INDIRECT EFFECTS OF LOW AMPLITUDE ARVICOLINE CYCLES ON DAILY NEST SURVIVAL OF DUNLIN (*CALIDRIS ALPINA HUDSONIA*) IN A RAPIDLY CHANGING CLIMATE

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A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

GRADUATE PROGRAMME IN BIOLOGY
YORK UNIVERSITY
TORONTO, ONTARIO

JUNE 2022

ABSTRACT

The Alternative Prey Hypothesis (APH) states that predators switch to relatively more abundant prey when their main prey is scarce. Arctic lemming population cycles may indirectly affect predation risk on alternative prey such as shorebird nests as they share predators. I examined the indirect effects of arvicoline rodent cycles on Dunlin (*Calidris alpina hudsonia*) reproduction in Churchill, Manitoba. Using 10 years of field data, the study suggests collared lemming (*Dicrostonyx richardsoni*) cycles did not influence Dunlin nest success. Meadow vole (*Microtus pennsylvanicus*) cycles had an interactive effect with arctic fox (*Vulpes lagopus*) and red fox *(Vulpes vulpes)* abundance, indirectly affecting Dunlin nest success. North Atlantic Oscillations had a positive effect on Dunlin nest success. The results suggest that subarctic ecosystems are more complex than the High Arctic with multispecies trophic dynamics that can be used to predict the changing landscapes of the Arctic as the boreal forest expands northwards.

ACKNOWLEDGEMENTS

I want to first express my gratitude to my supervisor, Dr. Laura McKinnon, for her guidance on navigating this project under these uncertain circumstances. Both of my anticipated field seasons in Churchill were cancelled due to COVID-19, therefore I needed to quickly adapt my research plans by changing the thesis from a field-based project to the analysis of long-term data. Throughout my project, my supervisor provided countless resources and edits that helped make this project reach completion. I am also very grateful for all the opportunities that she has presented to me outside of my research which pushed me to gain experiences I would not have had the chance to otherwise, making me grow as a more well-rounded individual. For instance, granting me the opportunity to develop my field skills by suggesting I lead the local Killdeer monitoring project at Downsview Park, providing me with similar skills I would have gained in Churchill. I would like to next thank my committee member, Dr. Dawn Bazely, for her insightful feedback in the initial stages of my thesis, prompting questions I would not have thought to ask, and providing resources for my writing, whether that be related to my project or grants. Many thanks to Jim Roth for providing the fox and lemming data while taking time to thoroughly explain every question I had through lots of back-and-forth emails. Thanks also to the nest searching team of Dr. Erica Nol and Dr. Laura McKinnon. Thanks to my supervisor for providing her long-term data on Dunlin nest success, and to past lab members Taylor Brown, Leah Wright, and Victor Olek for helping me access the data and guiding me through them. I want to lastly thank Kenneth Tran for his moral support, listening to my presentation rehearsals, and taking time to help me automate calculations for this project so that I did not have to do them all manually.

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INTRODUCTION

Competition is the interaction between individuals or species for survival where shared resources are limited (Lang and Benbow 2013). Apparent competition occurs when prey species do not directly compete for shared resources but are able to indirectly influence each other’s abundance through a shared predator (Holt 1977, Lang & Benbow 2013). This interaction generally occurs in poor environments where the main prey is low in abundance, pressuring predators to forage for multiple prey items (Holt and Kotler 1987). The Alternative Prey Hypothesis (APH) states that predators can switch to relatively more abundant alternative prey when their main prey is scarce or inaccessible (Lack 1970). Predator-prey switching behaviour may thus result in short-term apparent competition between different prey types. Alternative prey species may experience negative effects such as increased predation risk when main prey types are low in abundance. However, as the main prey species decreases in abundance, mean hunting time for predators may increase, which then negatively affects predator reproductive success and population size (MacArthur & Pianka 1966, Oaten 1977). For example, a decrease in vole abundance (main prey; *Microtus agrestis* and *Myodes glareolus*) increased predation of common goldeneye (*Bucephala clangula*) nests (alternative prey) by pine marten (*Martes martes*) in Southern Finland (Pöysä et al. 2016). As such, a change in the abundance of a key prey species may alter nonlinear interactions between many species in the food web.

The APH has often been tested in the arctic tundra ecosystem due to the relatively simple trophic dynamics, short food webs and low species diversity (Bazely & Jefferies 1997, Krebs et al. 2003). Moreover, the presence of cyclic arvicoline rodent populations, such as voles (*Myodes* or *Microtus spp.*) or lemmings (*Lemmus* or *Dicrostonyx spp.*) facilitate empirical tests of the APH, as researchers can examine annual fluctuations in predation pressure on prey that share predators with the arvicoline rodents (McKinnon et al. 2014, Breisjøberget et al. 2018). In general, arctic predators mainly feed on rodents when their abundance is high, but when rodent populations crash, predators turn to feeding on similarly sized prey items like bird eggs or chicks (Angelstam et al. 1984). Lemmings are considered keystone species in the Arctic as they interact dynamically with many components of the food web. An important herbivore, lemmings are the main prey for various tundra predators such as the arctic fox (*Vulpes lagopus*), red fox (*Vulpes vulpes*), Snowy Owl (*Bubo scandiacus*) and jaegers (*Stercocarius* spp.; Gilg et al. 2009, Giroux et al. 2012). Their predictable population cycles of 3 to 5 years (Ims & Fuglei 2005) elicit both numerical and functional responses of predators (Gilg et al. 2006, Gilg & Sittler 2003). The strength of the numerical and functional responses of arctic predators depends on the extent to which they specialize on lemmings as prey (Angerbjörn et al. 1999, Schmidt et al. 2012).

Arctic foxes, a key mammalian arctic predator, are specialists for collared lemmings (*Dicrostonyx richardsoni*) (Bowler et al. 2020). As the main predators of lemmings, arctic foxes have been found to experience cycles correlated with lemming cycles (Angerbjörn et al. 1999, Roth 2002, Ims & Fuglei 2005, Schmidt et al. 2012). Indeed, some populations of arctic foxes have been found to mass migrate to southern Manitoba when lemming abundance declines (Wrigley and Hatch 1976). Red foxes, a more recent addition to the arctic ecosystem, are also generalists and overlap fundamental food niches with arctic foxes. Red foxes can outcompete arctic foxes because the former are more opportunistic foragers that take advantage of a wider range of additional food resources during low rodent years such as garbage and livestock (Elmhagen et al. 2017). As such, red foxes may show similar interannual fluctuations but often at smaller amplitudes (Roth 2003).

In the Arctic, lemming population cycles have been shown to indirectly affect predation risk on alternative prey such as shorebird eggs and chicks due to their shared predators. The amplitude of lemming cycles refers to the degree of fluctuation in population size throughout time. Cyclic patterns in predation pressure on ground nesting bird nests occur in response to lemming cycles (Bêty et al. 2002, McKinnon and Bêty 2009, McKinnon et al. 2014) are strongest in colder, high latitude regions where rodent population cycles exhibit greater amplitudes (Bowler et al. 2020). Arctic foxes are important predators of shorebird eggs and chicks (McKinnon and Bêty 2009, McKinnon et al. 2012). As lemming abundance increases, nest survival and breeding productivity also increase (Smith et al. 2007, McKinnon et al. 2014) and these effects can be detected at large spatial and temporal scales (Underhill et al. 1993, Summers et al. 1998).

Though recent studies have greatly increased our understanding of apparent competition between birds and lemmings in the Arctic, recent and rapid changes in climate will likely alter these key trophic interactions. Indeed, climate change has already altered the arctic tundra ecosystem and its food webs (Kausrud et al. 2008, Gilg et al. 2009). For instance, a decline in predator population size was associated with declines in vole populations in Sweden due to decreased winter stability (Hörnfeldt et al. 2005). Climate change is also thought to be responsible for the decrease in lemming abundance, causing their cycles to dampen or collapse, which in turn decreases predator population sizes (Schmidt et al. 2012, Row et al. 2014). If climate-induced changes to lemming cycles result in decreased population sizes, alternative prey populations may face increased predation risk and potential population declines (Ims and Fuglei 2005, Fraser et al. 2013). In the Subarctic (50° N to 60° N), located in the transition zone between the boreal forest tree line and the Low Arctic tundra (between 60° N to 70° N Love

1970)), arvicoline rodent cycles are of lower amplitude compared to populations in the High Arctic polar desert (north of 70° N), which is characterized by lack of standing vegetation (Hislop 2013, Derksen et al. 2014). Low amplitude cycles in the Subarctic, therefore, could illustrate the changes that may occur in the High Arctic if climate warming dampens lemming population cycles.

This study examined the indirect effects of low amplitude arvicoline rodent cycles on shorebird reproduction in Churchill, Manitoba. Shorebird populations in Churchill are at the southernmost range for the species, which can provide insight into how the populations farther north will respond to a warming climate. Using a decade of data from 2010 to 2019, this study investigated the indirect relationship between shorebird reproductive success and arvicoline rodent abundance due to shared predators in accordance with the APH. I hypothesized that predators will shift their diet from lemmings and voles (primary prey) to shorebird eggs (alternative prey) when lemming abundance declines. More specifically, I predicted that daily nest survival of shorebirds will increase as lemming and vole populations increase.

MATERIALS & METHODS

Study Area

This study used data collected during the shorebird breeding season from 2010 to 2019 at Churchill, Manitoba, Canada which is located on the west coast of Hudson Bay (58° 46 ’09” N, 94° 10 ’09” W; Figure 1) and where there are lower amplitude arvicoline rodent cycles (Roth 2017, Dudenhoeffer et al. 2021). This site is located within the transition zone from the northernmost limit of the boreal forest treeline to the southernmost limit of the subarctic tundra ecosystem. The combination of two major biotic regions and the Churchill River attracts a variety of species to Churchill (Jehl 2004). The region is characterised as having low relief, poor drainage, permafrost, and shallow lakes and ponds (Skeel 1983). Spring conditions at Churchill normally started in early June but have been advancing to May (Koes 1999, Senner 2012). The temperatures are positive from the summer months of May to October, while temperatures are negative from November to April (Gough and He 2015). The location was chosen due to the ease of accessibility to a high abundance and diversity of breeding shorebirds species in the summer (Jehl and Lin 2001). Breeding populations of Dunlin (*Calidris alpina*) were monitored at three sites that were 3.1 km to 11.5 km apart from each other and considered suitable for shorebird breeding: Fen (58° 40 ’03 ’’N, 93° 49 ’00 ’’W), Golf Balls (58° 45′ 11.57″ N, 93° 55′ 36.51″ W), and Gun Range (58° 44 ’34 ’’N, 93° 57 ’59 ’’W).

