capable of capturing and additional egg and can be seen carrying it away (C). The remaining two Whimbrel eggs later hatched successfully according to nest revisits.

Appendix IF4 Nest failure event captured by shorebird SPYPOINT ™nest camera resulting in trampling of a Least Sandpiper Nest. Caribou within a larger group can be seen entering the view of the nest camera (A-F) and can be seen stepping onto the location of the nest cup (circled in red). Approximately six minutes later, the adult L. Sandpiper can be seen entering the view of the nest camera (circled in blue) (G) and returned to the nest cup (circled in violet). L. Sandpiper eggs were confirmed to be destroyed during subsequent nest revisits.

APPENDIX II Semivariograms



Geostatistical Wizard - Empirical Bayesian Kriging

General Properties

Subset Size	100
Overlap Factor	1
Number of Simulations	1000
Output Surface Type	Prediction
Transformation	Empirical
Semivariogram Type	K-Bessel
Neighborhood Type	Smooth Circular
Smoothing Factor	0.2
Radius	0.02640877690842

Identify Result

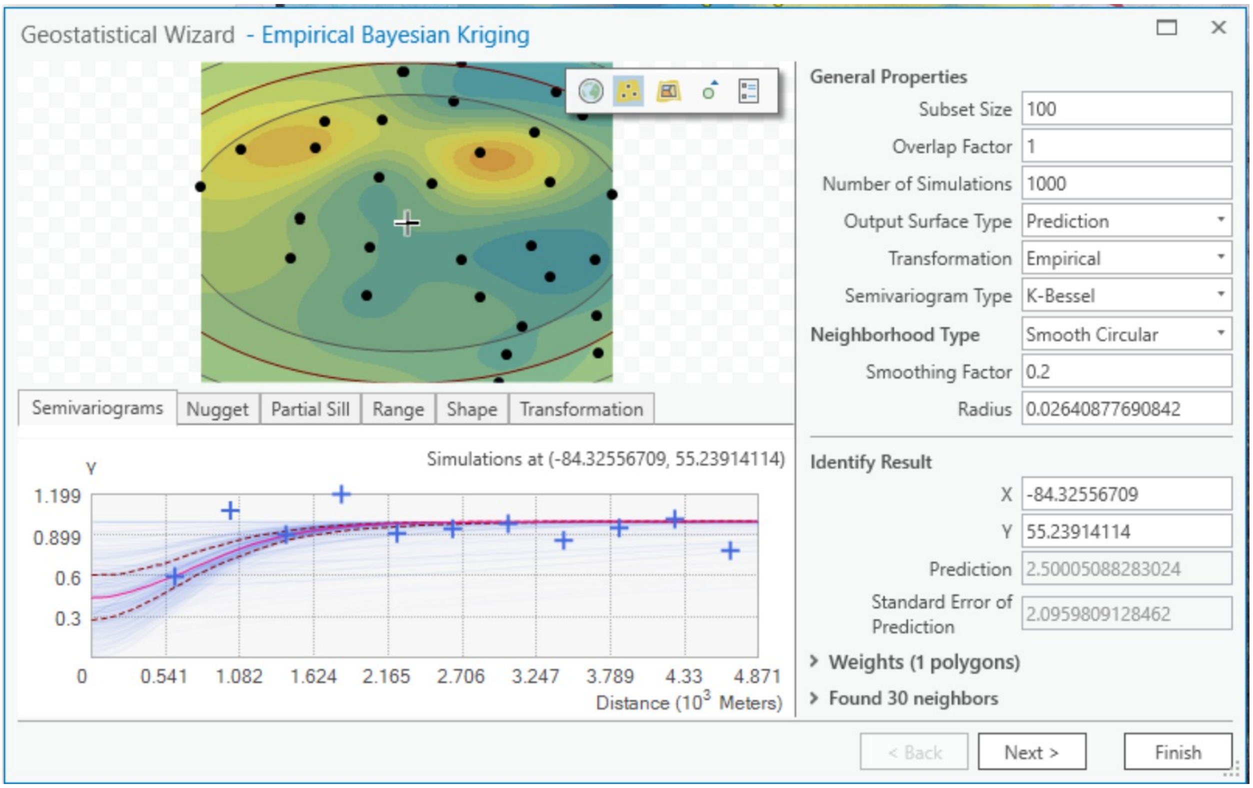
X	-84.32556709
Y	55.23914114
Prediction	2.35880412487783
Standard Error of Prediction	2.26310615381905

