Predicting the effects of climate change on the breeding distribution of Arctic shorebirds

by

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ABSTRACT

Climate change is recognized as one of the five key drivers of biodiversity loss. The Arctic is one of the most rapidly changing regions on earth. Arctic-breeding shorebirds have several traits that have been linked with sensitivity to climate change and there is concern that environmental changes to shorebird breeding habitats may increasingly cause additional stress in these declining populations. The objective of my thesis was to understand the influence of climate change on the distribution of shorebirds breeding in the Canadian Arctic. Over 25 years, in two Arctic regions, I found a strong positive relationship between changes in the occupancy of shorebird species, and their “species temperature index”, indicating that shorebird breeding ranges may be shifting northwards in response to climate change. I found that when predicting the current breeding distributions of Arctic shorebirds, additional variables beyond climate, such as land cover, topography, snowmelt, and geology, accounted for more than half of the explained variance in shorebird occupancy and that individual land cover variables were often stronger predictors than climate variables. If current shorebird habitat is not well captured by climate variables alone, the implication is that shorebirds responses to climate change are likely to be moderated by factors aside from climate, and that it is important to include these additional variables in projections of how shorebird habitat may shift in response to climate change. I projected how climate change may affect the area of suitable habitat for 13 shorebird species by 2075. I also assessed how six different modelling decisions contributed to the uncertainty in these estimates. By far, the choice
of method for variable selection was the most influential modelling decision. Choices
about the modelling algorithm, global circulation model and the pool of variables used
were minor sources of uncertainty, and carbon emissions scenario had a negligible effect.
The majority of these species are likely to lose suitable habitat, but there is a high degree
of uncertainty in these estimates. With more land mass further north than other Arctic
regions, Canada is an important refuge for shorebirds as the climate changes.
ACKNOWLEDGEMENTS

The Covid-19 pandemic was a difficult time to be a grad student. While working on my thesis confined in my house, a lyric from a song by Run the Jewels really got to me. “I used to wanna get the chance to show the world I’m smart. Isn’t that dumb? I should’ve focused mostly on the heart.” When I reflected on why I was so struck by this lyric, I realized it was because while doing a PhD, I was surrounded by many incredibly intelligent people. But what matters much more to me than their smarts are their kindness, curiosity, open-mindedness, and their collective resolve to improve our society’s relationships with animals, plants, land and water. What made working on a thesis during the pandemic difficult was being cut off from this wonderful group of people.

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THESIS FORMAT AND CO-AUTHORSHIP

This thesis follows an integrated thesis format, with a general introduction (Ch1), a general discussion (Ch5), and three data chapters which are written in manuscript format (Ch2-4). Each data chapter has been published in a scientific journal, or is submitted and under peer-review at the time of defence. Both published articles are freely available for reproduction under the terms of Creative Commons Attribution Licenses.

I was the primary author for each chapter, developing the ideas for each chapter, preparing the data, conducting the analyses, and writing the manuscripts. Paul Smith and Lenore Fahrig assisted with supervision and editing. Jennie Rausch and Paul Smith assisted with data collection, funding, and resources. Jean‐Louis Martin and Tanguy Daufresne assisted with field work and editing. I have received permission from my co-authors to reproduce our collaborative work in my thesis.


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CHAPTER 1 - INTRODUCTION

SHifting distributions in response to climate change

Climate change is recognized as one of the five key drivers of biodiversity loss (IPBES 2019), and is expected to become an increasingly important threat over the next several decades (Leadley 2010; Habibullah et al. 2022). The global average temperature has risen by 1°C in the last century, and is tracking towards a warming of 3°C - 4°C by 2100 (IPCC 2018). The alternative trajectories for climate change from different anthropogenic carbon emission scenarios will be critical for biodiversity, as the risk of species extinction increases with every extra degree of warming (Costello et al. 2022). Combined with other major drivers of global change such as land use change, overexploitation, invasive species, and pollution, climate change may lead to tipping points where major transformations in biodiversity will be widespread and difficult to reverse, and will have negative consequences for ecosystem services and human well-being (Leadley 2010; Cardinale et al. 2012). In response to this recent and ongoing climate change, species across the earth are altering their spatial distribution, their phenology, and/or their physiology (Bellard et al. 2012).

Studies of species’ range shifts show that on average species distributions are moving towards higher latitudes and higher elevations in response to increasing temperatures (Chen et al. 2011; Parmesan and Yohe 2003). The expected pattern is that under scenarios of warming, suitable climatic conditions shift northwards or upslope, and
species distributions track the climatic conditions they are adapted to. However, there has been considerable heterogeneity in the magnitude and the direction of range shifts (VanDerWal et al. 2013; Tingley et al. 2012). The strength of the relationship between climate and species distribution varies across and within taxonomic groups (Kharouba et al. 2013). Unexpected patterns in distribution shifts have been linked to complex interactions between climate and biotic relationships (Wisz et al. 2013; Lenoir and Svenning 2015). Interactions among species can play a strong role in facilitating or impeding species presence within a suitable climate, affecting how species respond to abiotic environmental changes (Gilman et al. 2010; Tylianakis et al. 2008). Given these and other uncertainties, we cannot assume that species distributions will shift as we might predict based on temperature alone.

Estimating how the distribution of species may respond to climate change in the future has become an active field of research, responding to concerns about how a growing human footprint and accelerating global environmental change will reshape the world’s ecosystems (Guisan and Thuiller 2005). Many of the methods used for these studies have been criticized for oversimplifying the factors that determine species distribution, as they often do not include biotic interactions or dispersal limitations (Davis et al. 1998). For example, for birds with strong associations with a particular tree species, using climate-only models for projecting changes in suitable habitat can result in predictions that are much more extreme than when vegetation and other biotic processes are included (Matthews et al. 2011). There is a divide among conservation scientists about whether these models are useful and important in planning for climate
change, or if climate-distribution forecasts should be avoided because of the high degree of uncertainty (Lawler and Michalak 2017).

Species redistribution will never be fully understood or completely predictable, as natural systems are highly complex and dynamic (Pecl et al. 2017). However, despite the challenges, the urgency of responding to climate change demands that we make decisions; taking conservation actions earlier can be much more efficient for preserving vulnerable populations than delaying actions to reduce uncertainty in climate change projections (Naujokaitis-Lewis, Pomara, and Zuckerberg 2018). If we acknowledge and quantify uncertainties in how species distributions will change in response to climate change, this information can be used in environmental planning to help select adaptation measures that are robust to uncertainty in future conditions (Veloz et al. 2013; Carvalho et al. 2011).

ARCTIC-BREEDING SHOREBIRDS

Understanding how ecosystems may respond to climate change is especially important in the Arctic, which has been warming 1°C per decade for the past 30 years, significantly greater than the global mean (Meredith et al. 2022). The Arctic is predicted to be one of the most rapidly changing environments on earth, as the loss of ice, snow and permafrost are amplified by positive feedbacks with increasing temperature (Serreze and Barry 2011). In terrestrial Arctic ecosystems, longer growing seasons are permitting
low Arctic trees and shrubs to expand northwards (Myers-Smith et al. 2011). Because the
tundra biome is bordered by the northern limits of land, the total area of tundra habitat
is predicted to shrink substantially, and may disappear entirely in Alaska and much of
Eurasia. The Canadian Arctic Archipelago is one of the largest land masses at high
latitudes, and is likely to be a key region supporting the northwards migration of Arctic
biota (Callaghan et al. 2004).

In contrast to the accelerated rates of climate change, relative to the rest of the
world, land use changes due to agriculture, industry and urbanization have thus far been
minimal in the North American Arctic (Newbold et al. 2015). Consequently, species’
responses to climate change may be detected more clearly in the Arctic in comparison to
areas where both climate and land use change are driving range shifts. However, the
same warmer temperatures and reductions in sea ice that are leading to shifting species’
distributions and also opening up new opportunities for northern industrial development,
underscoring the need to better understand species’ distributions and to develop new
frameworks for conservation in the Arctic (Chapin III et al. 2015).

Shorebirds (suborder Charadrii) are the most diverse and abundant group of birds
in many tundra habitats (Ganter and Gaston 2013) and are therefore a useful taxonomic
group for investigating shifting distributions. Arctic-breeding shorebirds have several
traits that have been linked with sensitivity to climate change. Multispecies, broad-scale
analyses of European birds have shown that habitat specialists, long-distance migrants,
and cold-associated species experience more negative effects of increasing temperature
than habitat generalists, short-distance migrants, and warm-associated species (Pearce-
Higgins et al. 2015; Tayleur et al. 2016). The life histories of Arctic-breeding shorebirds exemplify these traits associated with sensitivity to climate change. They migrate very long distances, ranging from 5000 to 14,000 km in a single season’s migratory journey (Anderson et al. 2019; Piersma 2007). Shorebirds time their long-distance migrations based on changing daylight levels and intrinsic cues (Piersma et al. 2008; Karagicheva et al. 2016), which may limit their ability to change their migration timing as climate change advances spring phenology in the Arctic (English 2022; Saalfeld and Lanctot 2017; Both et al. 2010; Gill et al. 2014). Another factor that makes Arctic-shorebirds vulnerable to climate change is their specialization on moist tundra habitats (Cunningham, Kesler, and Lanctot 2016; Smith, Gilchrist, and Smith 2007; Galbraith et al. 2014). As the climate changes, these habitats are expected to become increasingly dominated by shrubs (Myers-Smith et al. 2011), and increasingly dry (Meredith et al. 2022), both of which will reduce their suitability for shorebirds. Shorebirds also rely on the great burst of ephemeral invertebrate prey that emerge across the tundra each summer. The timing of breeding of shorebirds and the development of invertebrates may respond differently to climate change, leading to phenological mismatch (McKinnon et al. 2012; Kwon et al. 2019).

Half of all North American shorebird species breed in the Arctic (Brown et al. 2001; Donaldson et al. 2000). Most of these species have declined dramatically in abundance since the 1970s, and declines in shorebird abundance are accelerating (Smith et al. 2023; Andres et al. 2012). These declines are attributed to several threats. Significant amounts of shorebird habitat at migratory stopover or non-breeding sites has been degraded, disturbed or replaced by human development in coastal areas (Thomas,
Lanctot, and Szekely 2006; Niles et al. 2009; Pfister, Harrington, and Lavine 1992; Prosser et al. 2018; Studds et al. 2017). Other threats include potentially unsustainable harvest of shorebirds around the Caribbean Basin (Watts and Turrin 2016; B. Watts, Reed, and Turrin 2015), and negative indirect effects from hyperabundant geese at Arctic breeding sites (Flemming et al. 2016). In light of these existing threats, and given that climate change in the Arctic is expected to be rapid and severe, there is concern that environmental changes to shorebird breeding habitats may increasingly cause additional stress in these declining populations (Galbraith et al. 2014).

THESIS OBJECTIVES

The overall objective of my thesis is to understand the influence of climate change on the distribution of shorebirds breeding in the Canadian Arctic. The main questions I will address are:

- Is there evidence that shorebird distributions have changed in response to the observed climate change in Canada?
- How strong is the relationship between the present distribution of shorebirds and the climate?
- How might suitable breeding habitat for shorebirds change by 2075?
- What are the sources of uncertainty when estimating the future suitable breeding habitat for shorebirds?
In Chapter 2, I looked for evidence that Arctic-breeding shorebird distributions may have already shifted in response to climate change. To date, it has not been possible to identify shifts in the distributions of most Arctic species due to a lack of regularly-repeated, large scale surveys. Using a unique set of observations, made 25 years apart in two mid-Arctic regions, I developed a novel method to look for evidence of distribution shifts, testing if there was a relationship between changes in shorebird species occupancy over time and their “species temperature index”, a simple version of a species climate envelope.

In Chapter 3, my goal was to assess the strength of the relationship between present shorebird distributions and climate. Climate change may affect the breeding distribution of shorebirds through either direct or indirect effects. However, there may be additional predictors determining suitable shorebird habitat that are independent from climate. Understanding the relative importance of climate and additional factors in predicting the current distribution of shorebird habitat will provide insights into the strength of the relationship we can expect between changes in climate and changes in shorebird distribution. This information is also useful for understanding which factors to include when projecting the future distribution of shorebird habitat. In this chapter, I quantify the direct and indirect effects of climate on shorebird habitat suitability using path analysis, and I assess the relative importance of climate and additional predictors in explaining the current distribution of shorebird habitat using deviance partitioning.

In Chapter 4, I had two complementary objectives. The first objective was to predict how the area of suitable habitat for shorebirds breeding in the Arctic might
change by 2075. The second was to better understand sources of uncertainty in these predictions, and how they influence the probability that shorebird species would lose or gain suitable habitat. I varied 6 different modelling decisions influencing the projections of present and future habitat for Arctic-breeding shorebird species, both to understand how each modelling decision influenced the projections, and to understand the collective importance of all modelling decisions relative to other sources of uncertainty inherent to sampling bird distributions.

In Chapter 5, I summarize the key results from chapters 2-4 and discuss their implications for Arctic-breeding shorebirds. I also review how my thesis more broadly contributes to the scientific literature on the effects of climate change on species distributions. I examine the limitations of my thesis and suggest future research priorities to build on this work.

Collectively, these projects contribute to a foundation of knowledge for understanding how shorebirds in North America will adapt to climate change. There are two main ways species can quickly respond to climate change: by shifting the timing of their activities, or their location. A PhD thesis by Kwon (2016) addressed the former, studying the impacts of climate change on the breeding phenology of Arctic shorebirds. My thesis addresses the latter, by offering the first evidence of distribution shifts, projecting future habitat changes, and clarifying which environmental relationships and modelling decisions should be considered when assessing the distributions of Arctic shorebirds.
CHAPTER 2 - CLIMATE-RELATED RANGE SHIFTS IN ARCTIC-BREEDING SHOREBIRDS

ABSTRACT

**Aim:** To test whether the occupancy of shorebirds has changed in the eastern Canadian Arctic, and whether these changes could indicate that shorebird distributions are shifting in response to long-term climate change.

**Location:** Foxe Basin and Rasmussen Lowlands, Nunavut, Canada.

**Methods:** We used a unique set of observations, made 25 years apart, using general linear models to test if there was a relationship between changes in shorebird species’ occupancy and their Species Temperature Index, a simple version of a species climate envelope.

**Results:** Changes in occupancy and density varied widely across species, with some increasing and some decreasing. This is despite that overall population trends are known to be negative for all of these species, based on surveys during migration. The changes in occupancy that we observed were positively related to the Species Temperature Index, such that the warmer-breeding species appear to be moving into these regions, while colder-breeding species appear to be shifting out of the regions, likely northwards.
Main Conclusions: Our results suggest that we should be concerned about declining breeding habitat availability for bird species whose current breeding ranges are centred on higher and colder latitudes.