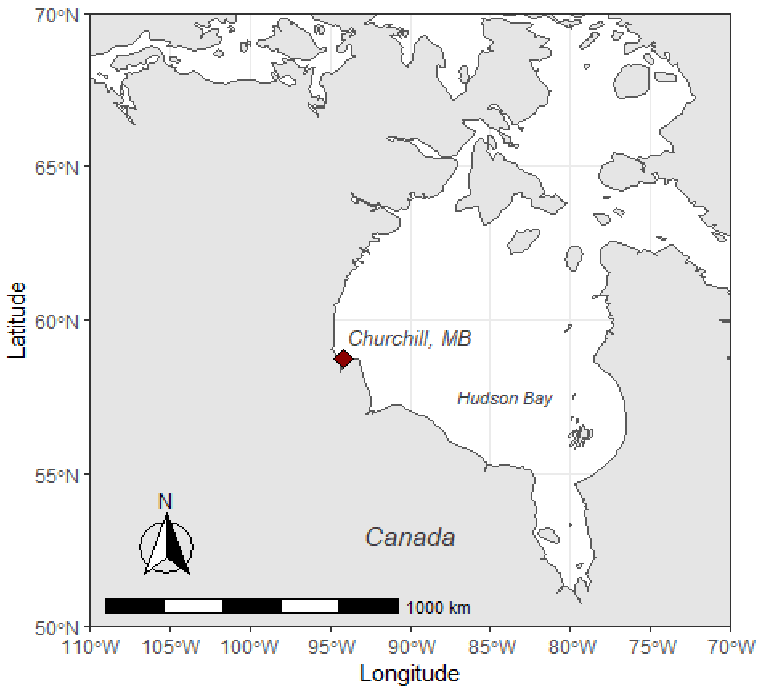

Figure 1. Map of the study location, Churchill, Manitoba on the west of the Hudson Bay.

Study Species

The Dunlin (*Calidris alpina*) is a shorebird with 11 subspecies that breeds in the Arctic and Subarctic during the summer (Fernández et al. 2010). They are long-distance migratory birds that are abundant in the Northern Hemisphere with a circumpolar breeding distribution. The three known subspecies that breed in North America (*C. a. arcticola, C. a. pacifica, C. a. hudsonia*) have different distribution ranges between subspecies (Fernández et al. 2010). The *C. a. arcticola* breeds in northern Alaska and resides from Japan to China in the nonbreeding season, while *C. a. pacifica* breeds in western Alaska and distributes along the Pacific coast of southern British Columbia to northwestern Mexico in the nonbreeding season (Fernández et al. 2010). The *C. a. hudsonia* spends their breeding season in northern Canada and nonbreeding season in the Atlantic and Gulf coasts from Massachusetts to Mexico (Fernández et al. 2010, Wright et al.2022). All three subspecies are estimated to be declining in population size (Jehl and Lin 2001: 3).

Dunlin are commonly found in estuarine mudflats but are also found in a variety of habitats including freshwater to brackish wetlands and agricultural habitats throughout the year. Dunlin are categorised as moderate concern for conservation planning as their populations may decline over time due to known or potential threats (Hope et al. 2019). Current potential threats include habitat loss in their nonbreeding range and possible range restrictions from decreases in suitable habitat due to human disturbance (Fernández et al. 2010).

The *C. A. hudsonia* is a common summer resident of Churchill, MB (Jehl and Lin 2001). They lay one 4-egg clutch per year into shallow ground scrapes which are easily detected due to males showing flight displays around their territory (Jehl and Lin 2001). Dunlin are biparental (i.e., both parents care for their offsprings) and both sexes incubate between 19.5 to 23 days from June to late July (Jehl 2004). Depending on when predation events occur, Dunlin may renest in the nesting season, with high renesting rates in early incubation (82-95%) and moderate renesting rates in late incubation (35-50%) (Gates et al. 2013, Pakanen et al. 2014).

Arvicoline rodents (i.e. of the subfamily Arvicolinae) include voles, lemmings and muskrat, are the most abundant rodents found in the Northern Hemisphere and have a Holarctic distribution. The arvicoline rodent population of Churchill, Manitoba is dominated by collared lemming (*Dicrostonyx richardsoni*) and Eastern meadow vole (*Microtus pennsylvanicus*) populations. The collared lemming is an arvicoline rodent that exhibits large periodic outbreaks in their population cycles at 3–4-year intervals (Shelford 1943, Scott 1993, Reiter and Andersen 2008). These large fluctuations of peaks and crashes in population size influence the food web as lemmings are important herbivores and prey in the tundra food web. However, there is a latitudinal gradient for the amplitude of lemming cycles, where collared lemmings in the Subarctic exhibit low-amplitude cycles compared to brown lemming (*Lemmus sibiricus*) in the High Arctic (Gruyer et al. 2008, Fauteux et al. 2018). The collared lemmings in Churchill have been noted to be decreasing in peak densities over the years, with 63 per ha in 1967 (Wrigley and Hatch 1976), 12 per ha in the 1990s (Roth 2002), and 2 per ha in 2017 (Roth 2017). While most lemming species breed through summer and winter (Krebs et al. 1995, Millar 2001), collared lemmings only breed in the winter and litters born in the spring do not mature until the next winter (Krebs et al. 1995). Snow cover properties may predict collared lemming outbreaks as they rely heavily on snow cover during the winter for reproduction and protection from predators (MacLean et al. 1974, Duchesne et al. 2011, Ims et al. 2011). Less than ideal winter conditions (ex. increased snow hardness and humidity) were found to cause less frequent peaks and low-amplitude fluctuations (Kausrud et al. 2008). As climate change alters ideal winter breeding conditions for lemming outbreaks to occur (i.e., long and cold winters), collapsing of lemming cycles can be expected (Ims et al. 2008, Ims et al. 2011).

In the Subarctic, voles occur in sympatry with collared lemmings, and are often synchronous in their role as prey for tundra predators which can have a positive indirect effect on lemming populations (Ims et al. 2011, Ehrich et al. 2019). The Eastern meadow vole also experiences 3–4-year cycles (Ims et al. 2008). However, vole population peaks are less abrupt and steep than those of lemmings (Ims et al. 2011), possibly due to higher reproduction rates, better juvenile nest survival, and faster maturation for the summer breeding season (Krebs et al. 1995). In contrast to lemmings, meadow voles breed year-round but rapidly increase during the summer and decrease in the winter (Ford et al. 2007). A strong decrease in Scandinavian vole numbers in the winter was attributed to recent changes to the North Atlantic Oscillation associated with increasing mild and wet weather conditions (Hörnfeldt 2005). Vole and lemming cycles are synchronized in different sites across the central and eastern Canadian Arctic, possibly due to weather (Krebs et al. 2002). As such, climate change could result in the dampening and/or collapse of population cycles in both species.

The main predators of both arvicoline rodents and shorebird eggs include the arctic fox (*Vulpes lagopus*) and red fox *(Vulpes vulpes)* (McKinnon and Bêty 2009, Brown et al. 2022). Though sympatric in low and high arctic regions, the arctic fox is currently declining due to climate warming, whereas the red fox is currently increasing in numbers, expanding northward and dominating the southernmost region of the arctic tundra (Macpherson 1969, Killengreen et al. 2007). Arctic foxes exhibit seasonal movements, leaving summer home ranges in the fall to be nomadic for the winter before returning to inland den sites in the spring (Roth 2002).

Breeding dens are underground, with whelps born in late spring and weaned until late summer, after which the dens are abandoned for the season (Macpherson 1969). Red foxes are known to use the dens of arctic foxes (Elmhagen et al. 2017). Arctic foxes depend on lemmings and other small mammals for their diet (MacPherson 1969, Angerbjörn et al. 1999, Roth 2002). Based on arctic fox droppings, lemmings may account for up to 50-90% of their diet, with birds and their eggs as their next most important food source in May to June (4-29%; Macpherson 1969). Arctic foxes in Manitoba experienced regular 3-year peaks from 1919-1975 (Wrigley and Hatch 1976), coinciding with peaks in lemming abundance (Shelford 1943). The mortality of arctic fox pups may be attributed to food scarcity from low lemming years (Larson 1960, Macpherson 1969). Red foxes in the Low Arctic are positively associated with primary productivity, summer temperatures, human population density, cropland, and young forests due to high prey availability and anthropogenic resources (Elmhagen et al. 2017). It is likely their opportunistic feeding strategies that drive their current range expansion and the displacement of the arctic foxes.

Predator Abundance

Fox abundance was calculated based on counts of fox dens that were successful in producing offspring in the study sites between 2010 and 2019. A successful den was represented by a minimum of 2 adults actively foraging to feed themselves and at least 1 pup. The home range size for red and arctic foxes is approximately 20 km^2 in the summer (Roth unpubl. data), therefore, only dens located within a 20 km radius from the centre of the study site were included. Den counts were conducted during late July and most of the dens were used by red foxes. Dens were visited on the ground and surveyed by helicopter in late July or August. While thick vegetation can inhibit assessment from air, those biases have been consistent over the years, so den counts can be used as a relative index for the population. Den counts have a good level of accuracy in estimating fox abundance (Beltrán et al. 1991). Arctic fox dens were found at raised beach ridges and were easily located by lush vegetation surrounding them (McDonald et al. 2017). Den use was distinguished between arctic foxes from red foxes based on the shed hair in and around the burrows. A den was considered successful if pups were observed at a den in the late summer months (i.e., late July or August). Successful dens are distinguishable from non successful ones based on scat, tracks, prey remains and digging in burrows (McDonald et al. 2017).