› **Weights (1 polygons)**

› **Found 30 neighbors**

Simulations at (-84.32556709, 55.23914114)

Appendix IIF1 2018 SMN index semivariogram and geostatistical wizard setting in ArcGIS Pro



Simulations at (-84.32556709, 55.23914114)

General Properties

Subset Size: 100
Overlap Factor: 1
Number of Simulations: 1000
Output Surface Type: Prediction
Transformation: Empirical
Semivariogram Type: K-Bessel

Neighborhood Type: Smooth Circular
Smoothing Factor: 0.2
Radius: 0.02640877690842

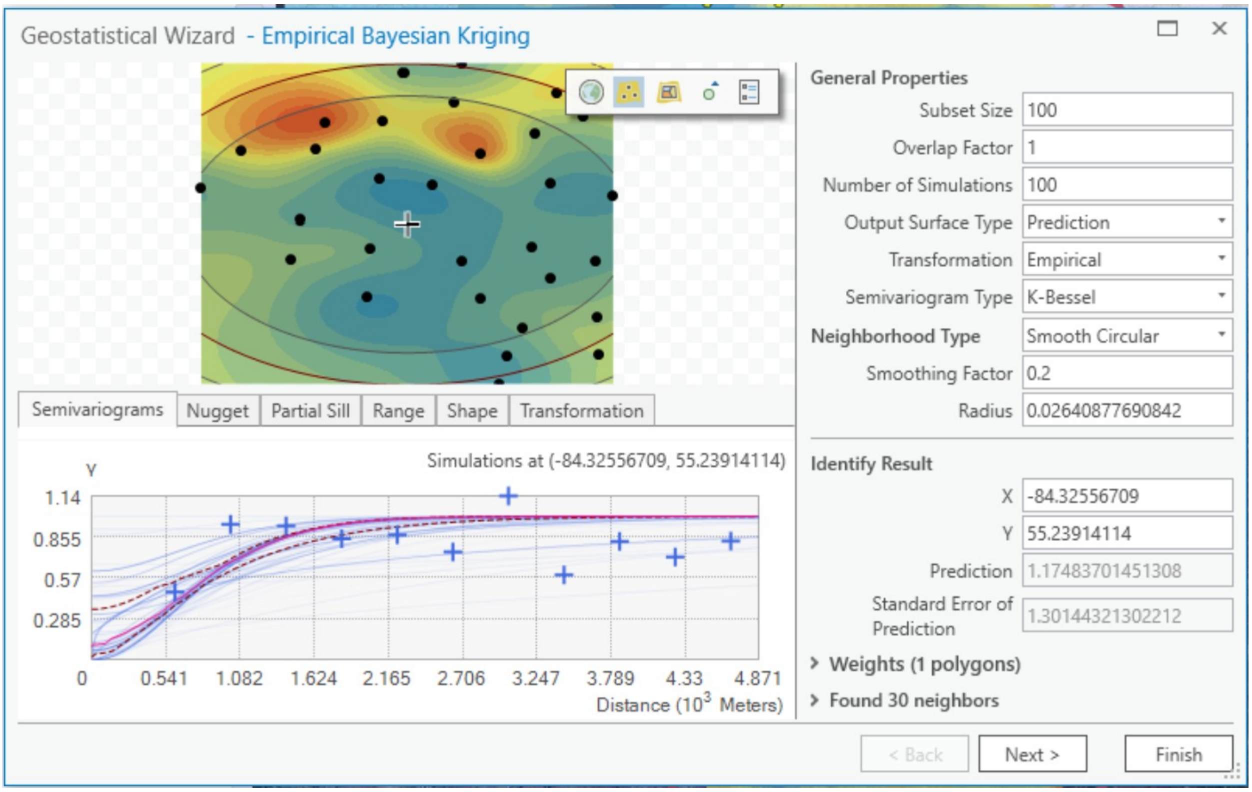
Identify Result

X: -84.32556709
Y: 55.23914114
Prediction: 2.50005088283024
Standard Error of Prediction: 2.0959809128462