INTRODUCTION

Over the past century, many species have shifted their distributions in response to anthropogenic influences. One increasingly important driver of distributional shifts is climate change, with species moving towards higher latitudes and higher elevations in response to a warming climate (Parmesan and Yohe 2003; Chen et al. 2011). For example, the northern limit of birds’ ranges measured by the North American Breeding Bird Survey shifted northward at a rate of 2.35 km/yr. between 1967 and 2002 (Hitch and Leberg 2007). Likewise, butterfly and moth ranges have expanded northward in Finland (Mikkola 1997), Great Britain (Hill et al. 2002) and across Europe (Parmesan et al. 1999). These changes in species’ range limits are an important measure of how species are redistributing in response to climate change. Patterns of species density and community composition are shifting as well, creating novel ecological communities (Devictor et al. 2012; Kampichler et al. 2012; Lurgi, López, and Montoya 2012). Estimating the distribution of species has become a very active field of research, responding to concerns about how accelerating global environmental change will reshape the world’s ecosystems (Guisan and Thuiller 2005).
Identifying shifts in distribution in response to climate change requires long-term and large-scale species data. However, the regions where the climate is changing fastest are often those where such data are sparse, making it challenging to measure shifts in species distribution (Shirey et al. 2021; Daskalova et al. 2023). For example, temperatures in the Arctic are rising three times faster than the global average (AMAP 2021). However, relative to other terrestrial biomes, consistent data collection efforts focused on describing species abundance and distributions are limited in the Arctic (Smith et al. 2020; Aronsson et al. 2021), due to logistical constraints associated with conducting field work at high latitudes (Mallory et al. 2018). Furthermore, citizen science programs such as the Christmas Bird Count, eBird, and Breeding Bird Survey programs (Curley, Manne, and Veit 2020; Devictor et al. 2008; Lindström et al. 2013; Johnston et al. 2021) are not viable in the Arctic because the region is very sparsely inhabited. As such, regularly repeated, large-scale surveys of vertebrate populations are currently lacking in the Arctic, which reduces the ability to assess patterns in species distributions as a function of shifts in climate conditions.

Despite the challenges, information about species distributions in the Arctic will be increasingly important for supporting conservation policies and protected areas being developed to protect northern species from increasing human presence and a rapidly warming climate. Melting ice is likely to lead to increases in shipping and resource extraction (Arbo et al. 2013). Arctic species are also particularly vulnerable to climate change due to three unique geographic factors that are leading to an “Arctic squeeze” which has the potential to dramatically limit the capacity of Arctic species to adaptively
shift their ranges (Vincent 2020; Meltofte et al. 2007). First, the surface area of the Earth decreases as latitude increases towards a fixed end point at the pole, limiting options for northern expansion of habitats (Gilg et al. 2012). Second, northern expansion of terrestrial habitats cannot occur in regions that are bordered to the north by the Arctic Ocean; in many locations there is no more northerly landmass available for terrestrial species to expand into (Wauchope et al. 2017). Third, the southern border of tundra habitat is moving northwards, as shrubs and trees also shift northwards in response to climate change, encroaching into the open habitats preferred by many tundra-breeding species (Martin et al. 2017; García Criado et al. 2020).

Here, we investigate whether the breeding distributions of shorebirds have shifted northward over a 25-year period in the Canadian Arctic. We focus here on shorebirds, the most abundant and diverse group of birds in many tundra habitats (Figure 2-1; Smith et al. 2020). These species are likely to be particularly sensitive to climate change because of their highly migratory life history, as Arctic-breeding shorebirds undertake long, energetically expensive migrations, only have a short window available for breeding in the Arctic, and depend on ecological synchronicities with their invertebrate prey (Hector Galbraith et al. 2014; Kwon et al. 2019). Surveys providing an index of shorebird abundance during their migrations through southern Canada and the United States suggest that shorebird populations have experienced pronounced declines in the past 50 years, including all of the species studied here (Bart and Johnston 2012; Smith et al. 2020; Smith et al. 2023). These declines are often attributed to habitat loss and degradation at migratory stopovers and non-breeding sites (Thomas, Lanctot, and
Szekely 2006), but given that climate change in the Arctic is expected to be rapid and severe, there is concern that environmental changes to shorebird breeding habitats may increasingly cause additional stress in these declining populations (Hector Galbraith et al. 2014).

We used a unique set of observations, made 25 years apart across 50,000 km² of mid-Arctic tundra habitats, to test whether the occupancy of shorebirds has changed over time, and whether these changes could indicate that distributions are shifting in response to long-term climate change. These data were collected as part of the Arctic Program for Regional and International Shorebird Monitoring (PRISM), an unprecedented Arctic-wide survey that will eventually track changes in the population size, trends and distribution of shorebirds (Bart and Johnston 2012). The observed summer temperature in northern Canada has increased by 1.6°C between 1948 and 2016 (Zhang et al. 2019). We therefore predicted that at mid-Arctic latitudes, species associated with warmer Low Arctic breeding habitats should be moving into the region and observed more frequently, and species associated with colder High Arctic habitats should be moving out of the region and observed less frequently (Jiguet et al. 2010; Figure 2-2). To test this prediction, we represented species temperature associations using the Species Temperature Index (STI), a simple version of a species climate envelope. Given that the population trends for these species are negative, we were interested to look at overall trends in survey counts in these regions to give context to any potential distribution shifts.
The STI is the long-term average temperature experienced by individuals of a species across their breeding range (Devictor et al. 2008). While species distributions are much more complex than simple climate relationships, this index has been a useful approach for describing how population trends and demography of bird populations are responding to climate change (P. Gaüzère et al. 2020; Princé and Zuckerberg 2015; Godet, Jaffré, and Devictor 2011). The collective contributions of individual species responses can give an indication of how the ecological community is responding to change (Curley et al. 2022; Pierre Gaüzère et al. 2019). Species with low STI consistently show more negative population trends in response to high temperatures (Pearce-Higgins et al. 2015). We thus predicted a positive relationship between STI and the temporal change in shorebird occupancy, with occupancy increasing for warmer-breeding species and occupancy decreasing for colder-breeding species over 25 years. Given that the large-scale population trends for these species are negative (Bart and Johnston 2012; Smith et al. 2023; Smith et al. 2020), for any species that have positive regional trends, this can be interpreted as reflecting distributional change, rather than change in population-level abundance.
METHODS

**SHOREBIRD SURVEYS**

Surveys were conducted as part of the Arctic PRISM shorebird monitoring program (Bart and Johnston 2012). These surveys were designed to estimate population sizes and habitat relationships for shorebirds breeding across the whole of the North American Arctic, only recently completing the first round of surveys that covers each of the 19 PRISM survey regions. Here, we include data from the first two regions to be surveyed for a second time in the Canadian Arctic. We surveyed 25,000 km² in the Rasmussen Lowlands, a coastal plain wetland complex located at the base of the Boothia Peninsula, designated as a Ramsar Wetland of International Importance (Carp 1980) and a Canadian Important Bird Area (Aguilar Mugica et al. 2009). We also surveyed a 25,000 km² area in Foxe Basin including the coastal wetlands and inland dry areas on Prince Charles Island, several nearby islands, and a portion of western Baffin Island (Figure 2-3). Both regions, approximately 750km apart, include a wide variety of land cover types, such as intertidal flats, low-lying salt marshes, flat marshy tundra, heath tundra, dry grasslands, beach ridge complexes and unvegetated broken shale (Bart and Johnston 2012). Within each region plots were selected by random sampling, stratified by habitat. The proportion of plots in wet, moist and dry habitats varied by region depending on habitat abundance (See Bart & Johnston, 2012 for more details), but on average 16%, 29%, and 56% of plots were in wet, moist, and dry habitats respectively. Based on these
random samples, the densities we present reflect the average densities across the study regions. These two regions are well suited for the current study because they are high quality shorebird habitat, containing a good diversity and abundance of shorebirds, and because they are located at mid-Arctic latitudes, therefore hosting both colder- and warmer-breeding species.

Each region was surveyed twice, 22-25 years apart. The Rasmussen Lowlands region was surveyed in 1994-95 and 2019, while the Foxe Basin region was surveyed in 1996-97 and 2019. While the earlier surveys of each region were completed over sequential two-year periods, the later surveys in both regions were completed simultaneously in one season owing to increased funding and resources. We excluded the 1996 data because of unusually poor weather and flooding that disrupted the normal behaviour of the birds (Bart and Johnston 2012). Each plot was surveyed once per survey period (1994-1997 and 2019). Surveys were conducted between June 18 and July 15, during late courtship and early incubation, when breeding territories could be identified from the birds’ territorial displays. The detectability of birds is believed to change throughout the season, as birds settle on their nests and incubation progresses. The late-courtship to early incubation period maximizes detectability. Detectability could vary slightly even within this time window, and most certainly varies due to weather and other factors. This variability in detection could introduce imprecision into the estimates. However, we do not expect that this would contribute to bias because surveys in both time periods occurred over a number of days during late courtship-early incubation. The PRISM surveys include a sub-sample of intensively surveyed plots to estimate detection
rates directly (see Bart and Johnston 2012), but these are intended to address changes in
detection rate at a large spatial scale, across regions, and were not used in these
analyses.

In both time periods, 28 plots were surveyed in the Rasmussen Lowlands and 36
plots were surveyed in Foxe Basin (64 plots total). Plots were 16 ha (400m by 400m).
Surveyors recorded the proportion of each plot covered by upland habitat (e.g. mesic
grasslands or heath habitats, sparsely vegetated xeric habitats) or lowland habitat (e.g.,
hydric areas of grass/sedge, polygonal wetlands, saltmarsh). In our analyses, we
categorized a plot as upland or lowland depending on which habitat type was
predominant.

Following PRISM protocols (Bart and Johnston 2012: “rapid surveys”), surveyors
searched the plot walking straight-line transects, covering a breadth of 50m with the
observers situated 25m apart, using a GPS to ensure complete coverage of the entire
plot. Surveys took approximately 90 mins. Observers recorded the number and species of
all birds observed within each plot. Birds were included in the count if they were
observed on the ground within the plot boundaries during the survey. Altogether we
observed 12 species of shorebirds: American Golden-Plover (*Pluvialis dominica*), Baird’s
Sandpiper (*Calidris bairdii*), Black-bellied Plover (*Pluvialis squatarola*), Buff-breasted
Sandpiper (*Tryngites subruficollis*), Dunlin (*Calidris alpina*), Pectoral Sandpiper (*Calidris
melanotos*), Red Knot (*Calidris canutus*), Red Phalarope (*Phalaropus fulicarius*), Ruddy
Turnstone (* Arenaria interpres*), Semipalmated Sandpiper (*Calidris pusilla*), Stilt Sandpiper
(*Calidris himantopus*), and White-rumped Sandpiper (*Calidris fuscicollis*).
**Analyses**

We tested whether the occupancy of breeding shorebirds, as well as species richness and density of shorebirds changed over time in a Generalized Linear Model (GLM) framework. We used logistic models for occupancy, and log-linear models for species richness and density, using a negative binomial distribution to account for extra zeros in the count data. We considered a structurally identical model for each response variable. Our inferential model consisted of an additive categorical effect of time period (i.e., 1994-1997 or 2019), which served as our index of temporal shifts in species distribution. Likewise, we considered additive categorical effects of region (i.e., Rasmussen or Foxe Basin) and habitat type (i.e., upland or lowland) to account for patterns in community structure associated with space and habitat, respectively.

We then tested whether species associated with warmer breeding habitats were moving into the region and species associated with colder habitats were moving out of the region. We modeled the relationship between the percent change in a species’ observed occupancy and its Species Temperature Index (STI), the long-term average temperature across the species’ breeding range (Devictor et al. 2008). The two species with the lowest and highest STI, respectively Red Knot and Stilt Sandpiper, were excluded from this analysis as they were not observed during the early survey effort. To calculate STI, we used the breeding season occurrence maps available from Birdlife International to define the North American breeding range of each species (BirdLife International and
Handbook of the Birds of the World 2020). We calculated the mean June temperature (1970-2000) for each species’ breeding range from the WorldClim 2.1 dataset, which has a 30 arc second (~1km2) resolution (Fick and Hijmans 2017). We chose to use this long-term average climate to match with the spatial temporal scale that seems relevant to the species range data described above, which is necessarily coarse. We used the mean June temperature because shorebirds arrive in the region, initiate their nests, and begin incubation in June, and temperature influences these behaviours (Meltofte et al. 2007). We clipped the mean June temperature grid to our breeding range polygons, and calculated a mean value for June temperature across the whole of each species’ breeding range. Finally, we used a linear model to test if there was a significant relationship (p < 0.5) between the percent change in a species’ occupancy and its STI. The data used for these analyses is published in Anderson et al. (2022).

All analyses were done using R 4.2.1 (R Core Team 2022) and RStudio 2022.7.2.576 (RStudio Team 2022) and the tidyverse package 1.3.2 (Wickham et al. 2019).

RESULTS

There was considerable variability in the occupancy, richness and density of breeding shorebirds between plots, therefore there was no significant difference between 1994-97 and 2019 (Table 1). The occupancy of breeding shorebirds per plot (all
species combined) in the two study regions was 79% in 1994-97 to 81% in 2019. The median (±SD) species richness per plot was 2 (±1.42) species per plot in 1994-97 and 2 (±1.64) species per plot in 2019 (Figure 2-4). The median density (±SD) of breeding shorebirds was 44 (±59) birds/km² in 1994-97 and 25 (±94) birds/km² in 2019 (Figure 2-4).

Changes in occupancy were highly variable between species (Figure 2-5). Occupancy by Baird’s Sandpiper, Buff-breasted Sandpiper, Black-bellied Plover, Pectoral Sandpiper and Red Phalarope declined (Table 2-2). Occupancy by Ruddy Turnstone and White-rumped Sandpiper increased moderately, and occupancy by Dunlin, American Golden Plover and Semipalmated Sandpiper increased considerably.

Interestingly, these same three species that increased substantially are the three species with the highest STI (Table 2-2). As predicted, there was a significant, positive relationship between the change in a species’ occupancy and its STI (Figure 2-6; Intercept = -95.49, Slope = 55.72, SE = 17.32, p = 0.01, Adjusted R² = 0.51). STI ranged from -1.3°C for Red Knot to 5.3°C for Stilt Sandpiper (Table 2-2).

**DISCUSSION**

Our results indicate shifting distributions for shorebirds in Arctic Canada at a large spatial scale, over a period of 25 years. We found occupancy varied widely across species, some increasing, some decreasing, despite the negative population trends observed for
these species based on migratory data from southern Canada and the United States (Bart and Johnston 2012; Smith et al. 2020; Smith et al. 2023). The changes in occupancy that we observed were positively related to STI. The increases in occupancy by and Dunlin, American Golden Plover and Semipalmated Sandpiper, the warmer-breeding species, indicate that these species may be moving into these regions. Most of the colder-breeding species, namely Baird’s Sandpiper, Buff-breasted Sandpiper, Black-bellied Plover, Pectoral Sandpiper and Red Phalarope, were observed less frequently, potentially as their ranges shifted northwards.

Species distributions are shaped by complex interactions between abiotic conditions, biotic interactions, dispersal capabilities and historical events, operating at different intensities at different spatial scales (Gaston 2003). Climate is widely recognized as one of the most common, influential drivers of species distribution, through both direct and indirect effects (Grinnell 1917; Root 1988a). All of the species considered here have breeding ranges centred at Arctic latitudes, but their breeding distributions nevertheless vary widely in terms of climate. Arctic-breeding shorebirds arrive to breed as the snow recedes in May and June, and their fledged young must depart before snow returns in August and September; temperature and weather during this brief window can have a profound effect on reproductive success (Meltofte et al. 2007). This may be through direct effects on incubation and chick survival during extreme events, or through indirect effects on invertebrate prey availability, the timing of snow and the vegetation community (Pearce-Higgins et al. 2010; Tulp and Schekkerman 2006; Kwon et al. 2019; Swift, Rodewald, and Senner 2017). Climate change during the non-breeding season also
plays a role, for example through inundation of coastal habitats (H. Galbraith et al. 2002). Decreased survival during the non-breeding season could influence distributions on the breeding grounds if there is strong migratory connectivity between breeding and wintering sites (Iwamura et al. 2013).