Arvicoline Rodent Abundance

Lemming and vole abundance was estimated using Sherman live-traps set along two 300 m long transects near Churchill Northern Studies Centre in the collared lemming's preferred habitat. Each transect consisted of 20 stations set 15 m apart. At each station, 3 traps were set 5 m apart. Sherman live-traps were baited with peanut butter, oats, and apple (Roth 2002, McDonald et al. 2017). The traps were checked every 4-6 hours over a 48-hour period and the rodents were marked by hair clipping for individual identification (McDonald et al. 2017). One trapping season was conducted each year at this study site shortly after snowmelt. Traps were kept open continuously in June for two nights for each year from 2010 to 2019. The total number of trap nights per year was calculated as the following:

$$Totalnumberoftrapnights = totalnumberoftraps \times numberofnightsperyear$$

The index of arvicoline rodent abundance was calculated as the number of rodents caught per 100 trap nights:

$$Rodents\ caught\ per\ 100\ trap\ nights = \frac{(number\ of\ captures \times 100)}{total\ number\ of\ trap\ nights}$$

Lemming and vole captures were calculated separately and categorized together as arvicoline rodents:

Arvicoline rodent abundance per year = lemming abundance per year + vole abundance per year

Weather

Climate can have direct effects on physiology and indirect effects on resource availability and habitat suitability for arctic-nesting shorebirds (Meltofte et al. 2007). Variation in weather is one exogenous variable affecting reproductive success of shorebirds (e.g., temperature: Hötker & Segebade 2000). Later snow melt and low temperatures result in fewer snow-free areas for nesting, which can increase predation risk (Machin 2019). Summer temperatures have a significant positive effect on breeding success of shorebirds (Aharon-Rotman et al. 2015), with climate warming enhancing that effect with earlier snowmelt and shortening incubation by 1.42 days for Dunlin (*C. a. articola*) (Weiser et al. 2018). To account for the potential important effects of weather and climate on daily nest survival, we included mean local temperature and North Atlantic Oscillation (NAO) values as variables in our models. NAO is the standardised difference in air pressure between the Azores High and the Iceland Low, which drives seasonal variability in the global atmosphere (Wanner et al. 2001). High NAO values are indicators of an earlier spring and wet spring and summer (Møller 2002).

Historical weather data recorded by Environment and Natural Resources Canada (https://climate.weather.gc.ca/historical_data/search_historic_data_e.html) were taken from 2010 to 2019 for Churchill, MB. Daily averages from the weather station Churchill A (58°44’21.000” N, 94°03’59.000” W) were converted into monthly averages for May, June, and July to correspond with nesting data. The monthly averages were then converted into one average for each year from 2010 to 2019.

Shorebird Nest Monitoring

Nests were monitored beginning 2010 to 2019 from early June to mid-July. Nests were found by flushing or following individuals returning to their nest (details in McKinnon et al. 2013). For each nest found, the number of eggs and/or young was recorded upon hatch. Nests were considered successful if one or more eggs hatched as indicated by either: (1) presence of chicks, (2) eggshells with intact membrane close to the estimated hatch date, (3) signs of hatching (starred or pipped eggs) on the last date visited and nest is empty during the latest visit, and/or (4) an empty nest, but the adult was later seen with the chicks. Failed nests were those that were depredated or abandoned. Depredated nests were indicated by the absence of eggs prior to estimated hatch and/or no eggshell fragments in the nest. Nests were considered abandoned if the eggs were cold on two consecutive visits over at least 4 days.

Data Access and Management

Data were collected for long-term monitoring projects led by Dr. Laura McKinnon (shorebird data) and Dr. James Roth (fox and lemming data). There were no formal sharing agreements made to use the data but it was informally agreed that any peer-reviewed publications made from this thesis based on the data would be co-authored by Dr. McKinnon and Dr. Roth.

The data were provided in Microsoft Excel and Access sheets. The details of the long-term data collected over 10 years were verified by examining data in field notebooks of all field personnel and final field data sheets for each nest that were entered in the database. More specifically, first day found, last day seen alive, last day visited and fate for each nest were double checked between the existing database and original field notes.

Statistical Analyses

Daily nest survival rate (DSR) is defined as the probability of a nest surviving from one day to the next throughout incubation. The nesting season is considered to have started on the day the first nest is found and ends on the last day any nest was checked. All daily nest survival models were constructed using the R package *Rmark* (v.2.2.5, Laake 2013). *Rmark* estimates daily nest survival by considering that successful and unsuccessful nests are not found with equal probability, and that nests found later during the incubation periods will have a bias towards higher nesting success (Rotella 2006). To reduce this bias, calculations of daily nest survival take into account the number of exposure days for each nest. Five pieces of information were required to build each model: 1) day the nest was found within the nesting season, 2) last day nest was checked alive, 3) last day nest was checked, 4) nest's fate (0 = successful, 1 = depredated), and 5) number of nests with the same encounter history (Dinsmore and Dinsmore 2007).

To test the main hypothesis of the indirect effect of lemming and vole abundance on Dunlin nest survival rates, 35 *a priori* nest survival models were compared (Table 1). The *a priori* models were made based on biologically sound combinations of variables that are known to affect shorebird reproduction (e.g., Smith et al. 2010, Robinson et al. 2014). Due to the relatively low variation in lemming, vole, and arvicoline rodent abundance, these variables were also included as categorical variables classified as low (absent during trapping) or high (present during trapping). A correlation matrix using Spearman's rank correlation was used to avoid multicollinearity in the *a priori* models. Dependent variables that were highly correlated (≤0.6) were not used in the same model. Several variables were considered highly correlated and so they were not included in models together (Table 2): 1) fox abundance and mean temperature, 2) fox abundance and categorical lemming abundance, 3) mean temperature and categorical lemming abundance, 4) mean temperature and categorical vole abundance, 5) mean temperature and categorical arvicoline rodent abundance, 6) NAO and categorical lemming abundance, 7) NAO and categorical vole abundance, 8) NAO and categorical arvicoline rodent abundance. Given that the effect of arvicoline rodent abundance could vary based on predator abundance, we also included models with an interaction between arvicoline rodent variables and fox abundance.

The model with the lowest AIC_c score was considered the best fitting model and was used to describe variation in Dunlin daily nest survival (Burnham and Anderson 2002, Arnold 2010).

All statistical analyses were conducted using R (3.6.1, R Core Team 2019). All protocols were approved by the animal care committee of York University.

Table 1. Complete list of *a priori* models used to explain daily nest survival rates of Dunlin in Churchill, MB. Note: explanatory variables *lemming abundance*, *vole abundance, arvicoline rodent abundance, fox abundance*, *mean temperature*, *North Atlantic Oscillation* were denoted as *lemming, vole, rodent, fox, temperature,* and *NAO* respectively. Categorical lemming, vole, and arvicoline rodent variables were simplified into *catLemming*, *catVole*, and *catRodent.*

No.	*Hypotheses*	*Candidate model*	*No.*	*Hypothesis*	*Candidate model*
1	Null	Intercept	18	Vole abundance and mean temperature	Intercept+vole+temperature
2	Lemming abundance	Intercept+lemming	19	Arvicoline rodent abundance and mean temperature	Intercept+rodent+temperature
3	Vole abundance	Intercept+vole	20	Lemming abundance and North Atlantic Oscillation	Intercept+lemming+NAO
4	Arvicoline rodent abundance	Intercept+rodent	21	Vole abundance and North Atlantic Oscillation	Intercept+vole+NAO
5	Categorical lemming abundance	Intercept+catLemming	22	Arvicoline rodent abundance and North Atlantic Oscillation	Intercept+rodent+NAO
6	Categorical vole abundance	Intercept+catVole	23	Fox abundance and North Atlantic Oscillation	Intercept+fox+NAO
7	Categorical arvicoline rodent abundance	Intercept+catRodent	24	Lemming abundance, fox abundance and North Atlantic Oscillation	Intercept+lemming+fox+NAO
8	Fox abundance	Intercept+fox	25	Vole abundance, fox abundance and North Atlantic Oscillation	Intercept+vole+fox+NAO
9	Mean temperature	Intercept+temperature	26	Arvicoline rodent abundance, fox abundance and North Atlantic Oscillation	Intercept+rodent+fox+NAO
10	North Atlantic Oscillation	Intercept+NAO	27	Lemming abundance varies by fox abundance	Intercept+lemming*fox
11	Year	Intercept+year	28	Vole abundance varies by fox abundance	Intercept+vole*fox
12	Lemming abundance and fox abundance	Intercept+lemming+fox	29	Arvicoline rodent abundance varie by fox abundance	Intercept+rodent*fox
13	Vole abundance and fox abundance	Intercept+vole+fox	30	Categorical vole abundance varies by fox abundance	Intercept+catVole*fox
14	Arvicoline rodent abundance and fox abundance	Intercept+rodent+fox	31	Categorical arvicoline rodent abundance varies by fox abundance	Intercept+catRodent*fox
15	Categorical vole abundance and fox abundance	Intercept+catVole+fox	32	Lemming abundance varies by fox abundance and North Atlantic Oscillation	Intercept+lemming*fox+NAO
16	Categorical arvicoline rodent abundance and fox abundance	Intercept+catRodent+fox	33	Vole abundance varies by fox abundance and North Atlantic Oscillation	Intercept+vole*fox+NAO
17	Lemming abundance and mean temperature	Intercept+lemming+temperature	34	Arvicoline rodent abundance varies by fox abundance and North Atlantic Oscillation	Intercept+rodent*fox+NAO

* interactive effect
\+ additive effect

	Lemming Abundance	Vole Abundance	Arvicoline Rodent Abundance	Fox Abundance	Mean Annual Temperature	NAO	Categorical Lemming Abundance	Categorical Vole Abundance	Categorical Arvicoline Rodent Abundance
Lemming Abundance	1.00	0.51	0.89	-0.27	0.07	0.06	0.40	-0.32	0.34
Vole Abundance		1.00	0.79	-0.18	0.36	0.36	0.37	0.00	0.54
Arvicoline Rodent Abundance			1.00	-0.19	0.18	0.24	0.37	-0.15	0.48
Fox Abundance				1.00	**-0.87**	-0.42	**-0.71**	-0.40	-0.56
Mean Annual Temperature					1.00	0.62	**0.73**	**0.69**	**0.76**
NAO						1.00	**0.74**	**0.73**	**0.86**
Categorical Lemming Abundance							1.00	0.52	**0.92**
Categorical Vole Abundance								1.00	0.65
Categorical Arvicoline Rodent Abundance									1.00

Table 2. Spearman correlation matrix for lemming abundance, vole abundance, arvicoline rodent abundance, fox abundance, mean annual temperature, and averaged annual North Atlantic Oscillation (NAO) index of May, June, and July, and categorical lemming, vole and arvicoline rodent abundance. Variables that were considered highly correlated are in bold and were not included together in *a priori* models to avoid collinearity.