› **Weights (1 polygons)**

› **Found 30 neighbors**

Appendix IIF2 2019 SMN index semivariogram and geostatistical wizard setting in ArcGIS Pro



Geostatistical Wizard - Empirical Bayesian Kriging

General Properties

Subset Size	100
Overlap Factor	1
Number of Simulations	100
Output Surface Type	Prediction
Transformation	Empirical
Semivariogram Type	K-Bessel
Neighborhood Type	Smooth Circular
Smoothing Factor	0.2
Radius	0.02640877690842

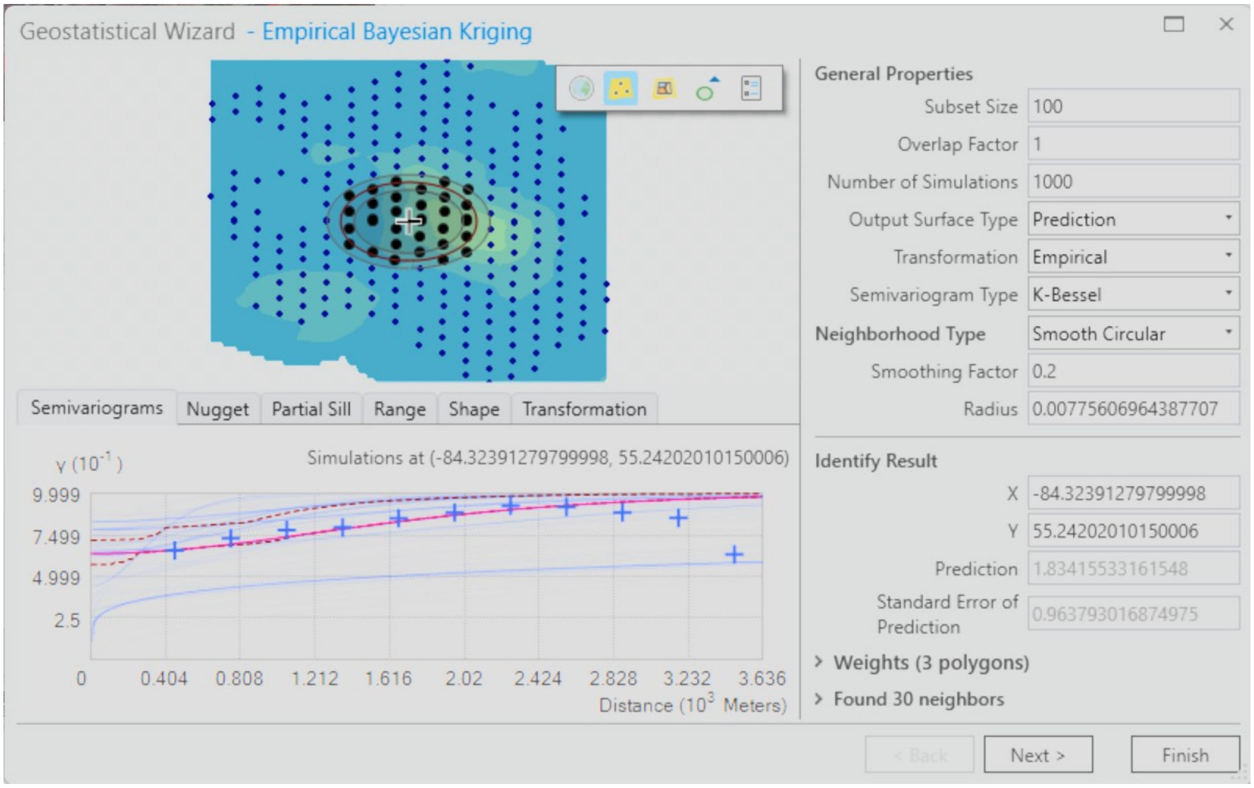
Identify Result

X	-84.32556709
Y	55.23914114
Prediction	1.17483701451308
Standard Error of Prediction	1.30144321302212