Climate change could also have indirect effects on shorebird distributions through its effect on biotic interactions (Blois et al. 2013). Climatic shifts appear to lengthen lemming population cycles in the Arctic, and decrease their maximum population densities (Gilg et al. 2012). This is likely to affect shorebird distributions, as the presence of lemmings provides alternative prey for Arctic foxes (Gilg and Yoccoz 2010; Léandri-Breton and Béty 2020), reducing predation risk for shorebird nests. Climate-related northward shifts of nest predator distributions could also increase nest loss through predation at higher latitudes, nest predation risk having been shown to decrease with latitude (McKinnon et al. 2010).

The status and distribution of shorebirds is undoubtedly influenced by non-climatic factors as well. The densities of Dunlin, Pectoral Sandpiper, Red Phalarope, Semipalmated Sandpiper and White-rumped Sandpiper are depressed in the vicinity of Snow Goose (*Anser caerulescens*) and Ross’ Goose (*Anser rossi*) colonies, for which populations and colonies have increased dramatically in the past century, in large part due to increasing agricultural food subsidies in their overwintering areas (Flemming et al. 2019). In their migration and wintering habitats, shorebird survival has been negatively affected by processes including loss of coastal habitats to development (Fernández and Lank 2008; Murray and Fuller 2015), and unsustainable hunting of some species (Watts,
Semipalmated Sandpipers have shifted their stopover habitats in response to increasing predation as raptor populations recover from critical lows, a dynamic that is likely affecting other shorebird species as well (Hope et al. 2020).

All studied species, including the four species showing increasing occupancy in our two study regions, are thought to be declining in total abundance, based on surveys during migration at temperate latitudes in Canada and the US (Smith et al. 2023). These declines average around 50% over 15 years and appear to be accelerating when compared to the previous 15 years. The mismatch between the trends we observed in the eastern Arctic and the overall population trends for Semipalmated Sandpiper, Ruddy Turnstone, Dunlin, and American Golden-Plover suggest that our study regions may have been closer to the margins of these species’ ranges 25 years ago, and that climate change has shifted their distributions such that our regions are now closer to the centre of their ranges, where occupancy is assumed to be higher. For the species showing declines in occupancy, our data are likely reflecting a shift or contraction of their ranges towards the north as well as overall population declines. The inference of range shifts is stronger for the four species showing simultaneously increased occupancy in our region and overall population declines. It is interesting to note that we also observed a decline in the density of all breeding shorebirds in these two regions, although the result was not significant.

A similar study of shorebird population trends in Fennoscandia found that there was no relationship between breeding latitude and species population trends (Lindström et al. 2019). The authors discuss how the relationship between climate and latitude in
this region is complicated by altitudinal west-east climate gradients. The area for which
they calculated a species mean latitude may also have been too small to fully capture the
range of conditions these species inhabit (14° of latitude vs 25° of latitude in the current
study). Using metrics such as STI which more closely reflect the conditions that species
experience is likely more useful than assessing relationships between species population
trends and latitude.

Given the numerous other factors and interactions influencing shorebird
distributions, it is notable that we detected an apparent signal of climate change through
our cross-species analysis. As climate change in the Arctic is expected to be rapid and
severe, environmental changes to shorebird breeding habitats may increasingly cause
additional stress in these species. Changing distributions on the Arctic breeding grounds,
including local increases in occupancy and density in some cases, indicate that suitable
habitat continues to exist in the Arctic for some species. However, there are limits to
these species’ capacity to shift their ranges, especially for colder-breeding species, not
least of which is the geographic limit imposed by the Arctic Ocean. The shift towards a
warmer-breeding community of species suggests that, in addition to the pressures on
shorebird species during the non-breeding periods, we should also be concerned about
decreasing breeding habitat availability for shorebird species whose current breeding
ranges are centred on higher, colder latitudes.
Figure 2-1: White-rumped Sandpiper, one of the 12 species of shorebirds observed in this study. Shorebirds are the most abundant and diverse group of birds in many tundra habitats.
Figure 2-2: Expected changes in plot occupancy as species distributions shift north in response to warming temperatures. Species are assumed to have higher occupancy in the centre of their range and lower occupancy at the edges of their range (Gaston et al. 2003; indicated in this figure by opacity of the orange and blue species ranges). Plots are surveyed within the study area outlined by the black box. The STI (mean June temperature of the range) for species 1 is 5 °C, in this case making it a colder-breeding species. At time 1, the mean temperature of the study area is also 5 °C, therefore the occupancy of species 1 is high. At time 2, the mean temperature of the study area has increased to 10 °C. Species 1 has shifted its distribution northwards. The study area is now on the southern edge of its range, and the occupancy of species 1 has declined. The STI of species 2, a warmer-breeding species, is 10 °C. At time 1 the study area is at the northern edge of its range, therefore the occupancy of species 2 at time 1 is low. At time 2, the study area is now in the centre of its range, and the occupancy of species 2 has increased.
Figure 2-3: Map of eastern Arctic study areas showing plots where breeding shorebirds were surveyed in 1994-97, and then 22 to 25 years later in 2019.
Figure 2-4: Species richness (right) and density of breeding shorebirds per km$^2$ (left) observed in the two time periods of our study, for both regions combined.
Figure 2-5: Change in individual species occupancy in plots surveyed in 1994-97 and 2019 (n = 64) in both study regions combined.
Figure 2-6: Linear model of the relationship between the percent change in occupancy of shorebird species from 1994-97 to 2019 and their Species Temperature Index. Intercept = -95.49, Slope = 55.72, p = 0.01, Adjusted $R^2 = 0.51$. The Species Temperature Index is the mean June Temperature from 1970 to 2000 across the species range. See Table 2-2 for a legend of 4-letter bird species codes.
Table 2-1: Generalized linear model results for change in occupancy, richness and density of breeding shorebirds (all species) from 1994-97 to 2019 in the Rasmussen Lowlands and Foxe Basin (n = 64). The models included time period as the main predictor of interest, region to control for any regional effects, and habitat to control for any habitat effects (of upland and lowland habitat). The model for occupancy used a binomial distribution, and the models for species richness and density used negative binomial distributions. The intercept represents the parameter estimate for reference categories (1994-97, Foxe Basin, lowland). The estimate for the parameters in brackets (2019, Rasmussen, upland) represent the difference for that category and the reference level.

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<th>Model</th>
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<th>Estimate</th>
<th>SE</th>
<th>Z</th>
<th>p</th>
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<td><strong>Richness</strong></td>
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Table 2-2: Species Temperature Index and change in occupancy between 1994-97 and 2019 for 12 shorebird species.

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<th>% Occupancy 2019</th>
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CHAPTER 3 - CLIMATE VARIABLES ARE NOT THE DOMINANT PREDICTOR OF ARCTIC SHOREBIRD DISTRIBUTIONS

ABSTRACT

Competing theoretical perspectives about whether or not climate is the dominant factor influencing species’ distributions at large spatial scales have important consequences when habitat suitability models are used to address conservation problems. In this study, we tested how much variables in addition to climate help to explain habitat suitability for Arctic-breeding shorebirds. To do this we model species occupancy using path analysis, which allow us to estimate the indirect effects of climate on other predictor variables, such as land cover. We also use deviance partitioning to quantify the total relative importance of climate versus additional predictors in explaining species occupancy. We found that individual land cover variables are often stronger predictors than the direct and indirect effects of climate combined. In models with both climate and additional variables, on average the additional variables accounted for 57% of the explained deviance, independent of shared effects with the climate variables. Our results support the idea that climate-only models may offer incomplete descriptions of current and future habitat suitability and can lead to incorrect conclusions about the size and location of suitable habitat. These conclusions could have important management implications for designating protected areas and assessing threats like climate change and human development.
INTRODUCTION

Habitat suitability models are used to describe the relationship between species’ presence in geographic space and the characteristics of the environment, and to estimate how likely a species is to occupy unsampled locations. Along with closely related species distribution models, environmental niche models, resource selection functions and bioclimatic envelope models (but see Peterson and Soberón 2012), these analyses are increasingly popular for addressing a wide range of questions, such as how species will respond to climate change (e.g. Ramirez-Villegas et al. 2014), identifying priority areas for threatened species (e.g. Fong, Viña Dávila, and López-Iborra 2015), managing landscapes (e.g. M.-G. Zhang et al. 2012), and understanding the spread of invasive species (e.g. Kramer et al. 2017). However, different theoretical perspectives about how these relationships between species and their environment are structured have important consequences for the variables included in these models, and therefore how we use them to address conservation problems.

One hypothesis suggests that climate is the dominant factor influencing species’ distributions at large spatial scales (Root 1988b; Soberón 2010). Climate influences species’ distributions directly, for example through thermal tolerances, and indirectly, for example through climate’s influence on land cover (Figure 3-1). Interestingly, many of the papers that invoke this hypothesis are studies of future species distribution based on climate-only models (e.g. Langham et al. 2015). One reason for this practice is pragmatic: often there are no future predictions available for the other potential covariates of
distribution such as land cover (Oliver and Morecroft 2014). However, these papers also often argue that at large spatial extents, such as entire ranges for widespread species, the direct and indirect effects of climate encompass the majority of the influences on species’ distributions (Pearson and Dawson 2003). ‘Climate-only’ models are often evaluated using a threshold, such as a model with an AUC of at least 0.7 has “good” explanatory power, and usually climate-only models exceed the threshold (Dyderski et al. 2018; Graham et al. 2019).

A competing hypothesis suggests that habitat suitability models need to be more comprehensive because there can be additional important factors shaping species distributions that may not be well described as an indirect effect of climate, as is often assumed in climate-only models. In contrast to the future-oriented models described above, papers estimating current species distributions often include a wide range of predictors, many of which are non-climatic, relating instead to resources and habitat structure (Elith and Leathwick 2009). Studies aimed at estimating current habitat suitability typically compare multiple models to identify a best model, which is rarely a climate-only model (e.g. de Araújo, Marcondes-Machado, and Costa 2014; Jenkins et al. 2020; Regos et al. 2019). In particular, biotic interactions may be important even at large spatial extents, not just at local scales (Wisz et al. 2013). For example, many species require the presence of specific plants as food or hosts to facilitate their presence in a region (Sexton et al. 2009). Precipitation is often a poor proxy for the water available to plants, as topography and soil substrate control how precipitation translates into soil moisture (Piedallu et al. 2013). Soil predictors such as pH and nutrients are important
predictors of plant distribution, are strongly influenced by underlying geology, irrespective of climate (Mod et al. 2016).

In this paper, we ask how much do variables in addition to climate help to explain habitat suitability? To do this we model species occupancy using path analyses, which allow us to estimate the indirect effects of climate on other predictor variables, such as land cover. We also use partitioning to quantify the total relative importance of climate versus additional predictors in explaining species occupancy. We addressed our question using data on the distribution of Arctic-breeding shorebirds. Most papers studying habitat suitability for Arctic-breeding shorebirds have been conducted at smaller extents, and for the most part they do not include climate variables, likely because climate does not vary enough over smaller extents to be a relevant predictor (e.g. Cunningham, Kesler, and Lanctot 2016; Smith, Gilchrist, and Smith 2007; Swift, Rodewald, and Senner 2017). The few large-extent models that have been used to predict habitat suitability for these species include a model that largely relies on climate predictors (Wauchope et al. 2017), but also a report suggesting that additional predictors beyond climate were important for predicting current and future occupancy of Red Knot (Calidris canutus) and Semipalmated Sandpipers (Calidris pusilla; Lathrop et al. 2019). Based on previous studies of Arctic shorebird habitat associations, the additional predictors we consider are land cover, snow cover, substrate chemistry, and elevation, and the standard deviation of elevation, as shorebirds prefer flat habitats (Cunningham, Kesler, and Lanctot 2016; Wauchope et al. 2017; Lathrop et al. 2019; 2018; Saalfeld et al. 2013).
A priori, we expected that the probability of shorebird occupancy at sites
distributed over large spatial extents can be estimated considerably better by explicitly
including additional variables in habitat suitability models, rather than assuming that
these additional variables are themselves driven by climate. If climate is the dominant
factor influencing the occupancy of breeding shorebirds across the Arctic, we expect that
the variation in shorebird occupancy is mostly explained by the combination of the direct
effects of predictors from climate-only models and their indirect effects through their
effects on the additional predictors. If, independent of climate, additional predictors have
important influences on the occupancy of breeding shorebirds across the Arctic, we
expect that a substantial amount of the explained variation in shorebird occupancy is
uniquely attributed to the additional predictors not found in climate-only models.

METHODS

OVERVIEW

To look at the predictors of shorebird occupancy, their interrelationships, and
their relative effect sizes, we developed a hypothetical path diagram outlining our
hypotheses about how climate predictors and additional environmental predictors are
interrelated (Figure 3-2). We identified predictors that have been important in other
models of habitat suitability for Arctic-breeding shorebirds (Cunningham, Kesler, and
Lanctot 2016; Wauchope et al. 2017; Lathrop et al. 2018; 2019; Saalfeld et al. 2013). We
used path analysis to verify the structure of our path diagram and assess the degree to which the effects of additional predictors are driven by climate. We then used a deviance partitioning approach to test whether the total (direct + indirect) effects of climate predictors explained most of the variation in shorebird occupancy. All analyses were performed using R Statistical Software v4.2.1 (R Core Team 2022).

**Shorebird Surveys**

Plots were surveyed for shorebirds across the Canadian Arctic as part of the Arctic Program for Regional and International Shorebird Monitoring (PRISM; Bart and Johnston 2012), which covers all of Arctic North America as defined by the Circumpolar Arctic Vegetation Map (Walker et al. 2002). The Canadian PRISM data used here includes 2336 plots across the Canadian Arctic (Figure 3-3), an area of 3.5 million km². Given this massive area, surveys were completed over a number of years, from 1994-2018, with a majority of the sampling effort concentrated between 2003 and 2018. The Canadian Arctic was divided into 12 regions based on logistical considerations. Within each region plots were selected by random sampling, stratified by habitat. The proportion of plots in wet, moist and dry habitats varied by region depending on habitat abundance (see Bart and Johnston 2012 for more details), but on average 16%, 29%, and 56% of plots were in wet, moist, and dry habitats respectively. In all years, surveys were conducted between June 18 and July 15. This corresponds with the latter part of shorebird courtship and the early part of incubation, when breeding territories could be identified from the birds’
territorial displays. Plots were typically 12-16 ha (400 m x 300-400 m). We excluded one set of surveys because extensive flooding led to very atypical breeding conditions. We also excluded surveys for which observers recorded nearby human development, which is rare across the study area and could potentially alter shorebird habitat preferences. For 211 plots that were visited in more than one year, we randomly selected one of the surveys to be included in the final dataset.