RESULTS

Predator Abundance

The number of fox dens, both active and inactive, found each year was relatively consistent ranging from 30 to 33 dens. The number of active fox dens averaged 6.1±1.8 across the 10 years (range 4 to 9; Figure 2). The highest abundance of foxes occurred in 2018 with 9 successful dens while the lowest abundance in 2013 and 2014 with 4 successful dens (Figure 2).

Arvicoline Rodent Abundance

Arvicoline rodent abundance ranged from 0 to 1.7 individuals per 100 TN (Figure 2). Lemming abundance ranged from 0 to 0.6 individuals per 100 TN. In 2013, 2014 and 2017, lemming abundance was 0.6 individuals per 100 TN. For all other years, lemming abundance was 0 individuals per 100 TN. In 2013 and 2018, meadow vole abundance was 1.1 individuals per 100 TN, and 0 in all other years.

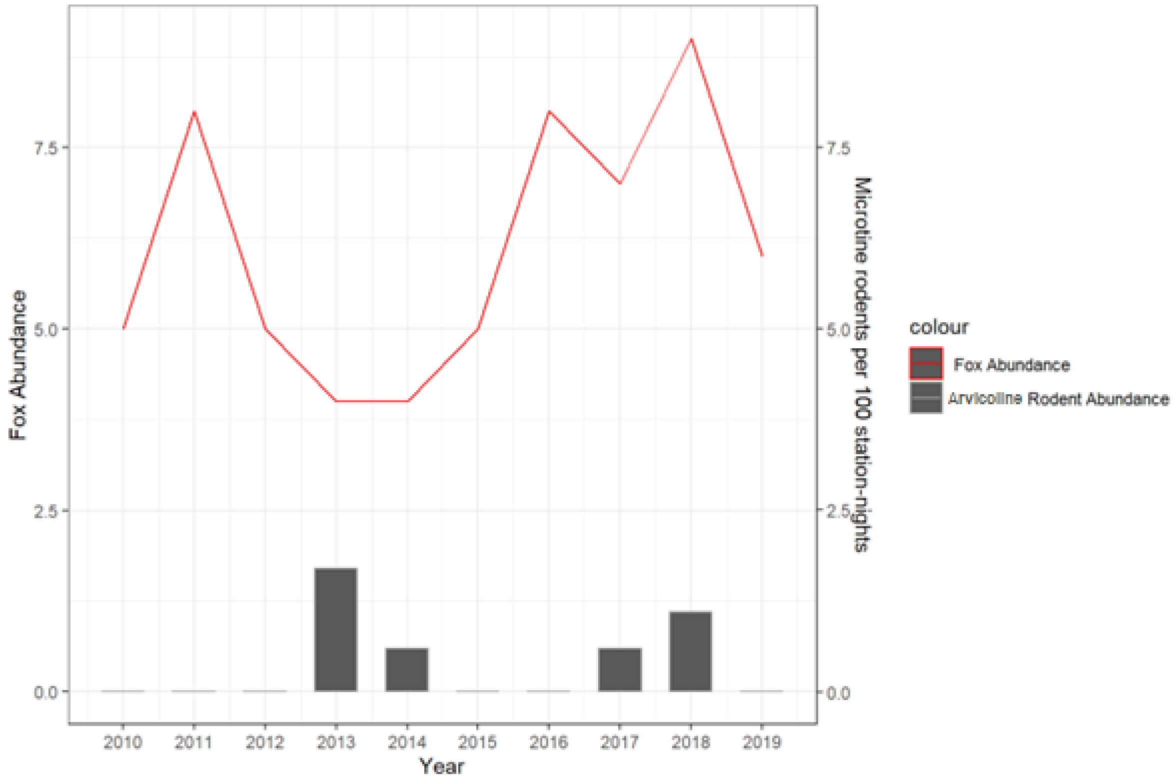

Figure 2. Index of arvicoline rodent abundance based on live trap census and fox abundance from 2010 to 2019. The arvicoline rodent abundance index was calculated as the number of individuals trapped per 100 trap-nights. Fox abundance was the number of successful fox dens in a year.

Weather

The minimum average summer temperatures from 2010 to 2019 ranged from 1.7±2.6°C (2011) to 3.7±1.9°C (2014) (Figure 3). The maximum average summer temperatures ranged from 11.0±1.6°C (2015) to 13.8±2.7°C (2013). The mean annual summer temperature ranged from 6.6±2.8°C (2011) to 8.4±2.4°C (2013). Both maximum and mean summer temperatures in 2013 were exceptionally high. In 2011, there was relatively lower minimum and mean summer temperatures compared to other years.

The peak summer averages of North Atlantic Oscillation (NAO) were in 2013 and 2018 at 0.59±0.04 and 1.53±0.31 respectively while the lowest NAO was found in 2012 and 2019 at -1.59±0.49 and -1.71±0.46 respectively (Figure 4).

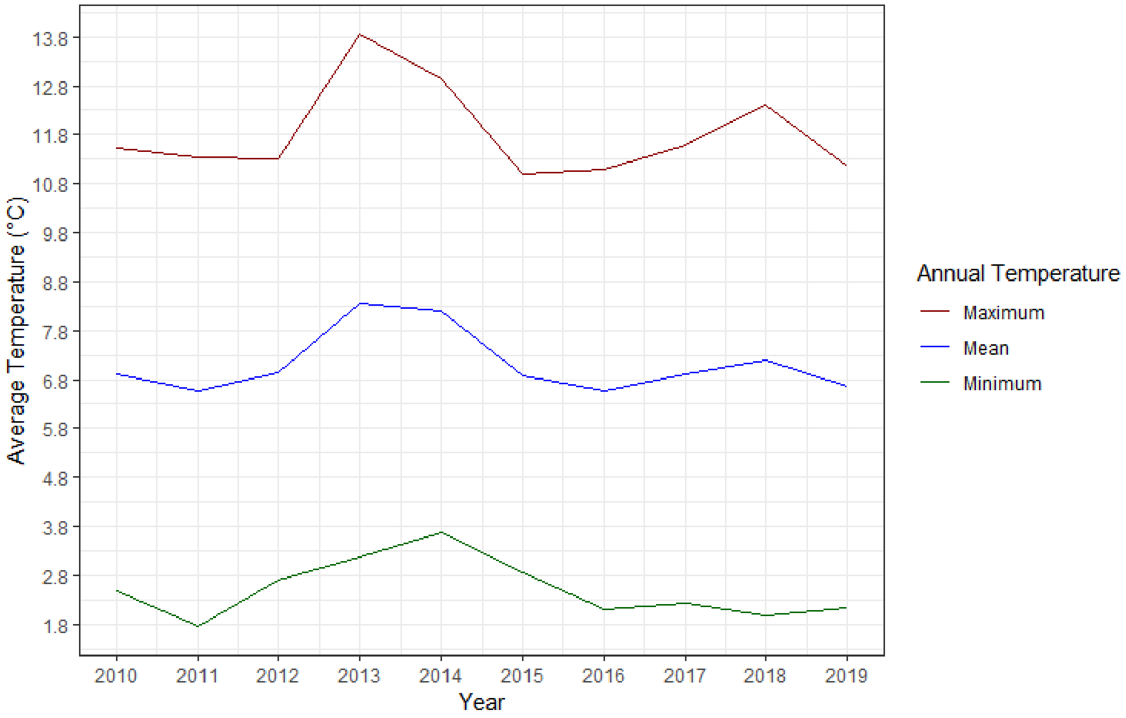

Figure 3. The maximum, minimum and mean of the averaged summer temperatures (May, June, July) from 2010 to 2019.

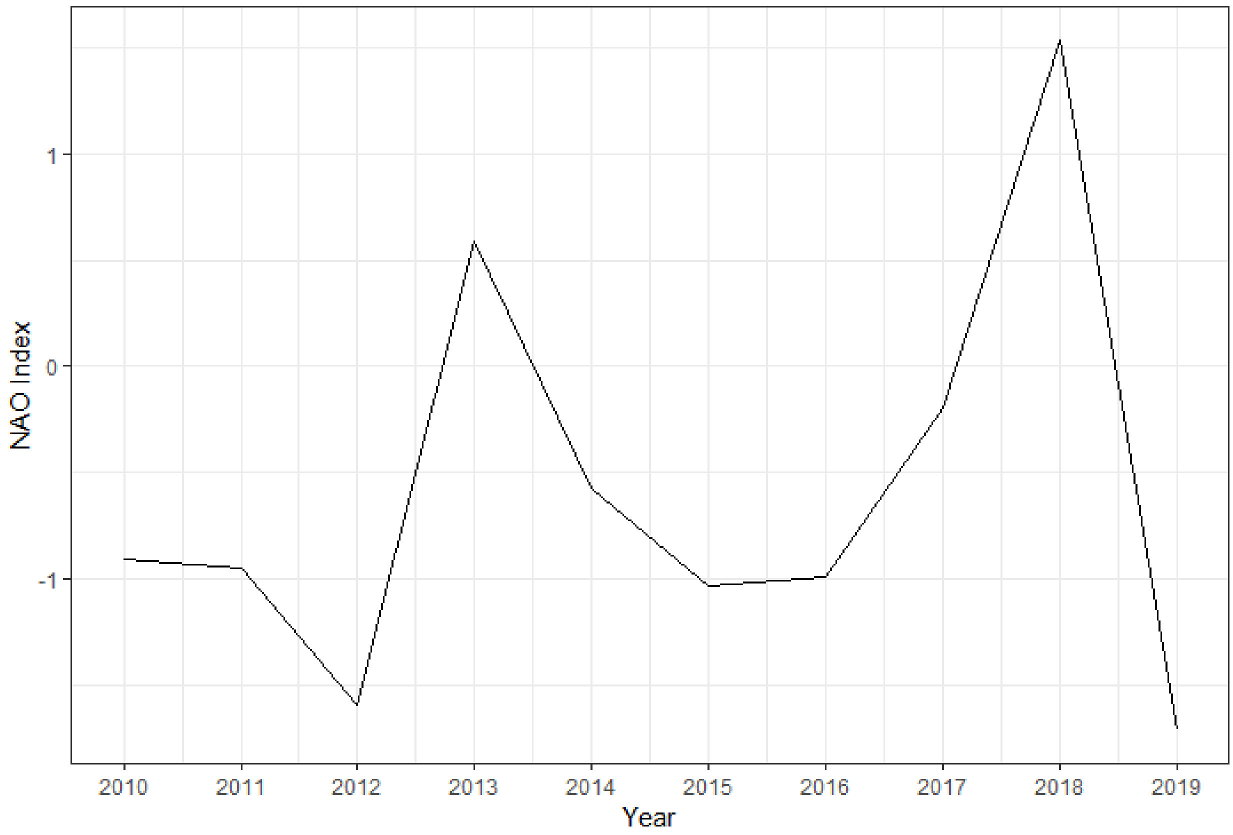

Figure 4. Time series of the summer averages of the North Atlantic Oscillation (NAO) index. The index was calculated as the averaged NAO of May, June, July from 2010 to 2019.