› Weights (1 polygons)

› Found 30 neighbors

Appendix IIF3 2021 SMN index semivariogram and geostatistical wizard setting in ArcGIS Pro



Geostatistical Wizard - Empirical Bayesian Kriging

General Properties

Subset Size	100
Overlap Factor	1
Number of Simulations	1000
Output Surface Type	Prediction
Transformation	Empirical
Semivariogram Type	K-Bessel
Neighborhood Type	Smooth Circular
Smoothing Factor	0.2
Radius	0.00775606964387707

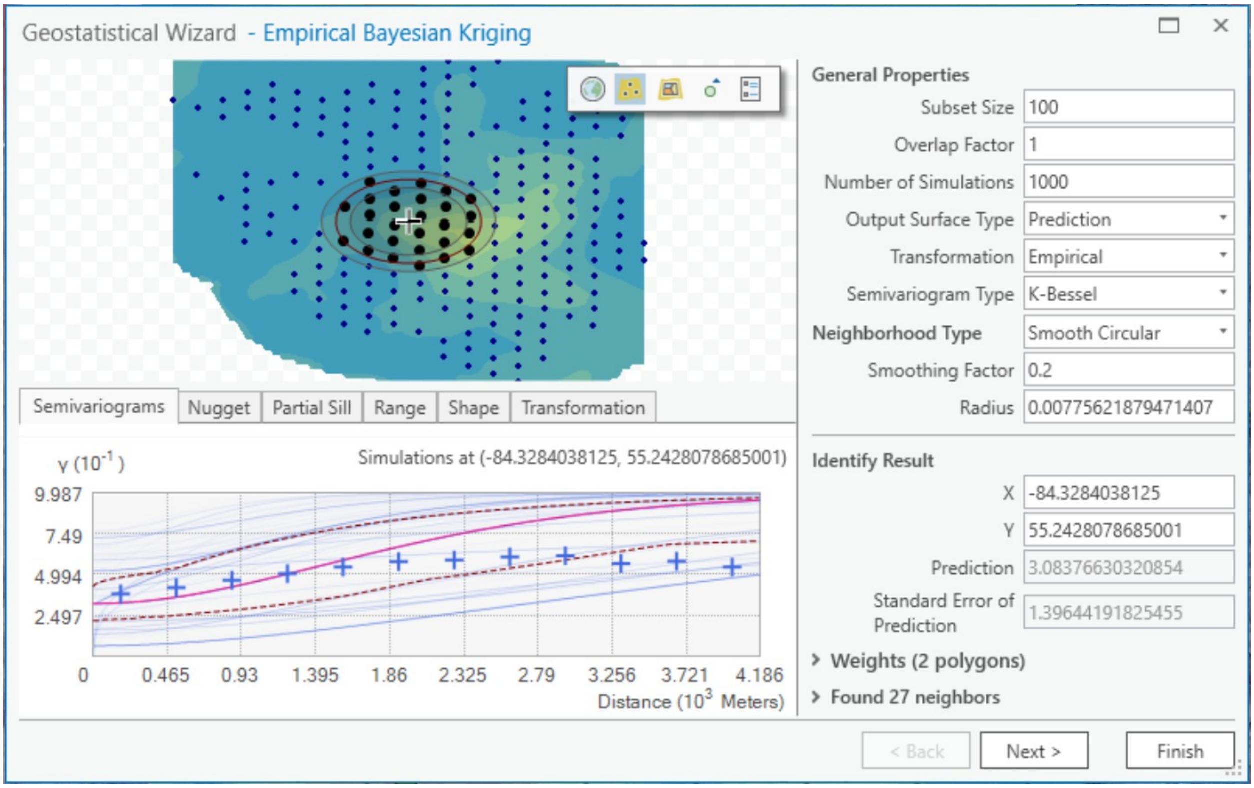
Identify Result

X	-84.32391279799998
Y	55.24202010150006
Prediction	1.83415533161548
Standard Error of Prediction	0.963793016874975