Plots were surveyed for breeding birds following PRISM protocols (Bart and Johnston 2012). Two surveyors searched the plot walking straight-line transects, covering a breadth of 50 m with the observers situated 25 m apart, using a GPS to ensure complete coverage of the entire plot. Surveys took approximately 90 mins. Observers recorded the number and species of all birds observed within each plot. Altogether we observed 19 species of shorebirds, 17 of which were observed in at least 30 plots, our minimum threshold for developing habitat suitability models: American Golden-Plover (Pluvialus dominica), Baird’s Sandpiper (Calidris bairdii), Black-bellied Plover (Pluvialis squatraola), Buff-breasted Sandpiper (Tryngites subruficollis), Dunlin (Calidris alpina), Least Sandpiper (Calidris minutilla), Pectoral Sandpiper (Calidris melanotos), Red Knot (Calidris cantus), Red Phalarope (Phalaropus fulicarius), Red-necked Phalarope (Phalaropus lobatus), Ruddy Turnstone (Arenaria interpres), Sanderling (Calidris alba), Semipalmated Sandpiper (Calidris pusilla), Stilt Sandpiper (Calidris himantopus), Wilson’s Snipe (Gallinago delicata), and White-rumped Sandpiper (Calidris fuscicollis). In our analyses we chose to model occupancy instead of density because shorebirds were observed at very low densities (average of <5 birds/survey for all 17 species, ranging from 0.03-0.68 birds
for each individual species), with frequent counts of 0 (no birds were observed in 54% of surveys). Surveys were observational, and involve no capture or sampling. Lands surveyed include Federal Crown Lands, Inuit Owned Lands, and Federal and Territorial Protected Areas. Access to these lands was granted through permits to JR including: Environment and Climate Change Canada (NWT-MBS-17-03, MM-NR-2022-NU-005, NUN-NWA-17-04, SC-NR-2001-NT-004, SC-NR-2022-NU-005), Government of Nunavut (WL2022-031), Kitikmeot Inuit Association (KTX115X007), Kivalliq Inuit Association (KVX15N05), Qikiqtani Inuit Association (Q14X001).

**Environmental Predictors**

We used two categories of environmental predictors of shorebird occupancy: predictors found in ‘climate-only models’, and additional predictors in ‘climate+additional models’. For the climate predictors we used the bioclimatic data available from WorldClim 2 at a 30 arc-second resolution (~1km; Fick and Hijmans 2017). This data is typical of that used in climate-only habitat suitability models because it is global in scope and easily accessible. We eliminated any predictors that had correlations higher than 0.7, selecting the 5 uncorrelated climate predictors that seemed most relevant to shorebird occupancy: annual mean temperature, temperature seasonality (standard deviation of mean monthly temperature x 100), mean diurnal range (mean of monthly max temp – min temp), annual precipitation, and precipitation seasonality (coefficient of variation of monthly precipitation).
Additional predictors in the climate+additional models of shorebird occupancy included topography, geology, snowmelt, and land cover variables. The topography predictors we included were elevation, the standard deviation of elevation, and distance to coast. We used elevation data available from WorldClim 2, also at a 30 arc-second resolution (~1km). From this, we derived the standard deviation of elevation over a 5km grid. We calculated distance to coast from coastline data available from Natural Earth (Patterson and Vaughn Kelso 2022). To represent geology, we used substrate chemistry data from the Circumpolar Arctic Vegetation map (Walker et al. 2002), which includes 3 categories: acidic (pH < 5.5), circumneutral (pH 5.5-7.2) and carbonate (pH > 7.2). Snowmelt timing was derived from an 8-day composite MODIS product, and we used the day of 50% snowmelt per 500m pixel (O’Leary III et al. 2019). We used land cover data from the Circa-2000 Northern Land Cover Map of Canada. This dataset derives 15 land cover classes from Landsat data 1999-2002 at a 30m resolution (Olthof, Latifovic, and Pouliot 2009).

**Statistical Analyses**

Before building models of habitat suitability for each species of shorebird, we first determined the spatial extent at which day of snowmelt and each land cover predictor most strongly affected each species, their "scale of effect" (Jackson and Fahrig 2012). Habitat selection is scale dependent, therefore identifying the appropriate scale at which species respond is important for making correct inferences about the relative importance
of environmental variables (McGarigal et al. 2016). We did not complete this step for climate, topography or substrate because these variables were measured at much larger spatial resolutions, and show little variation at small spatial resolutions. To find the scales of effect, we first filtered the plots to a reduced set that were at least 10km from each other. We calculated the mean day of snowmelt and the proportion of each land cover type at multiple scales, centered on the middle of each plot. We tested spatial scales from a radius of 200m, approximately covering the plot itself, to 10km, increasing by increments of 100m up to 2500m and by increments of 500m thereafter. We created a series of logistic regression models relating the occupancy of each of the 17 shorebird species to each predictor at each spatial scale. Then for each predictor, we identified the scale of effect for that species as the extent where the model had the lowest AIC value. In the models described below, we entered the snowmelt timing and land cover predictors at their scales of effect.

We used path analysis to test whether the effects of the additional variables on habitat suitability for shorebirds were largely explainable as indirect effects of climate. Path models were fit using the R package piecewiseSEM (Lefcheck 2016). We fit a path model for each of the 17 shorebird species, following the causal structure illustrated in Figure 3-2. We also included correlated error terms among all climate variables, and among all land cover variables. All models included an offset for plot size. We used a test of directed separation (d-sep) to evaluate the goodness-of-fit for our hypothesized path model, assessing the conditional independence between pairs of variables in the model. Significant d-sep test results indicated associations between substrate and climate, and
substrate and shorebird presence, so we included these links as correlated error terms as well. For each species model, the median standardized effects and 95% confidence intervals were estimated using nonparametric bootstrapping from 10,000 resamples using the R package semEff (Murphy 2022). The path coefficients we present are semi-partial correlations, which are the correlation between the unique components of predictors (residualised on other predictors) and the response variable. Note that this approach controls for multicollinearity between predictors, whereas many path analyses present standardized partial regression coefficients which do not control for multicollinearity, which often creates an upward bias in perceived effect sizes (Keith 2015). Model fit was assessed with Fisher’s C statistic, for which a significant value indicates that no potentially significant missing paths were excluded, as well as visually using plots of residuals calculated from the median coefficient values. To assess the relative strength of individual predictors, we compared the absolute values of their total effects on shorebird species occupancy. The total effect of a predictor is the sum of its direct effects (the path coefficients between the predictor and the shorebird response) and its indirect effects (the product of the path coefficients between the predictor, intermediate predictors, and the shorebird response). Effects were considered to be significant when 95% confidence intervals did not contain 0.

To assess the overall relative contribution of climate-only model predictors and additional predictors to shorebird occupancy, we used a deviance partitioning approach. We used Generalized Linear Models (GLMs) with a binomial distribution to determine the deviance explained by climate and additional predictors. Species were analysed
separately. Deviance was partitioned using the ratio of the null deviance and the deviance explained by each of the following factors: climate predictors, additional predictors, deviance shared between climate and additional predictors, and unexplained deviance.

RESULTS

We observed 11,636 shorebirds in surveys of 2336 plots from 1994-2018. At least one shorebird was observed on 54% of plots. By species, occupancy varied from 1% (Red Knot) to 14% (Semipalmated Sandpiper); the average (±SD) species occupancy was 6 ± 4%. Descriptive statistics of the environmental predictor values are in Appendix A Table A2. The mean scale of effect for land cover classes was 4400m (median = 3000m). For virtually all land cover classes, the scale of effect varied from the smallest possible scale (200m, just covering the plot) to the largest possible scale (10km) depending on the species. Similarly, each species responded to the different land cover classes at very different spatial scales (Appendix A Table A3). The median scale of effect for snowmelt timing was 5000m (median = 3500m)

Direct effects of climate-only model predictors accounted for on average 17% of the total explained deviance in shorebird occupancy (Figure 3-4). The total effect of climate-model predictors (direct effect + shared/indirect effect) accounted for on average 43% of the total explained deviance in shorebird occupancy. The unique effects
of additional predictors included in climate+additional models, beyond the indirect effects of climate through these predictors, accounted for on average 57% of the total explained deviance in shorebird occupancy (Figure 4-5). Depending on the species, the ratio of deviance explained by climate-only predictors vs additional predictors ranged from 80% climate/20% additional to 10% climate/90% additional. The mean explained deviance for our models of shorebird occupancy was 27% (ranging from 9%-42%). The mean AUC of our models of shorebird occupancy was 0.87 (ranging from 0.72-0.93). The full results of the GLMs used for deviance partitioning can be found in Appendix A Table A4.

Overall, the total effect sizes of climate predictors (direct + indirect sizes; Figure 3-2) and additional predictors on shorebird occupancy were similar (Figure 3-5). Our path model included the paths illustrated in Figure 3-2 (Fisher’s C statistic = 3.14, P = 0.21). The 5 predictors with the largest significant absolute effect on shorebird occupancy were additional predictors, specifically the predictors that described the proportion land cover at the species-specific scale of effect of high shrub, dwarf shrub, sparsely vegetated till, dry graminoid dwarf shrub, and non-tussock graminoid. The climate predictors with the largest significant absolute effect on shorebird occupancy were mean diurnal range and mean annual temperature (Figure 3-5). A summary of the significant total effects of predictors on shorebird occupancy can be found in Appendix A Table A6. The full results of the 17 species-specific path models, including summaries of the direct, indirect and total effects of the paths between all variables can be found in Appendix A Table A6.
DISCUSSION

Our results suggest that the direct and indirect effects of climate variables are not enough to explain the range-wide variation in the occupancy of Arctic-breeding shorebirds. Individual land cover variables are often stronger predictors than the direct and indirect effects of climate combined. In models with climate+additional variables, on average the additional variables accounted for more than half of the explained deviance, independent of shared effects with the climate variables. Our results support the idea that climate-only models may offer incomplete descriptions of current and future habitat suitability, and can lead to incorrect conclusions with important management implications.

Even at broad spatial scales, Arctic-breeding shorebirds typically have distinct land cover preferences that are stronger predictors of habitat suitability than climate, and we show here that land cover is not a simple derivative of climate. Aside from climate, tundra vegetation and soils are also the product of the geological parent material and water drainage (Walker 2000). Acidic and non-acidic tundra soils have substantially different biogeochemical fluxes, which in many cases are larger differences than between bioclimatic vegetation zones (Walker 2000). These land cover and vegetation characteristics, which are only partly predicted by climate, are well established predictors of shorebird habitat. For example, Dunlin and Red Phalaropes are more likely to be present in moist, lowland habitats (Cunningham, Kesler, and Lanctot 2016), while Red Knots prefer sparsely vegetated habitats (Lathrop et al. 2018). Habitat suitability models
for eight shorebird species on the Alaska North Slope showed that all species were much less likely to be breed in upland shrub habitats (Saalfeld et al. 2013). Semipalmated Plovers commonly nest on stony shorelines, which helps them avoid nest predation by Arctic Foxes (Léandri-Breton and Bête 2020).

We should expect a spectrum of how well habitat suitability for individual species can be predicted by climate. For example, Pöyry et al (2008) found that butterflies with high mobility were modelled less accurately by climate-only models than species with low mobility. Species that use a wide range of climates are generally modelled less accurately than species found in a limited range of climatic conditions (Kadmon, Farber, and Danin 2003). The shorebirds studied here breed in the Arctic, and winter in tropical and subtropical areas, encountering vastly different climatic conditions throughout their annual cycle. Here, we saw that within closely related shorebird taxa in the same Arctic ecosystem, the total effect of climate explained anywhere from 10% to 80% of the explained deviance in shorebird occupancy.

In the debate about whether climate-only models are adequate for describing habitat suitability, one important factor that leads different papers to come to different conclusions is the spatial scale at which studies are conducted (Wiens 1989). Even Pearson and Dawson (2003), advocates of climate-only models, recommend that these analyses be undertaken with careful consideration: “...bioclimate envelope models can provide a useful starting point when applied to suitable species and at appropriate scales.” However, it seems that whether or not a climate-only model is appropriate for the given species and scale is often assumed rather than tested. For example, Wauchope
et al. (2017) write “Data were interpolated to a spatial grain size of 10 x 10 km to reflect the approximate resolution of most of the distributional records and a scale at which climate, rather than microhabitat factors, is more likely to be limiting (Mackey and Lindenmayer 2001)”.

Identifying which predictors are relevant at a particular spatial scale requires consideration of both the grain and the extent (Wiens 1989). Spatial grain has been demonstrated to influence the relative importance of climate predictors. For example, Luoto et al. (2006) found that climate-only models of bird distributions in Finland were improved by including land-cover at 10km and 20km resolutions, but not at 40km and 80km resolutions. The spatial extent of a study also plays a significant role in defining how much variability we find in each of the predictor variables. The extent of our study covers only a part of the breeding range of some species, and just beyond the range of others. Studies with much larger extents, covering the full range of climate conditions across the continent would have a stronger signal for climate, identifying a wider range of conditions species do not use. Habitat selection is a hierarchical process (Johnson 1980). Identifying the appropriate spatial scale for the type of habitat selection being studied will help identify when climate-only models are sufficient, and when other predictors such as land cover are important.

Optimizing the scale of effect for land cover and other predictors that can be measured at a range of spatial scales is an important step that is often neglected (McGarigal et al. 2016). Here, we found that Arctic-breeding shorebirds were responding to land cover at a radius of up to 10km, but that the scale of effect differed across species.
and land cover categories. A single-scale study of vertebrates in Florida (Bucklin et al. 2015), contrary to our results, found that including additional predictors had a relatively minor effect on the accuracy of climate-only habitat suitability models. They suggested that the 4km grain of their study may have been too coarse to resolve the land cover associations for their study species, following the hypothesis that biotic interactions are most important at smaller spatial scales. Another important difference between our study and that of Bucklin et al. (2015) may be that the spatial extent of our study area was approximately 20x larger; therefore, there may be more available variation in land cover across our sites, increasing its importance. Single-scale studies may therefore miss important predictors, because they are not measuring the predictors at the scale at which species are responding to the predictor (Wiens 1989).

Other reasons that climate-only models may be preferred are purely practical. Although important, additional predictors are often neglected because they are unavailable, or harder to obtain at the extent and resolution needed (Dubuis et al. 2013; Mod et al. 2016). Particularly for future predictions of habitat suitability, future climate projections are widely available, while other future projections such as land cover are much more limited in their availability, their spatial resolution, their accuracy, and the level of detail that they provide in terms of the number of classification categories (Titeux et al. 2016; Verburg et al. 2013).