Shorebird Nest Survival

The daily nest survival rate (DSR) for Dunlin nesting in Churchill ranged from 0.931±0.03 to 1±0.00 (Figure 5), which translates to a range in nest success from 21% to 100%. The highest daily nest survival rates occurred during 2010 and 2019, with the lowest daily nest survival rate in 2018. The DSR was best described by an interactive effect of vole and fox abundance, and an additive effect of NAO (ΔAIC = 0.000; Table 3). The DSR increased as fox abundance increased during low vole years (Figure 6), whereas the DSR decreased as fox abundance increased during high vole years (Figure 7). The NAO index had a positive effect on DSR.

Table 3. Models examining the ecological factors influencing daily nest survival rates in Dunlin nests at Churchill, MB based on Akaike's information criterion. Hypotheses tested include the effects of lemming abundance (lemming), vole abundance (vole), arvicoline rodent abundance (rodent), fox abundance (fox), North Atlantic Oscillation (NAO), categorical lemming abundance (catLemming), categorical vole abundance (catVole), categorical arvicoline rodent abundance (catrodent), average summer temperature (temperature), and year. k = number of parameter models, AIC_c = Akaike information criterion, ΔAIC_c = change in AIC_c relative to the top model, and w_i = AIC_c weight.

No.	*Model*	*k*	AIC_c	ΔAIC_c	w_i	*No.*	*Model*	*k*	AIC_c	ΔAIC_c	w_i
33	**Intercept+vole*fox+NAO**	2	**314.872**	**0.000**	$\mathbf{4.182\times10^{-1}}$	7	Intercept+catRodent	2	332.930	18.058	5.013×10^{-5}
3	Intercept+vole	2	317.062	2.190	1.399×10^{-1}	2	Intercept+lemming	2	333.290	18.418	4.188×10^{-5}
18	Intercept+vole+temperature	4	317.542	2.671	1.100×10^{-1}	31	Intercept+catRodent*fox	4	333.317	18.445	4.132×10^{-5}
13	Intercept+vole+fox	3	318.283	3.411	7.596×10^{-2}	16	Intercept+catRodent+fox	3	333.780	18.909	3.277×10^{-5}
21	Intercept+vole+NAO	3	318.470	3.598	6.920×10^{-2}	17	Intercept+lemming+temperature	3	334.660	19.788	2.110×10^{-5}
25	Intercept+vole+fox+NAO	3	318.971	4.099	5.387×10^{-2}	12	Intercept+lemming+fox	3	334.752	19.881	2.015×10^{-5}
28	Intercept+vole*fox	2	319.704	4.832	3.733×10^{-2}	9	Intercept+temperature	2	334.829	19.957	1.940×10^{-5}
34	Intercept+rodent*fox+NAO	3	320.605	5.733	2.380×10^{-3}	20	Intercept+lemming+NAO	3	334.988	20.116	1.791×10^{-5}
30	Intercept+catVole*fox	2	321.609	6.737	1.440×10^{-2}	10	Intercept+NAO	2	335.705	20.833	1.252×10^{-5}
4	Intercept+rodent	2	321.631	6.759	1.425×10^{-2}	8	Intercept+fox	2	335.714	20.843	1.246×10^{-5}
14	Intercept+rodent+fox	2	321.704	6.832	1.374×10^{-2}	5	Intercept+catLemming	2	335.751	20.879	1.223×10^{-5}
29	Intercept+rodent*fox	2	322.294	7.422	1.023×10^{-2}	6	Intercept+catVole	2	335.806	20.934	1.190×10^{-5}
26	Intercept+rodent+fox+NAO	4	323.600	8.728	5.323×10^{-3}	24	Intercept+lemming+fox+NAO	4	336.323	21.451	9.189×10^{-6}
22	Intercept+rodent+NAO	3	323.635	8.764	5.229×10^{-5}	23	Intercept+fox+NAO	3	337.563	22.691	4.944×10^{-6}
27	Intercept+lemming*fox	3	328.046	13.174	5.763×10^{-4}	15	Intercept+catVole+fox	3	337.719	22.847	4.573×10^{-6}
32	Intercept+lemming*fox+NAO	2	329.171	14.299	3.284×10^{-4}						
11	Intercept+year	2	331.590	16.718	9.797×10^{-5}						

* interactive effect
\+ additive effect

Table 4. Parameter estimates of the top-ranked model explaining Dunlin nest survival rates.

				95% confidence intervals	
Dependent Variable	*Parameter*	*Estimate*	*SE*	*Lower*	*Upper*
Daily nest survival	Intercept	1.389	0.902	2.620	6.157
	Vole	1.140	1.139	-1.093	3.374
	Fox	0.140	0.155	-0.165	0.444
	NAO	0.852	0.346	0.174	1.531
	Vole*Fox	-0.566	0.231	-1.018	-0.114

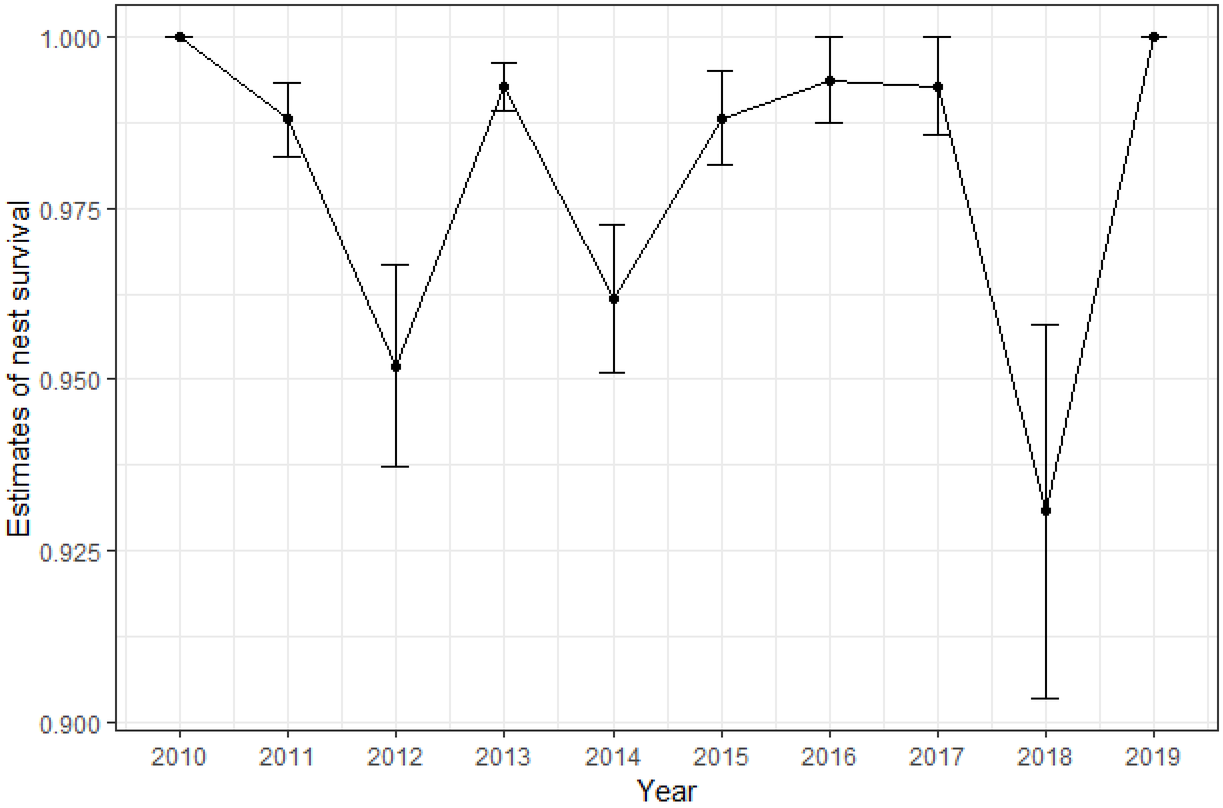

Figure 5. Interannual variation in DSR for Dunlin in Churchill, MB from 2010 to 2019. Error bars represent 95% confidence intervals for all estimates.