› Weights (3 polygons)

› Found 30 neighbors

Appendix IIF4 2018 predator index semivariogram and geostatistical wizard setting in ArcGIS Pro



Simulations at (-84.3284038125, 55.2428078685001)

General Properties

Subset Size	100
Overlap Factor	1
Number of Simulations	1000
Output Surface Type	Prediction
Transformation	Empirical
Semivariogram Type	K-Bessel
Neighborhood Type	Smooth Circular
Smoothing Factor	0.2
Radius	0.00775621879471407

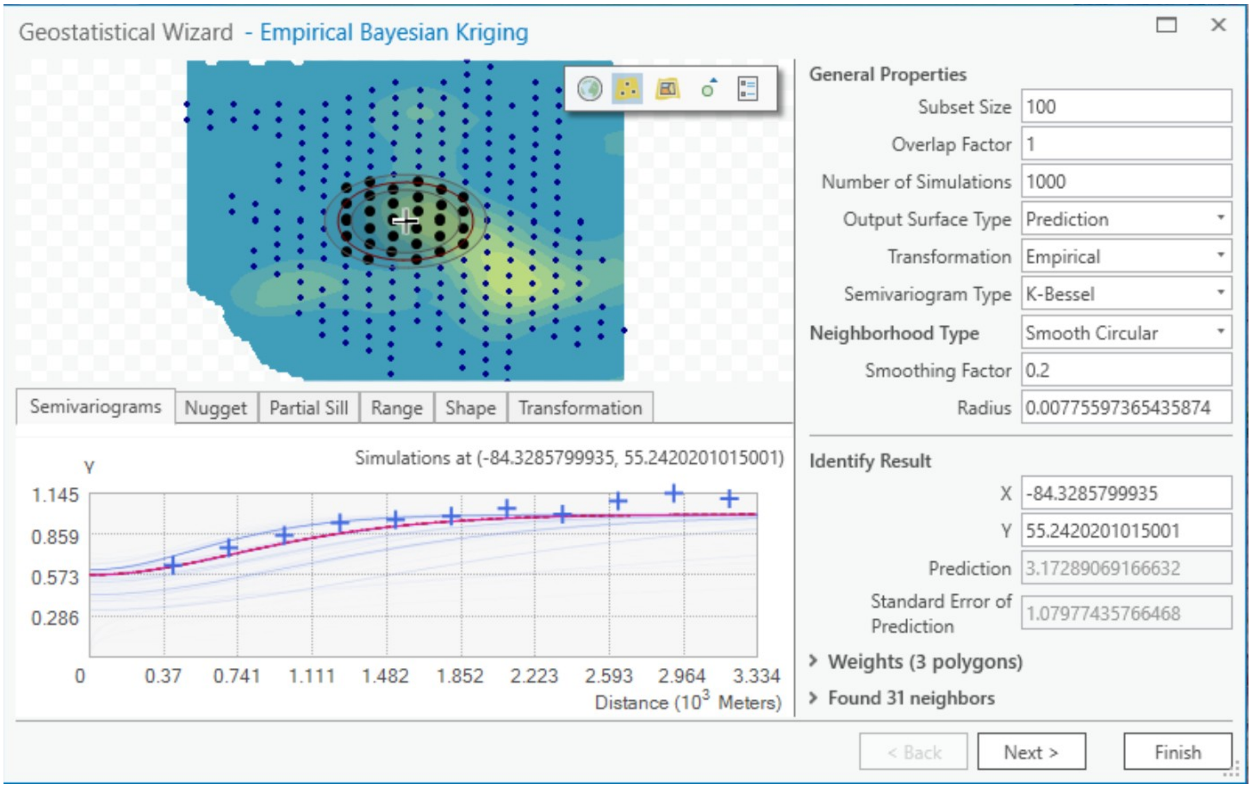
Identify Result

X	-84.3284038125
Y	55.2428078685001
Prediction	3.08376630320854
Standard Error of Prediction	1.39644191825455