We conclude that environmental predictors beyond climate are important for improving the accuracy of habitat suitability models explaining species distributions. We found that a large portion of explained deviance in shorebird occupancy is related to
direct effects of additional predictors, such as elevation and land cover, and that these
effects are not well captured as indirect effects of climate. It is therefore unwise to
assume that climate models are always sufficient for explaining habitat suitability. By
making these assumptions, we place unnecessary limits on our understanding of species
relationships with their environment. Incorrect conclusions from habitat suitability
models could have important management implications for designating protected areas
and assessing threats like climate change and human development. As many countries
seek to expand their protected areas networks to meet international commitments
under the Convention on Biological Diversity (Le Prestre 2017), a more complete
understanding of species’ distributions can have important management implications
now and especially in the future, under scenarios of climatic change.
FIGURES

Figure 3-1: Conceptual relationships between the drivers of species occupancy. Illustration of the common assumption that, over large spatial extents, climate predictors drive the probability of species occupancy. Such climate-only models imply that the total effects of climate predictors, i.e., both their direct effects ($a$) and their indirect effects through their effects on additional predictors such as land cover ($b*c$), are much greater than the direct effects of these additional predictors ($c$). The underlying assumption is that climate is the main driver of variation in the predictors that influence species occupancy, and so it is only necessary to include climate predictors in habitat suitability models.
Figure 3-2: Path diagram of the hypothesized relationships among predictors of shorebird occupancy. Groups of predictors with a blue label are included in climate-only models, and groups of predictors with an orange label are additional predictors included in climate+additional models. Arrows indicate direct causal paths between all combinations of variables in the respective groups are included in the path model of occupancy for each shorebird species. For example, the arrow from climate to land cover represents 60 arrows, one from each climate variable to each land cover variable.
Figure 3-3: Map of survey locations. 2336 plots were surveyed for breeding shorebirds across northern Canada, 1994-2018. Reprinted from ArcGIS under a CC BY license, with permission from Esri, original Copyright 2022 Esri (Basemaps supported by Esri, HERE, Garmin, OpenStreetMap contributors, and the GIS User Community).
Figure 3-4: Deviance partitioning for GLMs predicting the occupancy of each of 17 shorebird species. Each bar represents the total deviance explained for each species. The direct effects of climate, the proportion of explained deviance attributed to predictors from the climate-only model, is dark blue. The indirect effects of climate, the proportion of deviance that is explained by both climate and additional variables, is light blue. The total effect of climate on the occupancy of each species is the sum of the dark and light blue segments. The proportion of explained deviance attributed only to the additional predictors from the climate+additional models is orange. For half of the species shown, the unique effects of the additional variables explain more deviance in shorebird occupancy than the total effect of climate.
Figure 3-5: Total effect sizes of significant paths. Box and whisker plots showing the median and interquartile range of the absolute total effect sizes of significant (p>0.05) paths from individual path models of occupancy for the 17 most abundant shorebird species in the Canadian Arctic. Survey data was collected from 1994-2018 (Fig 3). The total effect sizes for each variable are the sum of its direct and indirect effects on shorebird occupancy (Fig 2). The predictors with the five largest effect sizes were additional variables. The magnitude of the effect sizes for climate and additional variables fall in a similar range.
CHAPTER 4 - UNEXPECTED SOURCES OF UNCERTAINTY IN PROJECTING HABITAT SHIFTS FOR ARCTIC SHOREBIRDS UNDER CLIMAT CHANGE

ABSTRACT

The Arctic is ideally suited for exploring uncertainty in climate-related projections, as many sources of uncertainty are exaggerated here. Expected climatic changes are more extreme than in other regions, and consistent data collection efforts are much more limited. However, in the last 30 years, shorebirds have been well monitored in an unprecedented arctic-wide survey. Our study had two objectives: 1) to develop probabilistic estimates of how the area of suitable habitat for 13 species of Arctic shorebirds in Canada will change by 2075, and 2) to assess how modelling decisions contribute to the uncertainty in these estimates. Our assessment of uncertainty included six distinct classes of modelling decisions, giving 216 unique projections of future habitat for each species. These six modelling decisions included the modelling algorithm, the carbon emissions scenario, and the global circulation model, plus three decisions that are less commonly explored - the pool of candidate variables, the method for selecting variables, and the maximum distance of tree line dispersal. We used a bootstrapping approach, creating a probability distribution for the proportional change in suitable habitat for each species. Our results showed that many Arctic shorebird species have a
considerable risk of losing over half of their suitable breeding habitat in Canada, but this projection is much less certain than has been described previously. We were surprised that the largest source of uncertainty was from our choice of method for variable selection, and that the other modelling decisions were relatively small sources of uncertainty. Despite the risks of losing shorebird habitat, the northward shift we predict in suitable shorebird habitat suggests that Canada will be an important refuge for Arctic breeding shorebirds, because in many other regions of the Arctic there is no land farther north for these species to shift northwards into.

INTRODUCTION

The location of many species’ habitat has been shifting in response to climate change, and forecasting these shifts has been an active area of research for more than 25 years (Carey 1996; Peterson et al. 2002). One of the most common ways to do this is with correlative approaches. Habitat is first defined by relating contemporary species occurrences to the resources and conditions in their environment, and then these relationships are used to project future habitat. Projections of how species’ habitat will shift in response to climate change have been useful for identifying the scale of change in species ranges that may occur in response to climate change (e.g. Loarie et al. 2008; Morato et al. 2020). They are also useful for identifying which species, habitats, and regions may be most sensitive to climate change (e.g. Chambault et al. 2022; Dyderski et al. 2018).
However, these projections are hampered by a high degree of uncertainty from numerous sources (Peterson, Cobos, and Jiménez-García 2018). All habitat suitability models are affected by uncertainty from sources such as limited sample sizes, measurement error, incomplete detection, imperfect understanding of what makes habitat suitable, lack of data for important predictor variables, and uncertainty in which model structures best represent the shape of ecological relationships (Barry and Elith 2006; Beale and Lennon 2012). However, for future projections of habitat suitability, additional sources of uncertainty must also be considered. These include uncertainty in how human behaviour will shape carbon emissions and land use, how the earth’s climate system is modelled, how climate changes will affect habitat, how species-habitat relationships may shift over time, and an inability to directly evaluate model accuracy using independent data (Heikkinen et al. 2006). There are many ways to categorize these sources of uncertainty, but two broadly important categories are epistemic uncertainty, i.e. uncertainty due to lack of knowledge, and stochastic uncertainty, i.e. uncertainty due to natural variability (Kirchner et al. 2021; Regan, Colyvan, and Burgman 2002).

A substantial body of scientific literature has developed to address epistemic uncertainty by identifying how modelling decisions affect future projections of habitat suitability. These papers have explored the relative importance of sources of uncertainty from model structure, such as modelling algorithm (Diniz-Filho et al. 2009; Pearson et al. 2006), approaches for variable selection, model parameter settings (Peterson, Cobos, and Jiménez-García 2018), thresholding procedures (Steen et al. 2017), and choice of predictor variables, which have been most commonly limited to various permutations of
climate variables for philosophical or practical reasons (Braunisch et al. 2013; Synes and Osborne 2011; van de Pol et al. 2016, but see Stralberg et al. 2015). Other sources of model uncertainty arise from decisions about the data inputs used to create projections, such as the global circulation models that describe spatiotemporal patterns in climate (GCMs; Braunisch et al. 2013) and the carbon emissions scenarios that force these models (Beaumont, Hughes, and Pitman 2008). Biotic interactions have been argued to be important for predicting how species distributions will respond to climate change (Van der Putten, Macel, and Visser 2010), but they are rarely included in future projections of species habitat.

In this paper, we apply compare sources of uncertainty in projections of how climate change may affect the breeding habitat of Arctic-breeding shorebirds. This system is ideally suited for exploring the sources of uncertainty in climate-related projections. Uncertainty is particularly important in the Arctic, as many sources of uncertainty are exaggerated here. Expected climatic changes are more extreme than in other regions; temperatures in the Arctic are rising three times faster than the global average, and impacts are expected to be rapid and transformational (AMAP 2021). Also, relative to other terrestrial biomes, consistent data collection efforts are much more limited, both for wildlife observations, and for habitat predictors such as climate and land cover variables (Aronsson et al. 2021). However, in the last 30 years, shorebirds have been well monitored in an unprecedented arctic-wide survey (Bart and Johnston 2012).

Arctic breeding shorebirds appear to be shifting their ranges northwards in response to recent climate change (Anderson et al. 2023a). A qualitative risk assessment
of the vulnerability of Arctic-breeding shorebirds to climate change in North America predicted that many of these species will lose more than half of their suitable breeding habitat, at a high level of subjective confidence (>70%) (Hector Galbraith et al. 2014). A correlative model projecting circumpolar changes in Arctic shorebird breeding habitat suggested that, globally, 66-83% of shorebird species could lose half of their suitable breeding habitat by 2070 (Wauchope et al. 2017). However, neither of these studies provide a comprehensive, quantitative picture of the uncertainty around these future projections of Arctic shorebird breeding, which we hypothesized should be very high.

Our study had two objectives. The first was to develop probabilistic estimates of how the area of suitable habitat for 13 species of Arctic-breeding shorebirds in Canada will change by 2075. The stochastic uncertainty from natural variation in ecological systems is difficult to predict, therefore one of the best ways to represent this uncertainty is as a probability distribution (Elith, Burgman, and Regan 2002). The second objective was to assess how modelling decisions contribute to the uncertainty in these estimates. Our assessment of uncertainty included six distinct classes of modelling decisions, three of which, to our knowledge, are not well studied in papers about uncertainty in species responses to climate change. First, we determined how the method for selecting habitat variables in habitat suitability models influences uncertainty, comparing a full model and two forward-selection methods based on cross-validation (see Dormann et al. 2008 for uncertainty from AIC-based methods). While older stepwise regression techniques have been out of favour for some time (Whittingham et al. 2006), methods based on spatial cross-validation are currently being debated as a modern
alternative (Meyer et al. 2018; Wadoux et al. 2021). Second, we compared the consequences of the pool of candidate variables available for selection. We compare such climate-only models and models including additional non-climate variables, which are important predictors of Arctic shorebird distributions (Anderson et al. 2023b). Third, we tested how assumed dispersal limits in projections of future vegetation affect uncertainty. In addition to these three novel classes of modelling decisions, we explored three more commonly tested classes of modelling decisions: the modelling algorithm, carbon emissions scenario, and global circulation model.

METHODS

OVERVIEW

Our study had two goals: 1) to develop probabilistic estimates of how the area of suitable habitat for 13 species of Arctic-breeding shorebirds in Canada will change by 2075, and 2) to assess how modeling decisions contribute to the uncertainty in these estimates. We varied 6 different modelling decisions, giving 216 unique projections of future habitat for each species. For each projection, we calculated the proportional change in suitable habitat as the future suitable area divided by the present suitable area. We used a bootstrapping approach, creating a probability distribution for the proportional change in suitable habitat estimated for each unique projection. We then combined these to create an overall probability distribution for each species that
captures both within- and between- model uncertainty. We compared sums of squares to determine the relative contributions of different modelling decisions to uncertainty in our estimates of the proportional change in suitable habitat. The analyses are summarized in Figure 2 and described below. All analyses were performed in R version 4.2.3, using packages tidyverse 2.0.0, caret 6.0-94, and terra 1.7-29. See Anderson et al. (2023c) for the full dataset used in our analysis.

**Shorebird Surveys**

Plots were surveyed for shorebirds across the Canadian Arctic as part of the Arctic Program for Regional and International Shorebird Monitoring (PRISM; Bart & Johnston, 2012), which covers all of Arctic North America as defined by the Circumpolar Arctic Vegetation Map (Walker, 2000). The Canadian PRISM data used here includes 1854 plots across the Canadian Arctic (Figure 4-1), an area of 3.5 million km². Given this massive area, surveys were completed over a number of years, from 1994-2018, with a majority of the sampling effort concentrated between 2003 and 2018. The Canadian Arctic was divided into 12 regions based on physiognomy and logistical considerations. Within each region plots were selected by random sampling, stratified by habitat. The proportion of plots in wet, moist and dry habitats varied by region depending on habitat abundance (See Bart & Johnston, 2012 for more details), but on average 16%, 29%, and 56% of plots were in wet, moist, and dry habitats respectively. In all years, surveys were conducted between June 18 and July 15. This corresponds to the latter part of shorebird courtship
and the early part of incubation, when detectability was highest, as breeding territories could be identified from the birds’ territorial displays. Although we use the uncorrected densities in our analyses, the PRISM survey also includes a subset of plots that are surveyed intensively, so that shorebird detectability could be estimated using double-sampling methods. The estimated detectability rate is 1.13, with no significant difference between species, indicating that occasionally birds visiting the plot were misidentified as breeding (J. Bart and P. Smith *unpublished*). Plots were typically 12-16 ha (400 m x 300-400 m). We excluded 23 surveys that were conducted in 1996 when extensive flooding led to very atypical breeding conditions. We also excluded 36 plots for which observers recorded nearby human development, which is rare across the study area and could potentially alter shorebird habitat preferences. Finally, 480 plots were excluded because not all necessary environmental predictors were available for them (for example, plots in areas close to shore which were in locations classified as ocean in the WorldClim dataset). Our final dataset consisted of surveys from 1854 plots. For 145 plots that were visited in more than one year, we randomly selected one year of data to include in the final dataset.

Plots were surveyed for breeding birds following PRISM protocols (Bart & Johnston, 2012). Two surveyors searched the plot walking straight-line transects, covering a breadth of 50 m with the observers situated 25 m apart, using a GPS to ensure complete coverage of the entire plot. The survey of a single plot took approximately 90 mins. Observers recorded the number and species of all birds observed within each plot. Altogether we observed 19 species of shorebirds, 13 of which had data sufficient for
projecting changes in the area of suitable habitat (observed in at least 30 plots, and containing at least 60% of their North American range within the study area): American Golden-Plover (Pluvialis dominica), Baird’s Sandpiper (Calidris bairdii), Black-bellied Plover (Pluvialis squatorla), Buff-breasted Sandpiper (Tryngites subruficollis), Dunlin (Calidris alpina), Pectoral Sandpiper (Calidris melanotos), Red Knot (Calidris canutus), Red Phalarope (Phalaropus fulicarius), Ruddy Turnstone (Arenaria interpres), Sanderling (Calidris alba), Semipalmated Sandpiper (Calidris pusilla), Stilt Sandpiper (Calidris himantopus), and White-rumped Sandpiper (Calidris fuscicollis). In our analyses, we chose to model occupancy instead of density because shorebirds were observed at very low densities (average of <3 birds/survey for all 13 species combined), with frequent counts of 0 (prevalence from 0.7% to 12.5% depending on the species). Surveys were observational, and involved no capture or sampling. Access to the plots was granted through permits to JR including: Environment and Climate Change Canada (NWT-MBS-17-03, MM-NR-2022-NU-005, NUN-NWA-17-04, SC-NR-2001-NT-004, SC-NR-2022-NU-005), Government of Nunavut (WL2022-031), Kitikmeot Inuit Association (KTX115X007), Kivalliq Inuit Association (KVX15N05), and Qikiqtani Inuit Association (Q14X001).

**ENVIRONMENTAL PREDICTORS**

For our habitat suitability models, we used two categories of environmental predictors of shorebird occupancy: climate predictors found in ‘climate-only models’, and additional predictors in ‘climate+additional models’ (see Anderson et al. 2023b for more
For the climate predictors, we used all 19 bioclimatic variables available from WorldClim 2 (Fick & Hijmans, 2017), which are interpolated from mean historical climate data covering 1970-2000 at a 30 arc-second resolution (~1km). Additional predictors in the ‘climate+additional’ models of shorebird occupancy included topography, geology, and land cover variables. The topography predictors we included were elevation, the standard deviation of elevation, and distance to coast. Elevation data were from WorldClim 2 (1km resolution), from which we also derived the standard deviation of elevation. We calculated distance to coast from coastline data from Natural Earth (Patterson & Vaughn Kelso, 2022). To represent geology, we used substrate chemistry data from the Circumpolar Arctic Vegetation map (CAVM; Walker et al., 2005), which includes 3 categories: acidic (pH < 5.5), circumneutral (pH 5.5-7.2) and carbonate (pH > 7.2). We used land cover data from the Circumpolar Arctic Vegetation Map (CAVM; Walker et al., 2005), which derived 17 land cover classes from AVHRR data from 1993-1995. We used 13 of these land cover classes, including barren, graminoid tundra, prostrate-shrub tundra, erect-shrub tundra, and wetland landcover classes. We excluded areas classified as glacier, mountain, water, and non-arctic areas from our analyses, as these areas were not surveyed and are not suitable shorebird habitat. Both CAVM datasets are vector maps with a minimum polygon edge size of 14km.