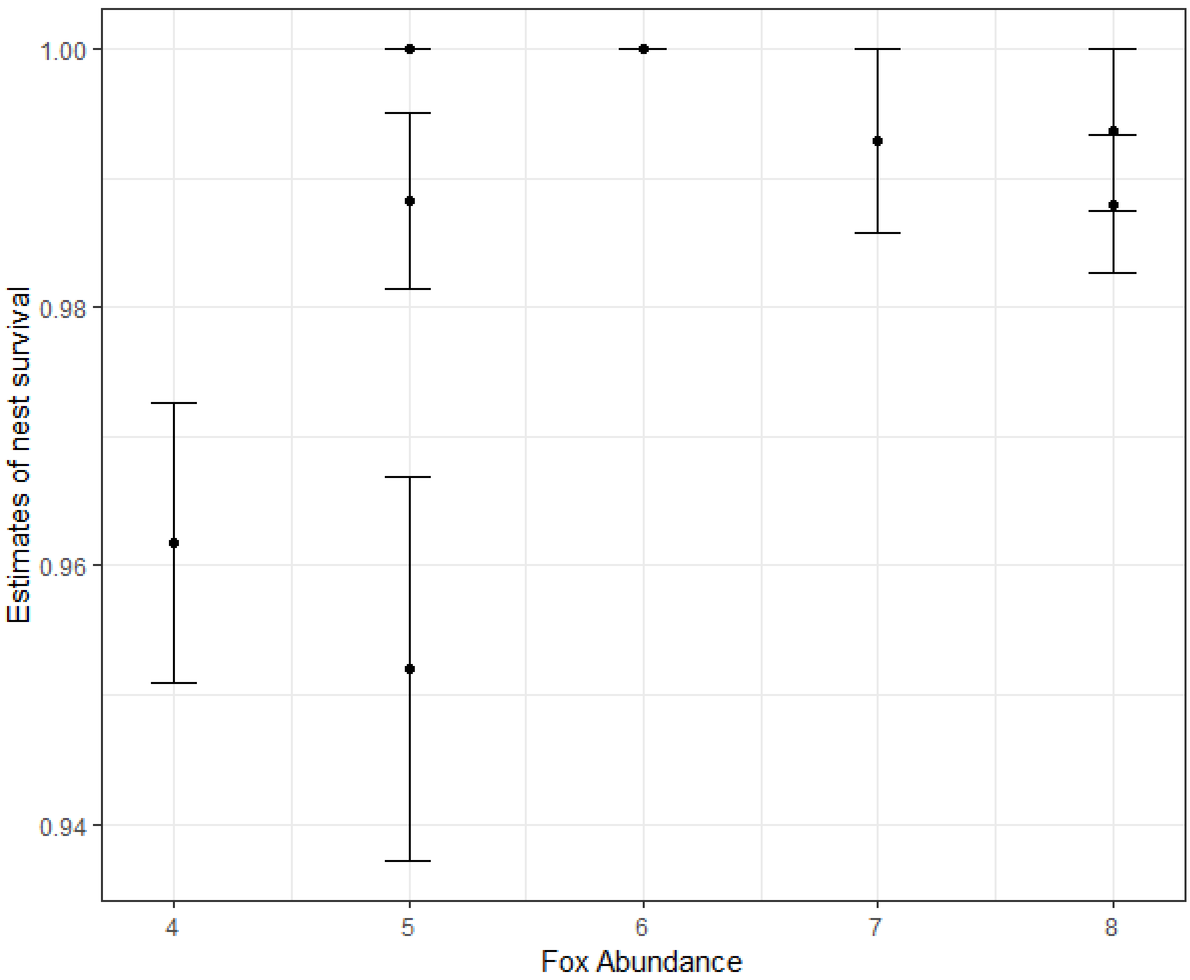

Figure 6. The estimated daily nest survival rate (DSR) of Dunlin plotted against fox abundance increases during years of low vole abundance (2010, 2011, 2012, 2014, 2015, 2016, 2017, and 2019).

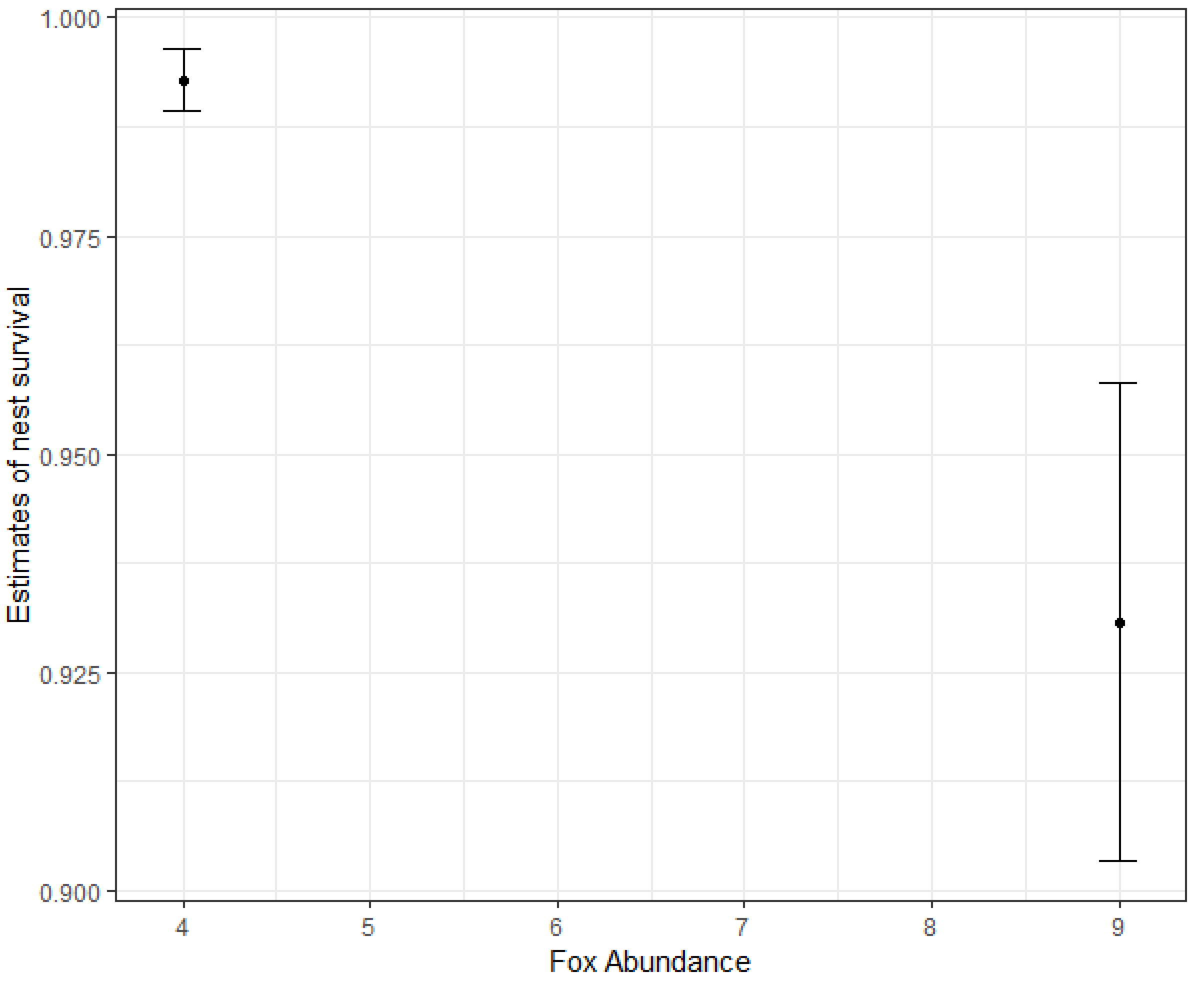

Figure 7. The estimated daily nest survival rate (DSR) of Dunlin decreases as fox abundance increases during years of high vole abundance (2013 and 2018).

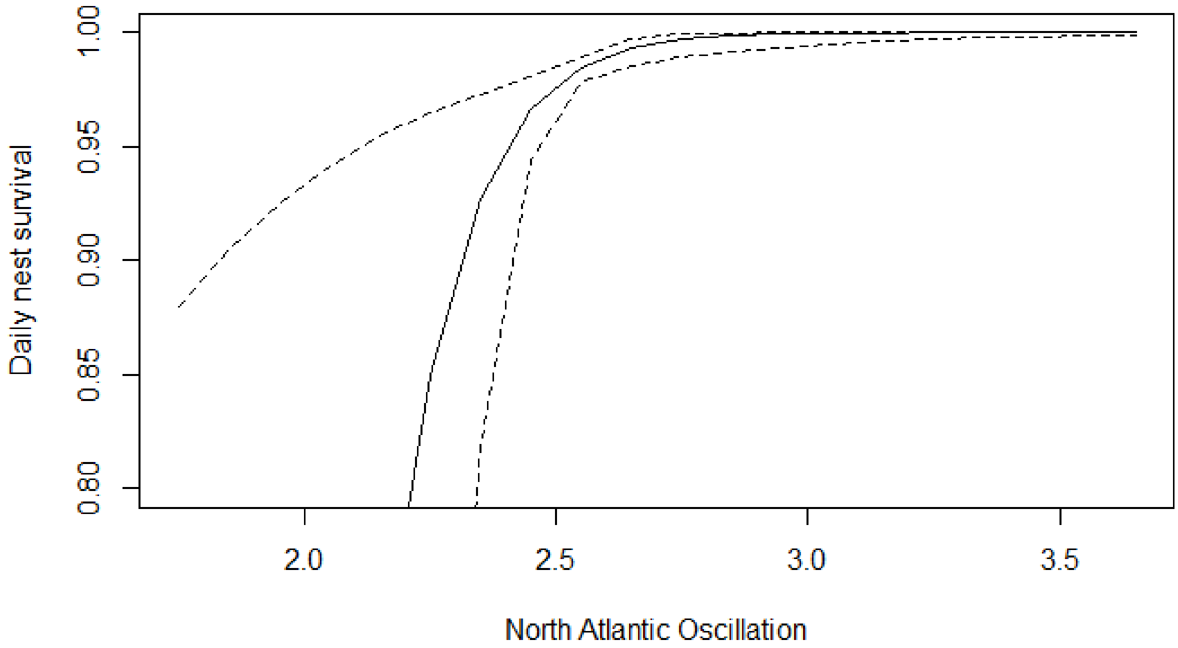

Figure 8. The daily survival rate (DSR) of Dunlin nests at Churchill increases as the North Atlantic Oscillation index increases. The solid line is the estimated DSR and the dashed lines represent 95% confidence intervals.

DISCUSSION

According to the APH, predators respond functionally and numerically to cyclic arvicoline rodent abundance which may then affect annual variation in predation risk on alternative prey such as shorebird eggs (Lack 1970, Angelstam et al. 1984). We found that over a 10-year period in the Subarctic, interannual variation in daily nest survival of Dunlin was best explained by an interactive effect of meadow vole abundance and fox abundance along with an additive effect of NAO. The abundance of lemming populations did not appear to have an effect on daily nest survival of Dunlin at this subarctic site. Thus, our prediction that decreases in arvicoline rodent abundance would increase the predation risk of Dunlin nests as suggested by the APH was not supported. The indirect relationship between arvicoline rodents and shorebird nest survival was opposite that expected and relatively more complex based on the significant interaction between vole and fox abundance. When meadow vole populations peaked, fox abundance also peaked and resultingly daily nest survival of Dunlin decreased. When meadow vole populations were low (virtually absent in our sampling), there was much more variation in Dunlin nest survival, and fox abundance appeared to have positive effect, the opposite of our predictions. The consumption of alternative prey like meadow voles has been increasing in importance as the Subarctic experiences rapid changes in climate (Dudenhoeffer et al. 2021). In general, voles have been expanding their northern range into the tundra as their preferred habitat continues to increase in these areas and suitable habitat for lemming decreases (Morris et al. 2011). My results indicate that in subarctic environments undergoing rapid ecological changes, recently established meadow vole populations (Smith and Foster 1957), not lemmings, have an unexpected indirect effect on shorebird nest survival in accordance with the APH.