› **Weights (2 polygons)**

› **Found 27 neighbors**

Appendix IIF5 2019 predator index semivariogram and geostatistical wizard setting in ArcGIS Pro



Geostatistical Wizard - Empirical Bayesian Kriging

Simulations at (-84.3285799935, 55.2420201015001)

General Properties

Subset Size 100
Overlap Factor 1
Number of Simulations 1000
Output Surface Type Prediction
Transformation Empirical
Semivariogram Type K-Bessel

Neighborhood Type Smooth Circular

Smoothing Factor 0.2
Radius 0.00775597365435874

Identify Result

X -84.3285799935
Y 55.2420201015001
Prediction 3.17289069166632
Standard Error of Prediction 1.07977435766468

› **Weights (3 polygons)**

› **Found 31 neighbors**

Appendix IIF6 2021 predator index semivariogram and geostatistical wizard setting in ArcGIS Pro

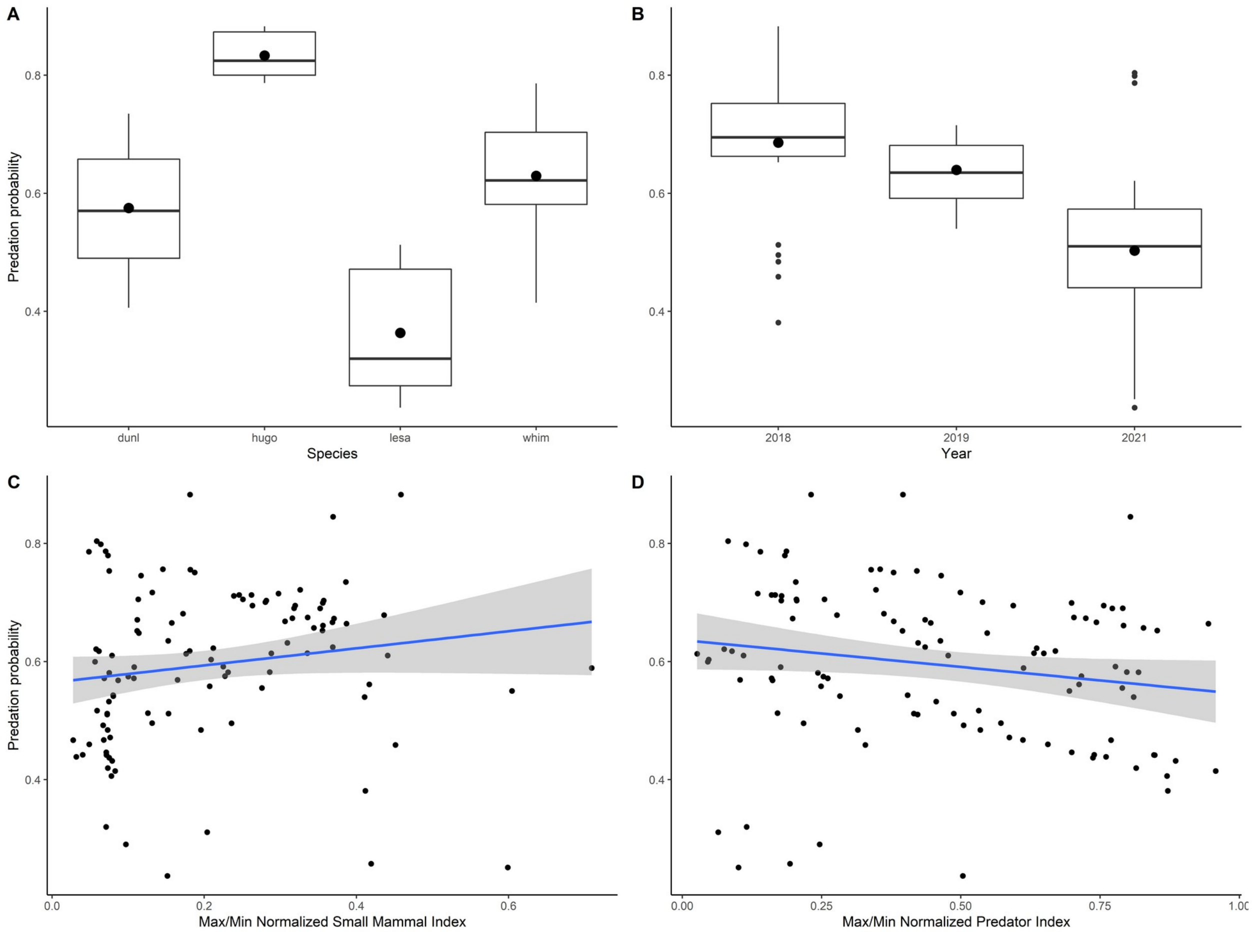
APPENDIX III Other candidate models

Nest predation risk model 1.1: Non-vegetation effects