For future projections of shorebird habitat, we used the above predictors for topography and geology, as well as future projections of bioclimatic variables and land cover for 2040-2060. We used several different sets of bioclimatic variables from the WorldClim 2 dataset (more details below). Future projections of the CAVM land cover
maps described above were created by Pearson et al. (2013), based on climate, geological substrate, and limitations on the distance that the tree line can shift northwards. Pearson et al. (2013) did not make future projections of land cover classes that do not have enough soil to support vegetation (barren land cover classes), because it is expected that these areas will remain unchanged. They also did not make projections for land cover classes that are highly influenced by hydrological processes (wetland land cover classes), because the changes could not be adequately predicted using data available at the time. For these areas, we based both recent and future habitat on the original CAVM classification. All recent and future predictors were resampled to a 5km raster grid using bilinear interpolation for continuous data and nearest neighbour resampling for categorical data.

Future projections created using habitat suitability models may perform poorly when extrapolating to environmental conditions which were not included in the training data (Fitzpatrick and Hargrove, 2009). To minimize extrapolation in our future projections, we mapped the range of values for both the recent and future environmental predictors to look for conditions that were far outside the sampled range of values. Future precipitation regimes in the Arctic Cordillera, and the eastern portion of Baffin Island, are predicted to diverge considerably from the climate conditions observed in areas that were sampled in this study. We therefore excluded these areas from predictions.
**Modelling Decisions**

To account for and assess how modelling decisions contributed to uncertainty in our estimates of the proportional change in suitable shorebird habitat, we varied six different modelling decisions in our analyses. Three of these decisions concerned the structure of our habitat suitability models, with 12 possible configurations, and three of these decisions concerned the environmental input scenarios for future projections, with 18 possible configurations. This created a total of 216 unique modelling decision configurations for each species (Figure 4-2).

The three modeling decisions about model structure that we varied were the pool of candidate variables, the modelling algorithm, and the selection of variables. For these three decisions, we evaluated options intended to represent a wide spectrum of decisions that are currently made in habitat suitability studies. For the pool of potential variables, we used with either ‘climate-only’ candidate predictor variables (e.g. Dyderski et al., 2018) or ‘climate+additional’ candidate predictor variables (e.g. Heikkinen et al., 2007; see Environmental Predictors section). For the modelling algorithm, we created habitat suitability models with either generalized linear models (GLM) with a binomial distribution (e.g. Chiaverini et al., 2023), or a Random Forest algorithm (Cushman & Wasserman, 2018). For selection of variables, beginning with the pool of candidate predictors, we used three different methods for selecting which variables to include in the final model: a full model including all candidate variables (e.g. Wauchope et al., 2017), a reduced model using forward variable selection with random cross-validation
(e.g. Hao et al., 2019), or a reduced model using forward variable selection with spatial cross-validation (e.g. Chambault et al., 2022). For both reduced models, we used the R package CAST forward feature selection method to select the most important variables by testing all possible two-pair permutations of variables (Meyer et al., 2023). We used Cohen’s Kappa statistic as our assessment metric for model accuracy, which measures the extent to which the agreement between observed and predicted values is higher than that expected by chance alone (Liu et al., 2011). A Kappa statistic of 0 indicates a level of agreement expected by chance, while a Kappa statistic of 1 indicates perfect agreement between observed and predicted values. The model with the highest Kappa statistic was selected, and the process was iteratively repeated, adding each of the remaining variables, until none of the remaining variables increased model performance. The Kappa statistic was calculated using 4-fold cross-validation in one of two ways: in random cross-validation, the data was randomly split into 4 folds, while in spatial cross-validation, the data was split into 4 folds based on the 12 survey regions, previously described in the Shorebird Surveys section (more details in Meyer et al., 2018).

The three modelling decisions about model inputs that we varied for future projections were the global circulation model (GCM), the carbon emissions scenario, and the maximum distance of tree line dispersal. For these three decisions, we evaluated the options as close as possible to those presented in Pearson et al. (2013), to ensure that we had land cover predictions to match each configuration of the modelling decisions. Thus, following Pearson et al. (2013), the GCMs we used were CanESM5, HadGEM3-GC31-LL, and ACCESS-CM2 (IPCC, 2022). Pearson et al. (2013) used SRES carbon emissions
scenarios B2b and A2a; we used close modern equivalents, CMIP6 Shared Socio-economic Pathways SSP 245 ("middle of the road" emissions) and SSP 585 ("fossil-fueled development" emissions (O’Neill et al., 2017). The future projections for land cover included three possible scenarios for how the tree line could disperse northwards: a maximum shift of 5km over 50 years, a maximum shift of 20km over 50 years, or an equilibrium scenario where there is no maximum distance imposed on the movement of the tree line.

**PROJECTING CHANGE IN SUITABLE HABITAT**

We created estimates of the area of suitable habitat for 13 Arctic-breeding shorebird species for two time periods, the recent past and the future. First, we estimate the area of suitable habitat for the period when the shorebird observation data was collected, 1994 to 2018. We refer to this time period as the estimates for 2010, which is the median year for the observations. In our models, there are lags between the observation period for shorebirds, and the observation period for the climate data (1970-2000) and the land cover data (1993-1995). We chose these data sets because they are the only options available that would allow us to include future land cover predictors and the influence of tree dispersal on shorebirds, which we identified as being important variables in Anderson et al. (2023b). We also believe there is likely a true lag in the responses between climate, landcover, and shorebird occupancy, so these time lags are a reasonable modelling assumption. The future climate predictions we use are for 2040-
2060, therefore we carry forward the 25-year time lag, and estimate the area of suitable shorebird habitat for 2065-2085. We refer to this time period as the estimates for 2075.

Probabilistic methods are a comprehensive and effective way to deal with compounded effects of uncertainty from within models, among candidate models, and among different future climate scenarios (Wenger et al., 2013). Our process for projecting the proportional change in suitable habitat for each shorebird species involved 4 steps (Figure 4-2). In Step 1, we built 12 habitat suitability model structures for each species, with all possible configurations of 3 modelling decisions (the pool of candidate variables, the modelling algorithm, and the selection of variables). In Step 2, we compiled 18 environmental input scenarios, with all possible configurations of 3 modelling decisions (GCM, carbon emissions scenario, and tree line dispersal). In Step 3, we created present and future projections for each of the 216 model structure x environmental-input configurations. We then calculated the proportional change in suitable habitat as the future suitable area divided by the present suitable area. The probability threshold for classifying a grid cell as suitable or unsuitable was calculated as the threshold that maximized the Kappa statistic. In Step 4, we repeated Step 3 with 500 bootstrapped resamples of the shorebird occupancy data for each of the 216 model configurations, estimating a probability distribution for the proportional change in suitable habitat. We combined the 216 probability distributions to create a single probability distribution for each species. Measurements of proportional change follow a non-linear scale (i.e. half as much habitat is a proportional change from 1 to 0.5, while twice as much habitat is a proportional change from 1 to 2). Therefore, in our models we compared the logarithm
of predicted proportional change so that increases and decreases would have values of comparable magnitudes (i.e. for half as much habitat, \( \log(0.5) = -0.69 \), and for twice as much habitat, \( \log(2) = 0.69 \)).

**Estimating Uncertainty due to Modelling Decisions**

To estimate how much of the uncertainty in the proportional change in suitable habitat was related to modelling decisions, we used their proportional contributions to the sums of squares in two ANOVA models. For the overall influence of modelling decisions, we included a factor with 216 unique levels reflecting all possible configurations of model structure and environmental input data, and we included species as a fixed effect to control for variation among species. In a second ANOVA, we included each of the six classes of modelling decisions as a fixed effect, to compare their relative effects on prediction uncertainty, and we included species as a random effect. We also included an interaction effect between the modelling algorithm and the selection of variables, as modelling algorithms can differ in their sensitivity to collinear predictors in a full model approach (Dormann et al. 2013).

We also present a set of ANOVA models designed to look at how modelling decisions influenced the likelihood of large changes in suitable habitat, which may be a more appropriate way to describe the results of highly uncertain future projections. For each predicted value in the bootstrapped probability distribution of proportional change
in suitable habitat, we calculated two binary variables describing whether the observation predicted that the species will have less than half as much suitable habitat in the future, or twice as much suitable habitat in the future. Again, we included each of the 6 modelling decisions as a fixed effect, and species as a random effect.

**Consensus Maps of Suitable Habitat**

For each of the 216 model configurations for each species, we created maps of suitable habitat for 2010 and 2075. For each time period, we created a consensus map, illustrating the proportion of the 216 models that predicted a grid cell to be suitable habitat, with suitable habitat identified as defined above, using the probability threshold that maximized the Kappa statistic. With the present and future consensus maps for each species, we assessed which areas were consistently predicted to be suitable in each time period, how these areas shifted over time, and which regions were consistently predicted to be suitable habitat for multiple species.

**RESULTS**

Compared to the area of suitable habitat predicted for 2010, the median predicted area of suitable habitat for 2075 ranged from 15% for Baird’s Sandpiper to 178% for Semipalmated Sandpiper (Figure 4-3). Across the wide range of modelling
decisions considered here, nine of 13 species were more likely to have less suitable habitat in 2075 than in 2010 (Baird’s Sandpiper, Pectoral Sandpiper, White-rumped Sandpiper, American Golden-plover, Buff-breasted Sandpiper, Sanderling, Red Phalarope, Black-bellied Plover, and Stilt Sandpiper; Table 3-1). These same nine species had at least a 30% chance of losing half their suitable habitat by 2075. Four species were more likely to have more suitable habitat in 2075 than in 2010 (Red Knot, Ruddy Turnstone, Dunlin, and Semipalmated Sandpiper; Table 3-1). These species, as well as Stilt Sandpiper, had at least a 30% chance of having twice as much suitable habitat in 2075.

Although the weight of evidence clearly suggests a loss of habitat is likely for the majority of these species, the uncertainty is substantial. For four species, there was at least a 20% chance of having both half or twice as much suitable habitat in 2075 (Pectoral Sandpiper, Buff-breasted Sandpiper, Black-Bellied Sandpiper and Stilt Sandpiper; Table 3-1). However, the degree of uncertainty varied considerably between species. Buff-breasted Sandpiper had the widest probability distribution (SD of 4.86) was five times broader than that for Semipalmated Sandpiper (SD of 0.88; Figure 4-3). The standard deviation in the proportion of habitat loss was higher for species that were rarer in our samples ($\beta = -0.01$, t value = -2.93, $p = 0.01$).

In our ANOVA model testing the overall influence of modelling decisions on proportional change in suitable shorebird habitat, we found that most of the uncertainty in our estimates of the proportional change in suitable habitat was unexplained by the factors we tested, and only 9% of the total sum of squares was related to modelling decisions (Figure 4-4 A). However, it is noteworthy that variation we observed among
modelling decisions is comparable to the variation we observed among species (11% of the total sum of squares), so it is also not inconsequential. See Discussion for a review of some of the sources of uncertainty that were not included in this model. In our ANOVA model of how the six individual modelling decisions affect predictions of proportional change, the largest source of uncertainty was related to the choice of approach for selecting the variables that were retained in the habitat suitability models, accounting for 69% of the sum of squares (Figure 4-4 B). Choice of GCM accounted for 10% of the total sum of squares, and choice of the pool of candidate variables accounted for 4%. The remaining modelling decisions contributed a small amount of uncertainty to the sum of squares: the choice of carbon emission scenario at 2%, and the choice of modelling algorithm and the maximum distance of tree line dispersal at less than 1%. The interaction between the choices of variable selection methods and modelling algorithms accounted for 14% of the uncertainty.

How we selected the variables that were retained in the habitat suitability models also had the by far strongest influence on the uncertainty in predicting whether a species will lose or gain a large amount of habitat, respectively accounting for 83% and 74% of the explained sum of squares in these models (Figure 4-4 C-D). The choice of GCM was the second largest source of uncertainty in our model of the probability that species would lose half of their suitable habitat, at 10% (Figure 4-4 C). The choice of modelling algorithm was the second largest source of uncertainty in our model of the probability that species would have twice the amount of suitable habitat, at 22% (Figure 4-4 D). The other modelling decisions accounted for less than 3% of the sum of squares in both
models. The interaction between the choices of variable selection methods and modelling algorithms was less important here; it accounted for less than 3% of the uncertainty in both the models of habitat loss and gain.

By plotting the probabilities of predicted half or twice as much suitable habitat associated with the choices for each modelling decisions across all 13 species, we can see that there was substantial overlap in the predicted probabilities for most modelling decisions (Figure 4-5). The largest difference in predicted probabilities is when different methods were used to select included variables. We can see that when all candidate variables are included, species are predicted to lose much less, or gain much more, habitat than when either of the two variable selection approaches was used (Figure 4-5). Likewise, we can see that GLMs consistently estimated more optimistic outcomes than Random Forest models.

Interestingly, the uncertainty arising from the carbon emissions scenarios was only 2% or less of the sum of squares in our models of how individual modelling decisions affected the proportional change in suitable habitat, and the probability of predicting half or twice as much suitable habitat (Figure 4-4 B-D). Compared to the SSP 245 scenario (“middle-of-the-road”), the proportional change in the area of suitable habitat in the SSP 585 scenario (“fossil-fueled development) ranged from 7% more habitat to 13% less habitat, depending on the species (mean = 4% less habitat). This translated to an average 1% higher probability of predicting half the area of suitable habitat in the SSP 585 scenario (0 to 10% by species), and an average 4% higher probability of predicting twice the area of suitable habitat (-1 to 3% by species). For context, the mean average annual
temperature in our study area was -12.6 °C from 1970-2000. By 2040-2060, it is predicted to increase to -6.5°C in the SSP245 scenario, and -5.3 °C in the SSP 585 scenario.

Mapping the consensus in the projections of suitable habitat across all model configurations illustrates a general trend where the location of suitable habitat for most species will shift north and west by 2075 (Figure 4-6). Even for species such as Stilt Sandpiper, Black-bellied Plover, Red Phalarope and Sanderling, which were predicted to be less likely to lose or gain a large amount of habitat, the location of their suitable habitat was predicted to shift considerably (Appendix B). Red Knot was the only species that did not show a substantial predicted shift in the location of its’ suitable habitat.

DISCUSSION

Our results showed that many Arctic-breeding shorebird species have a considerable risk of losing over half of their suitable breeding habitat in Canada, but this projection is much less certain than has been described previously. The probability distributions we projected for these 13 Arctic shorebird species showed that decreasing area of suitable habitat is the most likely prospect for 9 of the species. However, for most species, a wide range of scenarios from major losses to modest changes to major gains in suitable habitat were all possible. By contrast, previous studies of shorebird habitat shifts have claimed much higher certainty. Wauchope et al. (2017) predicted that globally, 66–83% of shorebird species would lose at least half their area of suitable habitat by 2070.
However, their exploration of uncertainty around these estimates was limited to the choices of GCM and emissions scenario, which we found to be relatively minor sources of uncertainty. Galbraith et al (2014) used a qualitative risk assessment framework to evaluate the vulnerability of North American shorebirds to climate change. They predicted that 10 of 13 shorebird species from our study will lose at least 50% of their breeding habitat, and claimed high confidence (>70% probability) in that prediction. One reason this study may have higher confidence in predicting major losses of breeding habitat is that it also included Alaska, where there is no land further north to accommodate range shifts northwards.

There are a number of reasons why Arctic-breeding shorebirds are likely to be vulnerable to climate change: they depend on ecological synchronicities with short peaks of invertebrate prey availability; they migrate very long distances; and they specialize on particular habitat types (Galbraith et al., 2014). Tundra habitats are experiencing a faster rate of climate change than those at lower latitudes, due to positive feedbacks from changes in snow and ice dynamics (Serreze & Barry, 2011), leading to increased shrub size and cover (Myers-Smith et al., 2011), which is reducing the habitat suitability for most shorebird species (Saalfeld et al., 2013).