Most studies examining the APH to date, have revealed indirect effects of lemming abundance on bird nest success, however most of these studies were situated in the High Arctic (e.g., Bêty et al. 2002, Blomqvist et al. 2002, McKinnon et al. 2014). The High Arctic trophic system is characterised as being simple due to having low species diversity and short food webs (Bazely & Jefferies 1997, Krebs et al. 2003;Figure 9). However, my study site in Churchill, Manitoba is situated at the northern limit of the boreal forest, and the southern limit of the tundra; this transition zone, characterized by relatively higher levels of biodiversity (Jehl 2004), exhibits more complicated trophic dynamics than other High Arctic sites (Figure 10). Moreover, the geographic range of many boreal species are currently expanding northwards due to climate change (Elmhagen et al. 2015), which may further complexify the trophic dynamics in subarctic regions. Regarding testing the APH, in Churchill, we are essentially investigating a multipredator, multiprey system. Churchill is home to both meadow voles and lemmings as main prey items for predators (Figure 9) whereas the High Arctic only has the latter (Figure 10; Ehrich et al. 2020). Furthermore, Churchill houses both red foxes and arctic foxes as the northern ranges of red foxes expand from the boreal forest into the tundra, which was once exclusively occupied by arctic foxes (Norén et al. 2017, Gallant et al. 2020). Though I did find an interactive effect of voles and fox abundance, one caveat of the study is that both red and arctic fox were combined during analysis, therefore it is unclear whether the effect on shorebird nest survival is due to a predator mediated effect via the red or arctic fox. In this sense, Churchill has a relatively more complicated Arctic system as several species occupy each trophic level.

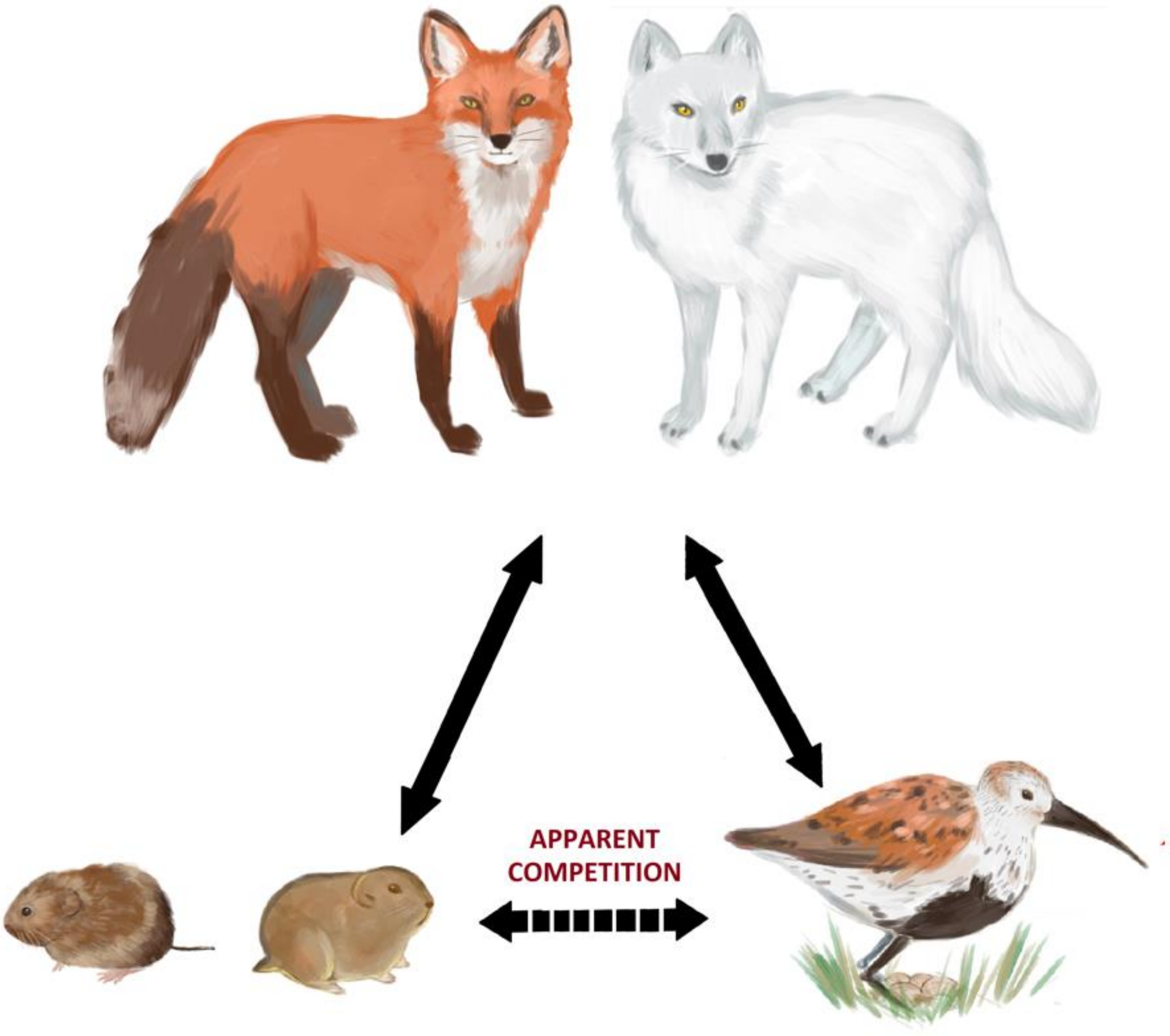

Figure 9. The trophic dynamics in the Subarctic showing a multipredator, multiprey system where the red fox and arctic fox (top) are the predators, and the meadow vole, lemming, and Dunlin (bottom) are the prey items.

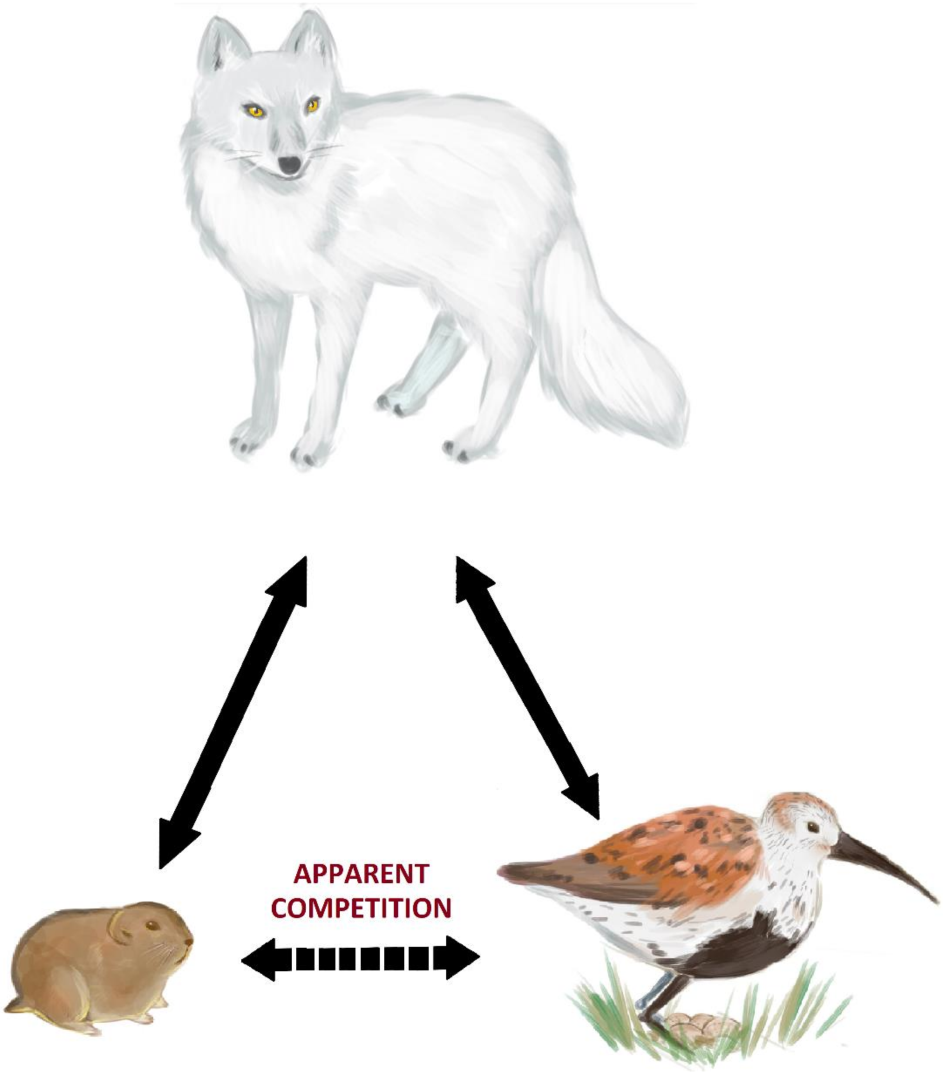

Figure 10. The trophic dynamics in the High Arctic showing a relatively simpler system compared to the Subarctic, where the arctic fox (top) is the predator and the lemming and Dunlin (bottom) are the prey items.