Appendix IIIT1: GLM model summary for the effects of species, year, predator density, and small mammal density on shorebird nest predation.

Shorebird nest predation

Predictors	Estimate	Statistic	p
(Intercept)	7.525 x 10^2	1.633	0.102
Year	-0.372	-1.631	0.103
Species [Hudsonian Godwit]	1.225	0.887	0.375
Species [Least Sandpiper]	-0.876	-1.378	0.168
Species [Whimbrel]	0.151	0.271	0.786
Predator index	-0.192	-1.045	0.296
Small Mammal Nest Index	-1.513	-0.240	0..811
Observations	111		
R^2 McFadden's	0.056		



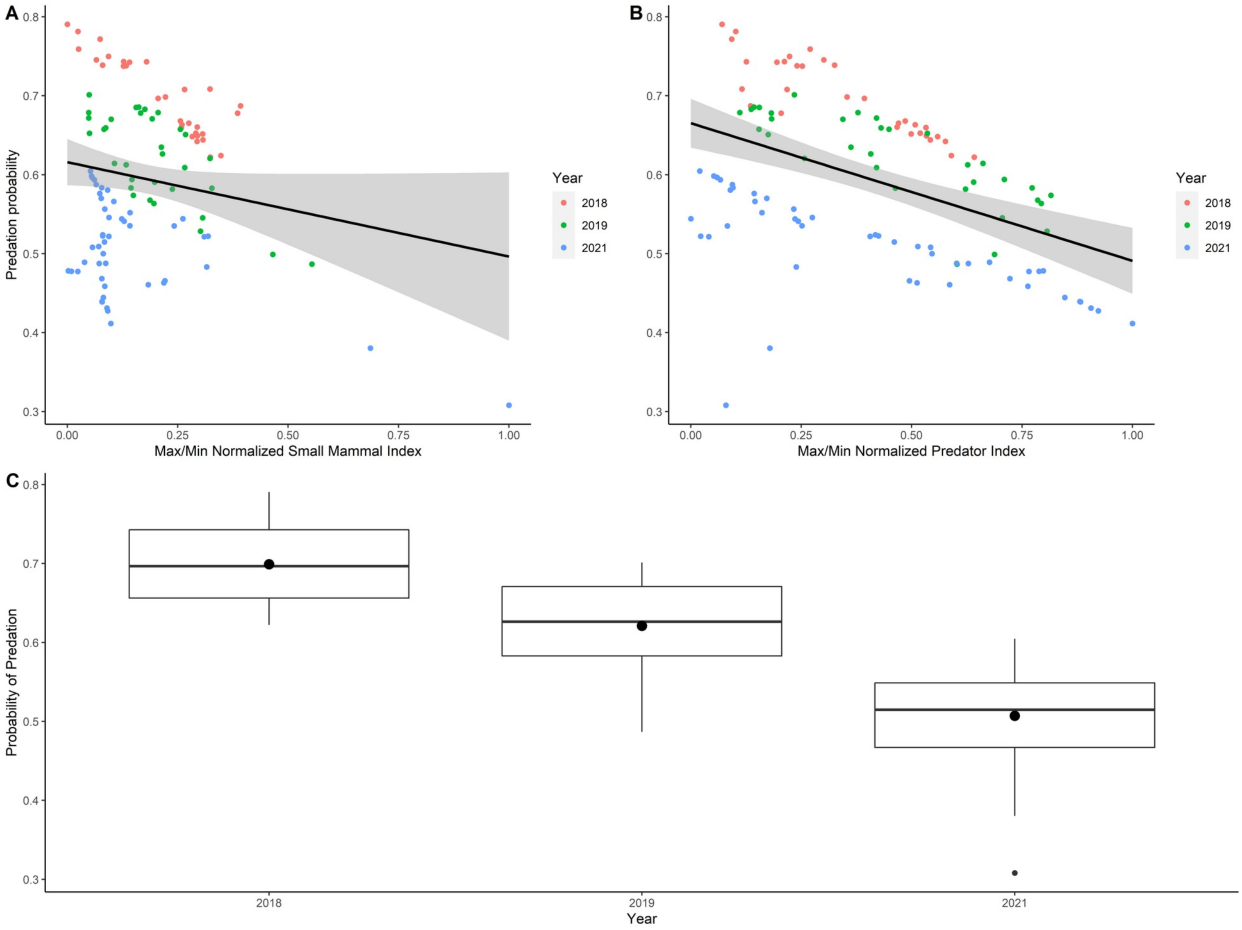
Appendix IIIF1: Shorebird nest predation probability according to A) species, B) year, C) SMN index and D) predator index. A and B are boxplots where the large black dot indicates the sample mean. Plots C and D illustrate the fitted GLM for predation probability (blue line +/- 95% confidence interval in grey).