We were surprised that, of the modelling decisions we assessed, the largest source of uncertainty in projections of habitat change was from our choice of method for selecting the variables that were retained in the habitat suitability models. Specifically, when all candidate variables were included, species were predicted to lose much less, or gain much more, habitat than when a variable selection approach was used. This was an
unexpected finding, as variable selection has not been previously identified as an
important source of uncertainty in projections of habitat change. Dormann et al. (2008)
concluded that the choice of variable selection was less important than the choice of
modelling algorithm as a source of uncertainty in climate change projections, but their
study only compared AIC-based methods. We found that variable selection was a much
larger source of uncertainty than either the modelling algorithm or the GCM, modelling
decisions that are regularly identified as significant sources of uncertainty in other studies
(Buisson et al., 2010; Diniz-Filho et al., 2009; Naujokaitis-Lewis et al., 2013; Pearson et al.,
2006). Our results showed that uncertainty stemming from variable selection depends on
the modeling algorithm used. The full model approach may be more applicable for
machine-learning methods, which may better cope with high-dimensional, collinear
datasets (Kampichler and Sierdsema 2018), but these methods may be less appropriate
for GLMs. The additional uncertainty introduced by collinear variables in the full model
approach is one area where uncertainty in future projections can be reduced by following
best practices in structuring habitat suitability models (De Marco and Nóbrega 2018,
Sofaer et al. 2019). Forward selection approaches, which are much more conservative
that a full model, purported to only include variables with actual predictive power
beyond the training locations (Meyer et al., 2019). There is no consensus on the best way
to select which variables are included in a model. Both full model and stepwise selection
approaches have been proposed to avoid overfitting models to the samples data (Harrell,
2001; Meyer et al., 2018). We recommend that future uncertainty analysis take variable
selection into account, and that further research should quantify uncertainty in habitat suitability projections across a larger array of variable selection techniques.

The limited influence of the choice of carbon emissions scenarios on the results is also notable. Similar to many other studies of uncertainty in projections of species distribution and habitat in response to climate change, we found that uncertainty from other modelling decisions greatly exceeds uncertainty from carbon emissions scenarios, the only modelling decision that reflects real-world decisions that we have some control over rather than a consequence of climate change or strictly a methodological uncertainty (Buisson et al., 2010; Garcia et al., 2012; Peterson et al., 2018; Synes & Osborne, 2011). The small differences in the probability of species predicted to lose or gain large quantities of suitable habitat with different carbon emissions levels suggests that many of the harmful effects of climate change on wildlife distributions are difficult to halt or reverse given plausible emissions scenarios.

It is important to note that we found that uncertainty in our projections stemming from modelling decisions was relatively small compared to uncertainty from other sources. Our study, like all correlational projections, is constrained by current observed species-habitat relationships. We found that there were higher levels of uncertainty for more uncommon shorebirds. One limitation of habitat suitability models is that for uncommon species, many areas of suitable habitat are likely to be unoccupied (Doncaster et al., 1996). Another limitation is that occurrence data may not adequately capture the niche of a species, either due small sample sizes or biases in sampling (Loiselle et al., 2007). Opportunistic species such as Pectoral Sandpipers have low site

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fidelity, and selection of breeding sites may be more closely tied to annual conditions rather than long-term climate averages (Saalfeld et al. 2015). Habitat suitability models are also limited in their ability to capture some important ecological processes that operate at a range of spatial scales to influence whether suitable habitat is actually used by a species, such as biotic interactions, dispersal limitations, and disturbance (Guisan & Thuiller, 2005). There is still much we do not know about the current distribution of shorebirds, and although we have some understanding of what defines suitable habitat for shorebirds, our ability to predict their distribution has limitations (Anderson et al., 2023b; Cunningham et al., 2016; Saalfeld et al., 2013). Any limitations in models of present habitat suitability persist in the future projections they are used to create. Similar to Hegyi and Laczi (2015), we found that the choice of variable selection method and other statistical modelling decisions have a smaller impact on the results of ecological models than the quality of the data.

Using probabilistic methods was key for understanding the relative importance of modelling decisions as a source of uncertainty. Araujo and New (2007) describe probabilistic forecasting as the ‘end game’ of multi-model ensemble forecasting, but these methods are still surprisingly infrequently used in projections of how species’ habitat will shift in response to climate change. By explicitly describing uncertainty in future projections of species habitat explicit, it can be incorporated into conservation planning to make decisions that are robust to uncertainty (e.g. Bagchi et al., 2013; Carvalho et al., 2011; Fuller et al., 2008). For example, if there is consensus between
multiple modelling methods that a particular site has a high conservation value, it’s protection can be prioritized over sites with greater uncertainty.

We have illustrated a high degree of uncertainty in how suitable breeding habitat for Arctic-breeding shorebirds will change under scenarios of climate change, but in fact the true uncertainty is even greater when we consider factors that were not possible to include in our models. For example, the future land cover predictions we included did not address changes in hydrology (Pearson et al., 2013). Shorebirds are likely to be sensitive to such changes, as many species rely on moist, lowland habitats (Cunningham et al., 2016; Saalfeld et al., 2013). However, these changes are very difficult to predict: annual rainfall is predicted to increase in the Canadian Arctic (Ford et al., 2018), but this may be offset by increases in evapotranspiration and decreases in permafrost, leading to soil drying (Meredith et al., 2022). Another source of uncertainty is the extent to which the modelling assumptions of habitat suitability models reflect the reality. For example, species-habitat relationships may change over time. Like all correlational habitat suitability models, our methods assume these relationships will be stable over time, but the relationship between species and their environment may change under scenarios of climate change. Our models also assume that these species are at equilibrium with their environment. Shorebird populations have declined and therefore some potentially suitable habitat may be unoccupied, which may result in habitat suitability models that underestimate the area of potential suitable habitat.

Despite the uncertainty, the consensus picture (Figure 4-6) suggests a northward and westward shift of breeding habitat for shorebirds in the Canadian Arctic. Several
areas that are currently considered good shorebird breeding habitat, including Victoria Island (Kitlineq), Southampton Island (Shugliaq), Prince Charles Island, and the Dewey Soper (Isulijarnik) Migratory Bird Sanctuary (Latour, 2008), were predicted to decline in the number of shorebird species they support. Red Knot was the only species that did not show a substantial predicted shift in the location of its’ suitable habitat. This is likely because Red Knots use barren land cover types where there is not sufficient soil for vegetation to develop and are therefore not predicted to shift in response to climate change in the near future (Lathrop et al., 2018; Pearson et al., 2013). Despite the risks of losing shorebird habitat, the northward shift we predict in suitable shorebird habitat suggests that Canada will be an important refuge for Arctic breeding shorebirds, because in many other regions of the Arctic there is no land farther north for these species to shift northwards into.

Future projections of habitat suitability and species distributions are frequently proposed as something to consider in the design of climate resilient protected areas networks (Araújo, 2009; Ochoa-Ochoa et al., 2016). Countries around the world are pursuing protection of 30% of their land mass under the Global Biodiversity Framework (Xu et al., 2021). However, comprehensive information about the degree of uncertainty in these projections is needed in order to understand whether this is desirable or even possible. The probabilistic methods we used here are important for presenting a more honest representation of the uncertainty around future projections of habitat suitability.

Unexpectedly, we identified that the modelling decision generating the most uncertainty in our predictions was how candidate variables were selected to be included
in the model, a source of uncertainty that has not been recognized in previous assessments of uncertainty in predictions of habitat suitability under climate change. Our study also sheds new light on the potential impacts of climate change on Arctic-breeding shorebird species in Canada. While previous studies have described a significant risk of losing more than half of their suitable breeding habitat, our findings indicate that this prediction is accompanied by a high level of uncertainty. Explicitly accounting for uncertainty when projecting how habitat of vulnerable species like shorebirds will shift in response to climate change is will be key for making conservation decisions that succeed across a range of potential futures.
Figure 4-1: Map of northern Canada showing the locations of plots used in analyses, where breeding shorebirds were surveyed, 1994-2018
STEP 1: Modelling decisions - 12 model structure configurations

STEP 2: Modelling decisions - 18 environmental input configurations

STEP 3: Present and future projections of suitable habitat

STEP 4: Bootstrapped probability distribution for change in suitable habitat
Figure 4-2: Figure on page 91. Methodology used to estimate the probability distribution of the proportional change from 2010 to 2075 in suitable breeding habitat for each of 13 shorebird species. In Step 1, we built 12 habitat suitability model structures for each species, with all possible configurations of 3 modelling decisions (the pool of candidate variables, the modelling algorithm, and the selection of variables). In Step 2, we compiled 18 environmental input scenarios, with all possible configurations of 3 modelling decisions (GCM, carbon emissions scenario, and tree line dispersal). In Step 3, we created present and future projections for each of the 216 model structure x environmental input configurations. We then calculated the proportional change in suitable habitat as the future suitable area divided by the present suitable area. In Step 4, we repeated Step 3 with 500 bootstrapped resamples of the shorebird occupancy data for each of the 216 model configurations, estimating a probability distribution for the proportional change in suitable habitat. We combined the 216 probability distributions to create a single probability distribution for each species.

Figure 4-3: Figure on page 93. Probability distributions for proportional change in suitable habitat (future area / present area) from 216 configurations of 6 modelling decisions (pool of candidate variables, model algorithm, selection of variables, global circulation model, carbon emissions scenario, and tree line dispersal). Probability distributions were calculated based on 500 bootstrapped resamples of shorebird occupancy data from the Canadian Arctic, 1994-2018 (see Figure 4-2). The black line indicates no change in the area of suitable habitat between 2010 and 2075. Red dashed lines indicate half or twice as much suitable habitat in 2075 compared to 2010. Grey lines indicate the minimum and maximum estimates for the change in suitable habitat for each species.
Figure 4-4: Figure on page 94. The proportion of the sum of squares attributed to different sources of uncertainty in ANOVA models of the proportional change in suitable habitat (A, B), the probability of predicting half the amount of suitable habitat (C), and the probability of predicting twice the amount of suitable habitat (D) in 2075 compared to 2010. In panel A, we compare the sum of squares attributed to model configuration, a factor with all 216 possible configurations of 6 modelling decisions, to the sum of squares attributed to species and the residual unexplained variation. In panels B-D, we break down the sum of squares attributed to model configuration to look at the uncertainty attributed to each of the 6 individual modelling decisions, with species as a random effect.

Figure 4-5: Figure on page 96. Across 13 Arctic-breeding shorebird species, the effects of six modelling decisions on the predicted probability that a species’ area of suitable habitat in 2075 will be half or twice as much as in 2010. The box and whiskers show the median, 25th and 75th percentiles, and 1.5 times the interquartile range, with individual dots for values outside this range. The box plot for each modelling decision includes all other possible combinations of the other 5 modeling decisions.
Figure 4-6: Consensus maps of the areas predicted to be suitable habitat for Arctic shorebird species in 2010 and 2075. The value in each cell is the number of species for which at least 50% of the 216 model configurations of 6 modelling decisions indicated suitable habitat.
### TABLES

Table 4-1: The probability that the area of suitable habitat for each shorebird species in 2075 will decrease compared to 2010 (proportional change < 1), will be less than half of the area of 2010 (proportional change < ½), or will be more than twice the area in 2010 (proportional change > 2). For each species, these values represent the cumulative probabilities beyond these thresholds, illustrated in Figure 4-2 as the areas above and below the red lines.

<table>
<thead>
<tr>
<th>Species</th>
<th>Decrease</th>
<th>Half</th>
<th>Twice</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baird's Sandpiper</td>
<td>0.90</td>
<td>0.78</td>
<td>0.03</td>
</tr>
<tr>
<td>White-rumped Sandpiper</td>
<td>0.75</td>
<td>0.40</td>
<td>0.05</td>
</tr>
<tr>
<td>American Golden-Plover</td>
<td>0.70</td>
<td>0.40</td>
<td>0.12</td>
</tr>
<tr>
<td>Pectoral Sandpiper</td>
<td>0.67</td>
<td>0.55</td>
<td>0.23</td>
</tr>
<tr>
<td>Buff-breasted Sandpiper</td>
<td>0.65</td>
<td>0.45</td>
<td>0.20</td>
</tr>
<tr>
<td>Sanderling</td>
<td>0.64</td>
<td>0.35</td>
<td>0.16</td>
</tr>
<tr>
<td>Red Phalarope</td>
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<td>0.30</td>
<td>0.14</td>
</tr>
<tr>
<td>Black-bellied Plover</td>
<td>0.53</td>
<td>0.36</td>
<td>0.26</td>
</tr>
<tr>
<td>Stilt Sandpiper</td>
<td>0.51</td>
<td>0.37</td>
<td>0.40</td>
</tr>
<tr>
<td>Ruddy Turnstone</td>
<td>0.39</td>
<td>0.16</td>
<td>0.40</td>
</tr>
<tr>
<td>Red Knot</td>
<td>0.34</td>
<td>0.14</td>
<td>0.34</td>
</tr>
<tr>
<td>Dunlin</td>
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<td>0.13</td>
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<td>Semipalmated Sandpiper</td>
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<td>0.06</td>
<td>0.42</td>
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</tbody>
</table>
CHAPTER 5 - CONCLUSIONS

SUMMARY

The objective of my thesis was to understand the influence of climate change on the distribution of shorebirds breeding in the Canadian Arctic. Each of the previous chapters investigated a different element of this topic. In Chapter 2, I assessed whether the breeding distributions of Arctic shorebirds have already shifted in response to climate change, using a dataset spanning 25 years. In Chapter 3, I tested the relative importance of climate and non-climate factors in predicting their breeding distributions across the whole of the Canadian Arctic. In Chapter 4, I projected how the area of suitable breeding habitat for Arctic shorebirds may change by 2075, and tested how modelling decisions contributed to uncertainty in these projections. In this final chapter, I review the key findings of each chapter, and discuss the general implications of my thesis, specifically for Arctic breeding shorebirds, and more generally for the study of climate change on species distributions. I also review the limitations of this body of research, and outline directions for future research to build on this thesis.

In Chapter 2, I looked for evidence that Arctic breeding shorebirds may have already shifted their distributions in response to climate change, which has been occurring more rapidly in the Arctic than other regions. Over 25 years, in two Arctic regions, I found a strong positive relationship between changes in the occupancy of shorebird species, and their “species temperature index”. This result indicates that
occupancy of species that prefer warmer climates has increased, while the occupancy of species that prefer colder temperatures had decreased. Our observations matched the pattern we had expected to see if species are moving northwards in response to observed climate warming in the Arctic.

In Chapter 3, I tested the hypothesis that predictors in addition to climate, such as land cover, snow melt, geology and topography, are important for predicting suitable habitat for Arctic-breeding shorebirds. Some portion of the influence of these additional variables can be attributed to indirect effects of climate, so testing this hypothesis required apportioning of the effects through path analysis and deviance partitioning. My results supported the hypothesis, indicating that the additional variables accounted for more than half of the explained variance in shorebird occupancy, independent of indirect effects from climate variables. Individual land cover variables were often stronger predictors than combined direct and indirect effects of individual climate variables. These results show that models with predictors in addition to climate were better than climate-only models at describing the present suitable habitat of shorebirds. If current shorebird habitat is not well described by climate variables alone, then shorebirds’ responses to climate change are also likely to be moderated by factors other than climate. It is therefore important to include these additional variables in projections of how shorebird habitat may shift in response to future climate change.