Though both red and arctic fox have been identified as the main predators of shorebird nests at several sites throughout the Arctic and Subarctic, the shorebird nest predator community of Churchill is not restricted to mammalian predators. Avian predators may also be an important factor in determining shorebird nest survival especially in the Subarctic (Ekanayake et al. 2015, Brown et al. 2022). Using camera monitoring of several shorebird species in Churchill, Brown et al. (2022) found that, although red and arctic fox were the primary predators at shorebird nests, avian predators such as Parasitic Jaegers (*Stercorarius parasiticus*), and Northern Harriers (*Circus hudsonius*) also depredate eggs, though in much smaller numbers. Using artificial nests, Brown et al. (2022) also demonstrated that predation risk on shorebird nests increased in proximity to Parasitic Jaeger nests. Several other studies have suggested that the diversity of avian predator species in the area may be associated with nest survival rates of shorebirds (McGuire et al. 2020, Brown et al. 2022). Unfortunately, I was not able to investigate the effects of avian predators across the entire 10-year study period. As Jaegers are also known to semi-specialize on lemming populations in the High Arctic (Flemming et al. 2019, Seyer et al. 2020), and they have only recently been confirmed as nest predators at my study site, a greater effort should be made to monitor the contribution of avian predators to the relationship between arvicoline rodents and shorebirds in subarctic systems.

Despite the interactive effect of voles and foxes on Dunlin nest success, it is worth noting that nest survival was relatively high across years, even in the years with low vole numbers and moderate to high fox numbers. One potential explanation for this is the presence of another conspicuous alternative prey. My study sites were located in proximity to a large subarctic-nesting goose colony (~30 km away). The colonial nesting Lesser Snow Goose (*Chen caerulescens caerulescens*) occupy the same trophic level as shorebirds and are an important alternative prey for both mammalian and avian predators. A high density of nesting geese may attract foxes during low arvicoline rodent years as an alternative food source (Bêty et al. 2001, Giroux et al. 2012, McKinnon et al. 2013). Fox dens closer to goose colonies had a greater probability of being used for reproduction during low lemming years in the High Arctic (Giroux et al. 2012). Goose eggs have also been found to be in the summer diets of the arctic fox (Roth 2002) while goslings were present in their diet in mid- to late June (Sammler et al. 2008). Lesser snow geese and Canada geese (*Branta canadensis interior*) are hyperabundant and stay into October, which means foxes can rely less on lemmings as a resource into the fall (McDonald et al. 2017). Cached goose eggs are important alternative prey items as they contain enough nutrients for arctic foxes to last through winter and spring (Careau et al. 2008). Goose eggs and goslings are abundant, detectable, and more profitable than shorebird eggs, so they would likely be more desirable to predators (McKinnon et al. 2014). Shorebirds have been found to nest at further distances from goose colonies (Lamarre et al. 2017) as shorebird nests found near goose colonies were subjected to a higher risk of predation (McKinnon et al. 2013, Flemming et al. 2016). The potential attraction of the goose colony could render our study site a refuge for shorebirds (McKinnon et al. 2013, Flemming et al. 2019), and result in lowered predation rates (Cresswell et al. 2010).

Dunlin are also one of 8 species of shorebird nesting in the study area. Sample sizes for other shorebird species were low and not consistent enough across the 10-year period to include in the analysis, however the presence of multiple other shorebird species as prey, could have a dilution effect on any indirect effects of arvicoline rodents on Dunlin. Our study found relatively consistent high nest survival rates. Etheridge (1982) and Weiser et al. (2018) found that Dunlin have a high proportion of hatching success relative to other Arctic-nesting shorebirds. In comparison to other shorebirds, Dunlin appear to have life history characteristics that are conducive to higher levels of nest survival. Dunlin are biparental and territorial (Jehl 2004), which may contribute to greater nest defence against predators (Smith and Wilson 2010). Additionally, they arrive later than other birds to their nesting sites, migrating two weeks after local birds have already started nesting. This late start to nesting could decrease the likelihood of having their nests depredated as foxes increase their foraging during early spring months with the birth of young (Sargeant 1978, Goszczyński 1989). Dunlin also have high renesting rates (Gates et al. 2013), which may inflate their nest survival rates as clutches laid later in the season are more likely to be found (Young et al. 2021), though we did not have evidence of renesting for our study site. Dunlin density is dependent on food availability (Etheridge 1982), which causes uneven spacing of nests that may make it harder for predators to find nests. Furthermore, Dunlin having the propensity to aggregate around a food source (Etheridge 1982) which may allow for nest group defence which could contribute to increased nest survival.

Distance from the town may be another important factor in daily nest survival. Shorebirds nesting near town have increased nest survival rates as there is less fox denning activity and a less diverse community of avian predators (Brown et al. 2022). Another reason Dunlin have high survival rates in this study may be that as foxes are opportunistic foragers located near the town of Churchill, scavenging for anthropogenic food sources during low lemming years may supplement their diet as an alternative food source (Elmhagen et al. 2017). Our study chose a 20 km radius around the Churchill Northern Studies Centre, which includes areas of high human activity and therefore provides anthropogenic food sources to the foxes living close by the town. As our study looked at nests from three different field sites within Churchill, future studies may need to investigate an effect of site as predation risk may vary with distance from town (Brown et al. 2022).

Finally, I cannot exclude that our unexpected results could be attributed to methodological issues regarding the estimation of fox and arvicoline rodent abundance. Our study used indirect methods to estimate relative fox abundance using field signs, which is the standard in ecology due to its ease and cost efficiency (Sadlier et al. 2004). Getting accurate estimates of fox abundance using direct methods is difficult as foxes are cryptic, nocturnal, and occur in low densities (Vine et al. 2009). Our study counted breeding dens, but this method may be complicated by the fact that females can split their litter between multiple dens, which could inflate abundance estimates, or if the litter is lost before emergence, can deflate the estimate (Sadlier et al. 2004). Employing methods such as radio-tracking and capture-mark-recapture would likely improve our estimates (Harris 1981, Sadlier et al. 2004). Though we did use capture-mark-recapture methods for arvicoline rodents, it is not clear how reliable these methods are when the densities are as low as those found in Churchill. Anthony Et al. (2015) found that Sherman live traps were efficient at capturing meadow voles in grasslands. However, Jung (2016) proposes that the environment the trap is set in matters, wherein he notes that Sherman live traps set in the Nearctic boreal forest were inefficient at catching small mammals, with voles being less likely to be recaptured again with these traps. Our study did see peaks for both arvicoline rodent cycles, but the peaks were defined by the capture of only 1 or 2 individuals.

The use of late spring and early summer North Atlantic Oscillation (NAO) in our study provides evidence that climate influences nest survival rates. Our results were as predicted with higher NAO values indicating warmer spring temperatures. Earlier snowmelt has been found to be associated with increased nest success possibly due to greater food availability during nesting

(Aharon-Rotman et al. 2015, Weatherhead 2005, Saafeld et al. 2019). Additionally, increased NAO index is related to earlier arrival date to breeding areas, which means earlier brood initiation (Dickey et al. 2008) and possibly even additional time to lay a second clutch. However, earlier and warmer springs may lead to asynchronous food availability for the chicks when they hatch (Dickey et al. 2008). As such, climate warming may advance the reproductive phenology of many Arctic-nesting birds but may reduce chick survival (Dickey et al. 2008, Saafeld et al. 2019). However, it is unclear if Dunlin show substantial phenotypic plasticity in reproduction to respond to long-term, rapidly changing climatic conditions. Dunlin may have a harder time adjusting to changing spring conditions due to less exposure to the different conditions over their breeding range as they are conservative species (i.e., strong site fidelity, territorial, consistent population densities; Saalfeld and Lanctot 2015), and they have a reduced ability to track annual spring conditions to time snowmelt for making settlement decisions (McGuire et al. 2020).

NAO has been used extensively as a proxy for annual weather conditions in ecological studies (Rodríguez and Bustamante 2003) as we do in this study. The benefits to using NAO is that it is readily available on the internet, has less measurement errors than local weather conditions that were taken at a short time interval, and it may be relevant to biological effects strongly influenced by global indices (Rodríguez and Bustamante 2003, Stenseth et al. 2003). A limitation to using a large-scale climate index such as NAO is that it may represent weather conditions too broadly and not capture the actual environmental conditions that were occurring locally (Rodríguez and Bustamante 2003). For instance, there was a year of flooding during the nesting season at Churchill that may have influenced nest survival. As such, there are meaningful variables that should be considered for future studies to fully encompass what the annual environmental conditions were like on a more local level, such as total annual rainfall

(Rodríguez and Bustamante 2003), nesting habitat (food availability: Martin 1987, microhabitat: Huey 1991, vegetative concealment: Etheridge 1982), and occurrence of flooding (Que et al. 2015, Plaschke et al. 2019). It is important to quantify local weather and habitat features in order to provide guidelines specific to a locality to create effective conservation actions.

We found evidence of vole population cycles playing a significant role in Dunlin nest survival, contrary to past findings suggesting that it is lemming cycles indirectly affecting shorebird nest survival. Few studies have explored the potential effects of vole cycles on shorebird nest survival, but we suggest that as the subarctic landscape rapidly changes, it is necessary to consider the interactions between multiple species within a trophic level as it becomes more complicated with food web change. It is clear from our multispecies study system that the effect of red foxes and meadow voles expanding their range northward into the tundra is creating new trophic dynamics. We recommend that future studies account for avian predators as well as they have too often been overlooked. Additionally, future studies will want to keep in mind that the APH may be operating at a larger spatial scale than the area of our study site in Churchill, especially when factoring in goose colonies which could present another alternative prey species and further complicate the trophic dynamics. Our study also highlights the importance of identifying effects of climate conditions on nesting success. Our results provide some evidence that our understanding of trophic interactions in the subarctic ecosystem, with its relatively more complex, multi species trophic dynamic, is still in its infancy. To fully test the APH in subarctic environments, researchers should focus on the simultaneous monitoring of multiple shorebird species, all possible alternative prey and all mammalian and avian predators. Once we have established a greater understanding of this dynamic system, we will be better positioned to predict the changing trophic interactions of the Arctic in the context of climate change.

Conservation Implications

This study found that voles interacted with fox abundance to affect the survival of Dunlin. As Dunlin may decline overtime (Fernández et al. 2010, Hope et al. 2019), it is important that conservationists better understand these predator mediated interactions in order to provide comprehensive conservation strategies for Dunlin. From this study we saw that the trophic dynamics in the Subarctic are different than those in the High Arctic, thus it is important to further study the Subarctic as trophic dynamics found in one ecosystem may not be generalizable to another to inform conservation strategies. Understanding the trophic interactions and the roles each species play is critical to creating effective conservation management and actions, especially as the Subarctic is rapidly changing and trophic dynamics evolve.

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