Nest predation risk model 1.2: Non-vegetation effects with nest species considered non-informative

Appendix IIIT2: GLM model summary for the effects of year, predator index, and small mammal index on shorebird nest predation, omitting species as a factor in the model

Shorebird nest predation

Predictors	Estimate	Statistic	p
(Intercept)	5.894 X 10^2	1.822	**0.0685**
Year	-0.2914	-1.819	**0.0689**
Predator index	-0.7391	-0.963	0.3357
Small mammal nest indext	-1.256	-0.864	0.3357
Observations	111		
R^2 Mcfadden's	0.0302		



Appendix IIIF2: Shorebird nest predation probability according to A) SMN index and D) predator index and C) year. Large black circle indicates the mean

SMN index did not significantly influence predation probability (slope = 0.120 x 10^-2, intercept = 0.594, p >0.05) (AIIIF2, AIIIT2). However, three clusters of points evident in the relationship between small mammal indices and predation probability is suspected to be due to a year effect as visually demonstrated by colour (AIIIF2A). This seemingly annual pattern in the distribution in predation probability can also be seen as it is affected by predation index (slope = 0.0253, intercept = 0.583, p>0.05) (AIIIF2B). Despite the lack of significance when modeled independently, there is an apparent relationship attributing predation probability to a year-index interaction with an apparent negative relationship. Where years 2018 demonstrated higher overall predation probabilities with indices, 2019 had intermediate predation probability, and 2021 demonstrated the lowest predation probabilities according to indices.

Year was the only, albeit marginal, significant predictor of predation probability (p = 0.0689) (AIIIF2C, AIIIT2). The highest probability of predation occurred in 2018 (mean = 0.698 +/- 8.890 x 10^-3 SE, median = 0.697, Q1= 0.656, Q3 = 0.743, min = 0.622, max = 0.7904). Predation probability reduced in 2019 (mean = 0.621 +/- 9.993 x 10^-3 SE, median = 0.626, Q1 = 0.583, Q3 = 0.671, min = 0.487, max = 0.701) and was lowest in 2021 (mean = 0.507 +/- 9.12 x 10^-3 SE, median = 0.514, Q1 = 0.467, Q3 = 0.549, min = 0.380, max = 0.604) (AIIIF2C).