In Chapter 4, I developed projections of how climate change may affect the area of suitable habitat for 13 shorebird species in the Canadian Arctic by 2075. Noting the importance of additional predictors in Chapter 3, I tested how the choice of the pool of
candidate variables (climate only and climate + additional) contributed to uncertainty in
the projections, as well as uncertainty in future land cover under different tree dispersal
scenarios. I also addressed four other modelling decisions. The modelling decision that
contributed the most uncertainty, by far, to our projections of change in suitable habitat
was the choice of method for variable selection. This was an unexpected result. Choices
related to the modelling algorithm, the global circulation model and the pool of variables
used were minor sources of uncertainty. Interestingly, I concluded that the carbon
emissions scenario had a negligible effect on the predicted area of suitable shorebird
habitat. Beyond modelling decisions, most uncertainty in these projections was
unexplained, signifying the importance of sampling error and natural variability. Even
with high uncertainty in the estimates, there was a clear trend that the majority (9/13) of
these species are likely to lose suitable habitat, with a considerable risk of losing 50% or
more of their habitat. For other species, the projected trends were more favourable,
including some with a high likelihood of gaining suitable habitat under scenarios of
climate change.

EVIDENCE FOR DISTRIBUTION SHIFTS

This work represents the first scientific study providing evidence that shorebirds
are responding to the rapidly changing Arctic climate by shifting their breeding
distributions. Shifting distributions are likely to lead to changes in Arctic food webs,
where the presence of lemmings and geese mediate predation on shorebird nests by
Arctic Foxes and avian predators like jaegers and gulls (McKinnon et al. 2013; Flemming et al. 2019; Lamarre et al. 2017). These changes, of course, have implications for modelling suitable habitat for shorebirds, a topic I address further below. Shifts in the breeding distributions of Arctic shorebirds also have consequences outside the Arctic. If shorebirds shift their breeding grounds further north, this will increase the length of their already extensive migrations. Longer migrations could mean shorebirds need to alter timing, stopover locations, and overall migratory strategies (Anderson et al. 2019).

This evidence that shorebirds are shifting their distribution in response to climate change rests on a key assumption that occupancy will be higher in the center of a species range than at the edges. This assumption is based on a hypothesis which has been supported in some studies, but not others (Dallas, Decker, and Hastings 2017; Sagarin and Gaines 2002; Guo et al. 2005). The evidence that we provide in Chapter 1 will be stronger if combined with evidence that Arctic shorebird populations do indeed conform to this biogeographical pattern. Another limitation of the evidence in Chapter 1 is that there is little nuance about the potential direction of range shifts. Many studies neglect to compare distributional shifts across multiple directions, however, complex interactions between changes in temperature, precipitation and other factors mean that range shifts can occur in a multitude of directions (Taheri et al. 2021; VanDerWal et al. 2013). Despite these limitations, the methods I developed for this chapter present a novel way to test whether species are shifting their ranges for circumstances where large-scale, regularly repeated surveys are not available.
Interestingly, the evidence that Arctic shorebirds are already shifting their distributions in response to climate change is further supported when the results of Chapter 2 and Chapter 4 are viewed together (Figure 5-5). In Chapter 1, I described a trend where occupancy increased for warm-adapted species, and occupancy decreased for cold-adapted species. There is a strong relationship between these observed trends in occupancy from Chapter 2, and the changes in the area of suitable habitat I projected in Chapter 4. This is another supporting line of evidence for shorebird ranges shifting northwards, following the projected shifts in suitable habitat.

Figure 5-1: In Chapter 1 (y axis), I calculated the percent change in occupancy of shorebird species from 1994-1997 to 2019 in the Rasmussen Lowlands and Foxe Basin. In Chapter 3 (x axis), I calculate the probability that each species would have less suitable habitat in 2075 and 2010. There is a strong relationship between observed changes in shorebird occupancy and projected future change in the area of suitable breeding habitat for Arctic shorebirds ($\beta = -393$, $SE = 156$, $t = -2.5$, $p = 0.036$).
Addressing these shortcomings, and a wide range of other analyses for assessing distribution shifts in Arctic shorebirds, will become possible after more Arctic regions are re-surveyed by the Program for Regional and International Shorebird Monitoring (PRISM). For example, after a second full round of surveys, it will be possible to compare distribution maps for two survey periods ~20 years apart. This will allow us to test whether observed changes are matching the predicted trajectories of habitat change presented in Chapter 3. Such analyses would allow us to test if there have been shifts in shorebird habitat use, both in geographic space and environmental space.

Another avenue to better understand how shorebird distributions are changing would be to document evidence of local colonization and extinction at long-term research sites, and test if these patterns match the shifts we expect under climate change. Range shifts are often driven by generational shifts in distribution, as birds typically disperse to new breeding sites as juveniles, allowing them to take advantage of improving conditions in previously unused locations (Gill, Alves, and Gunnarsson 2019; Veit et al. 2022). Anecdotally, there have been years with above-average numbers of second-year Western Sandpipers in Utqiagvik (Barrow, Alaska), and second-year Dunlin in Quaqsauquq (East Bay, Nunavut; W. English, personal communication, July 19, 2023). These species were not previously known to breed at these sites, and tended to be inexperienced breeders with incomplete clutches and high rates of nest abandonment. Systematically quantifying variation in species, age composition, and reproductive success of nesting shorebirds in relationship to patterns we would predict to see as
species shift their ranges in response to climate change could clarify the mechanisms by which shorebird ranges are shifting.

HABITAT SUITABILITY MODELLING

The habitat suitability models which I presented in chapters 2 and 3 define suitable shorebird habitat at a much larger extent than previous studies. This gives new insight into the factors that shape shorebird distributions, as species respond to different biological processes at different spatial extents (Yackulic and Ginsberg 2016). Some important predictors of shorebird habitat at the extent of the Canadian Arctic align with previous studies at regional and local extents: many shorebird species nest at lower elevations, closer to the coast, and are strongly influenced by the vegetation community (Cunningham, Kesler, and Lanctot 2016; Saalfeld et al. 2013). The timing of snowmelt influences the timing of breeding for Arctic shorebirds, and the degree of phenological match or mismatch with their invertebrate prey (Smith et al. 2010; Saalfeld et al. 2013). I found that these mechanisms also influence shorebird breeding habitat at a large spatial scale.

In contrast, some of the predictors of shorebird habitat at the extent of the Canadian Arctic are less relevant at smaller scales because they vary across larger scales. For example, substrate chemistry was an important predictor for most species. Of the climate variables we tested, temperature-related variables were better predictors of
shorebird habitat than precipitation-related predictors. Both substrate chemistry and climate indirectly affect shorebirds through their influence on vegetation. Temperature has direct effects on shorebirds’ decisions to breed, the timing of egg-laying, and the growth of chicks (Meltofte et al. 2007). We found direct effects of substrate on shorebird habitat suitability, but I speculate that these results may be influenced by other indirect effects of substrate on water chemistry, invertebrates or other elements of the vegetation community that were not captured in the path analysis in Chapter 2.

Pragmatic constraints meant that some modelling decisions needed to be altered for modelling future versus current distributions. For example, in my assessment of the factors that best predict current habitat for Arctic shorebirds (Chapter 2), I concluded that the optimal spatial scale for testing relationships between shorebirds and landcover differed across shorebird species and across landcover types. I also found that for some species, the date of 50% snowmelt was an important predictor. These factors were not addressed in Chapter 3 for practical reasons; future projections of land cover are much coarser, and future projections of snow melt dates are not widely available.

Much like my projections for future shorebird habitat, projections of future land cover are limited by both uncertainty in present relationships between vegetation and soil, hydrology and climate, and the compounding of these uncertainties as they are projected into the future. Over time, I expect that there will be improvements in our understanding of some of these processes, and data products describing them will be developed. Predicting how snow cover will change is currently an active area of research in geoscience and civil engineering (Javadinejad, Dara, and Jafary 2020; Mudryk et al.)
2017; Callaghan et al. 2011), and predictive maps such as those in the “Canada’s Changing Climate Report” (Derksen et al. 2019) may soon become publicly available. Maps of Arctic land cover have improved since the Pearson et al. (2013) projections I used were developed (compare Walker et al. 2005 to Raynolds et al. 2019), creating opportunities to improve future projections. Advances in these types of data products will be beneficial for predictive models of future wildlife distributions.

Other uncertainties in projecting future habitat and species distributions are more difficult to address. One limitation of habitat suitability models is that they do no address biotic interactions like competition, facilitation, predation, and disease. While I addressed the importance of vegetation in shorebird distributions in this thesis, future research could work to incorporate the co-occurrence patterns of shorebirds with a wider ecological community of species like Arctic Fox, geese, gulls, jaegers, and lemmings, or shorebirds’ arthropod prey. As an alternative to individual habitat suitability models, an alternative approach would be to use methods that dynamically link models for co-occurring species, or macroecological models that model the how communities occur along environmental gradients (Kissling et al. 2012; Clark et al. 2014; Mokany et al. 2012). However, these methods still do not address the appearance of “no-analog” communities, combinations of species do not currently exist (Williams and Jackson 2007; Fitzpatrick and Hargrove 2009). Another limitation of habitat suitability models is that they assume species are at equilibrium with their current environment, fully occupying all suitable areas, and not occupying any unsuitable areas. Dynamic occupancy models explicitly estimate colonization and extinction do not make this assumption, and could
improve predictions compared with static SDMs (Naujokaitis-Lewis & Fortin, 2016; Yackulic, Nichols, Reid, & Der, 2015).

CONSERVATION IMPLICATIONS

My thesis has two important implications for shorebird conservation in Canada. First, as shorebirds move their breeding sites further north in response to climate change, we should be concerned about declining breeding habitat availability for High Arctic shorebird species whose current breeding ranges are centered on higher, colder latitudes. These species will be limited in their ability to shift their breeding sites to find appropriate climates, as there is no landmass further north to shift into. Second, for species whose breeding ranges are currently centered in Low Arctic latitudes, Canada can be an important refuge as the climate changes. The breeding ranges of many of these species also extends into Alaska, Russia, and Europe. In these regions, shorebirds will be limited in the amount of land that is available to shift into, but in Canada, there is substantial landmass in the Canadian Arctic Archipelago that could become suitable habitat for these species as the climate warms. However, the slow rates of soil accumulation and vegetation in the Arctic will put some limitations on whether High Arctic sites can become suitable habitat for Low Arctic species in an appropriate time-frame.
The Canadian north is a unique socio-political environment for conservation. Issues surrounding conservation and wildlife are a major political focus, with a mixed economy that relies both on wage and subsistence activities (Natcher 2009). For example, two of the four main objectives of the Nunavut Land Claims Agreement are to ensure rights for Inuit to participate in decision-making concerning the use, management and conservation of land, water and resources and to ensure rights of Inuit to participate in decision-making concerning wildlife harvesting (The Tungavik and the Minister of Indian Affairs and Northern Development 1993).

A warming climate is facilitating new development activities related to mining, oil and gas, transportation and tourism in the Arctic; activities that are hoped to address longstanding inequalities in access to services and jobs (Government of Canada 2019; Klein et al. 2005). The social importance of wildlife in the Arctic and the political autonomy of Inuit has a significant influence on these new developments. In 2022, the federal government upheld the Nunavut Impact Review Board’s recommendation to reject a doubling in size of the Mary River Iron Mine on northern Baffin Island, citing observed negative effects on wildlife and fish habitat (NIRB 2022). Although shorebirds are not widely harvested by Inuit, and therefore are not a focal species of wildlife management organizations, they benefit from management by northern co-management boards, which incorporate indigenous views on and approaches to conservation (CWS 2006). These Indigenous-managed lands can support biodiversity as well as conventional protected areas (Schuster et al. 2019).
Developing conservation plans for Arctic shorebirds that take climate change into account will be challenging and could benefit from a wide range of approaches, including habitat suitability models, direct observations, paleoecological records, experimental manipulations, population models, ecophysiological models and traditional knowledge (Dawson et al. 2011; Riedlinger and Berkes 2001). This thesis contributes both habitat suitability models and direct observations to help us better understand how climate change is affecting shorebirds in the Arctic. Given all of the uncertainties around projecting species’ future habitat in response to climate change, habitat suitability models may have a bias towards over-estimating species vulnerability to climate change, and may be more useful for identifying potential new habitats than identifying where current habitats will no longer exist (Schwartz 2012). Habitat suitability models are also useful as a tool for identifying exposure to climate change, which can be combined with other diverse sources of information on species sensitivity to climate change and adaptive capacity to prioritize conservation actions for species and locations that are most vulnerable to climate change (Dawson et al. 2011).

One of my fears while writing this thesis is that I might be inadvertently contributing to a false sense of predictability about consequences of climate change. Despite our attempts to wrap our minds around the uncertainties of the consequences of climate change, I fear that driving to campus to work on this thesis and flying in planes and helicopters to study shorebirds could be contributing the causative elements of climate change that are far less uncertain. I’ve been thankful for the opportunity to wrestle with the implications of climate change as part of my work, and I hope that I can
in some small way contribute to the systemic change that needs to happen in our society
to follow a path where the environment still feels welcoming to most human and non-
human organisms. If I am blessed to be alive in 2075, I will be in my 80’s. I hope my
grandchildren will be able to stumble across a shorebird nest while tramping across Arctic
tundra, or watch a great flock of shorebirds depart on their migratory journey from my
grandparent’s home on the Bay of Fundy.
APPENDIX A - SUPPORTING INFORMATION FOR CHAPTER 3

Links to all supporting files for chapter 3 can be found at

https://doi.org/10.1371/journal.pone.0285115

Figure A-1: Maps of northern Canada showing where each species of breeding shorebirds was present during PRISM surveys 1994–2018. Reprinted from ArcGIS under a CC BY license, with permission from Esri, original Copyright 2022 Esri (Basemaps supported by Esri, HERE, Garmin, OpenStreetMap contributors, and the GIS User Community).
https://doi.org/10.1371/journal.pone.0285115.s001

Figure A-2: AIC values for all tested radii to determine the optimal scale of effect at which land cover and snow cover affect shorebird occupancy.
https://doi.org/10.1371/journal.pone.0285115.s002

Table A-1: Years in which each PRISM region was surveyed. See [29] for map of survey regions.
https://doi.org/10.1371/journal.pone.0285115.s003

Table A-2: Range of values for environmental predictors.
https://doi.org/10.1371/journal.pone.0285115.s004

Table A-3: Radius (m) of the optimal scale of effect at which land cover and snow cover affect shorebird occupancy, determined by AIC.
https://doi.org/10.1371/journal.pone.0285115.s005

Table A-4: Full results of GLMs used for deviance partitioning.
https://doi.org/10.1371/journal.pone.0285115.s006

Table A-5: Path analysis: Summary of the significant total effects of predictors on shorebird occupancy. https://doi.org/10.1371/journal.pone.0285115.s007

Table A-6: Path analysis: Full results of the 17 species-specific path models, including summaries of the direct, indirect and total effects of the paths between all variables.
https://doi.org/10.1371/journal.pone.0285115.s008
Figure B-1: Consensus maps of the areas predicted to be suitable habitat for 13 Arctic shorebird species in the 20 year periods centered on 2010 and 2075. The value in each cell is the proportion of the 216 model configurations of 6 modelling decisions that indicated suitable habitat.
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