

Factors Affecting Nest Survival and Nest Site  
Selection for the Lesser Yellowlegs (*Tringa flavipes*)

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# ABSTRACT

## Factors Affecting Nest Survival and Nest Site Selection for the Lesser Yellowlegs (*Tringa flavipes*)

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The Lesser Yellowlegs (*Tringa flavipes*) is a steeply declining shorebird that breeds across boreal North America. I studied nest survival in Anchorage, Alaska, USA and Churchill, Manitoba, Canada and nest site selection factors in Churchill. Nests were monitored at each site and daily nest survival rates (DSR) were calculated based on a maximum likelihood approach. Overall nest survival was ~63% for Anchorage (lcl–ucl = 0.450–0.773, n=49) and ~28% (lcl–ucl = 0.113–0.481, n=26) for Churchill. Earlier initiation dates, warmer mid-incubation temperatures and lower temperature variability during nesting were linked with higher DSR. I tested nest site selection at territorial and microhabitat scales using multiple logistic regression to compare nest sites with random points. Lesser Yellowlegs selected territories further from water and, at the microhabitat scale, taller shrubs. Projected climate-related shifts in weather and habitat will likely present both benefits and challenges to Lesser Yellowlegs.

**Keywords:** Lesser Yellowlegs, *Tringa flavipes*, shorebird, nest survival, nest success, nesting habitat, breeding habitat, boreal, sub-arctic, climate change, Anchorage, Alaska, Churchill, Manitoba

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# CHAPTER 1: General Introduction

## Background

Multiple lines of evidence point to a loss of nearly 3 billion birds in North America over the last 50 years (Rosenberg et al. 2019). Shorebirds, grassland birds and aerial insectivorous birds showed the most drastic declines based on evidence provided by multiple long-term standardized surveys including the North American Breeding Bird Survey (BBS) (Rosenberg et al. 2019; Sauer et al. 2017). This precipitous loss of avifauna is compelling evidence of deteriorating ecosystem integrity (Rosenberg et al. 2019). Not unlike the early warning provided by the canary in the coal mine, global bird health is an important indicator of conditions that affect our own health (Egwumah 2017; Lawler et al. 2003; Mekonen 2017). Shorebirds, a group of birds with some of the longest migrations in the world (Colwell 2010), are potentially a valuable indicator taxon to evaluate hemispheric ecosystem health and global environmental change (Piersma & Lindström 2004). The rates of decline are accelerating for a majority of shorebird species breeding in North America (Smith et al. 2023), a phenomenon that makes the call for effective conservation action all the more urgent.

The Lesser Yellowlegs (*Tringa flavipes*) is one of many declining species of shorebirds and among those whose populations are declining most quickly (Smith et al. 2023). Their breeding range spans the northern boreal forest of North America, from Alaska to central Quebec, and the non-breeding range

stretches from the southern U.S. and the Caribbean to Argentina (COSEWIC 2020; Tibbitts & Moskoff 2020) (Figure 1.1). The downward trend for Lesser Yellowlegs populations is well documented with multiple lines of evidence. Data from migration surveys conducted in North America show a statistically significant population decline of 60-80% since the 1970's (Smith et al. 2023). BBS data suggest a long term decline of 1.87% per year for Canada and the contiguous U.S. (Sauer et al. 2017), while off-road Alaska Landbird Monitoring Surveys and roadside BBS data for the NW Interior Forest Bird Conservation Region (an area covering over 50% of Alaska's landmass) indicated a 5.3% annual decline in Lesser Yellowlegs (Handel & Sauer 2017). Abundance surveys at multiple non-breeding sites in the Caribbean and in South America have provided further evidence of range-wide population loss (Nores 2011; Ottema & Ramcharan 2009). The total North American population was estimated to be at least 527,000 individuals in 2020, but if current trends continue, an additional 50% loss is projected over the next 10 years (COSEWIC 2020; R2R 2022). This trend was corroborated by Smith et al. (2023), who found that Lesser Yellowlegs declines have not only continued but have accelerated by approximately 3% per year over the last three generations for an annual decline of ~7%. As a result of these declines, the Lesser Yellowlegs has been federally designated as Threatened in Canada (COSEWIC 2020), listed as a Bird of Conservation Concern in the U.S. (USFWS 2021), and is considered a Species of Greatest Conservation Need in Alaska's State Wildlife plan (ADF&G 2015). In 2023, the Province of Ontario, Canada added the Lesser Yellowlegs to the list of Species at Risk in Ontario

under a Threatened status (COSSARO 2021; *Lesser Yellowlegs* | *Ontario.ca* 2023).

Lesser Yellowlegs face threats throughout the species' range (Clay et al. 2012; COSEWIC 2020; McDuffie 2022). I will discuss these according to geography. First, in the boreal forest, climate change modeling has shown that wetland drying may become a threat to breeding success as it may limit suitable nesting habitat (Bateman et al. 2020; Clay et al. 2012). Lesser Yellowlegs commonly nest 30 to 200 meters away from shallow wetlands used for foraging and for brooding chicks (Tibbitts and Moskoff, 2020). Since precocial chicks are not fed by their parents and must rely on foraging for invertebrates available in the immediate environment, diminishment of these wetland areas may increase juvenile mortality during the brooding stage (Silva-Monteiro et al. 2022). Second, threats during migration include loss of critical wetland stopover sites due to agricultural expansion and exposure to agricultural contaminants in North America's Prairie Pothole Region (PPR) and in the Mississippi Basin (Malaj et al. 2020; Clay et al. 2012). Neonicotinoids, a class of insecticide commonly used in the PPR, can negatively impact migration and reduce survival for migratory birds (Eng et al. 2019; Gibbons et al. 2015). Further south, in the tropics, conversion of wetlands to agriculture, as well as shoreline development, have led to decreases in stopover habitat for migrants (Clay et al. 2012). Third, a potentially significant source of mortality for southbound birds is sport and subsistence hunting in the Caribbean and in northeastern South America (McDuffie et al. 2022). Hundreds of thousands of shorebirds are harvested in these regions each year; however,

hunting of Lesser Yellowlegs is not currently practiced in other parts of the species' breeding, migration or non-breeding range (AFSI 2020). And finally, on the non-breeding range in South America, agrochemical contamination of foraging sites and conversion of wetlands to agriculture pose threats to the species (Clay et al. 2012).

Lesser Yellowlegs populations have declined precipitously. To reverse declines, we need to know where the greatest losses are occurring, not just geographically, but also within the life cycle (Byers et al. 2022; Weiser et al. 2020). Given these declines, it is apparent that individuals are lost faster than they are replaced. We do not know if this is because mortality of adults or juveniles is high or because the rate of replacement is too slow, or perhaps both. Answering these questions and responding with targeted management requires investigating the factors that govern Lesser Yellowlegs' population dynamics, i.e., demographics (Norris 2004; Weiser et al. 2020).

Demography is the statistical analysis of population drivers and how they change over time. Given the Lesser Yellowlegs' expansive range and the complex matrix of threats they face, reliable demographic data are crucial to informing targeted conservation efforts (Norris 2004). Changes in vital rates, chiefly survival and reproduction, govern population size (Abadi et al. 2010; Johnson et al. 2010). Measures of reproductive success, a population gains metric, are often inferred from estimates of nest success (Brown et al. 2014). There are myriad threats, many of which most likely impact all populations, leading to declines of Lesser Yellowlegs. Given that there are no known populations insulated from these

threats (e.g. outside of the western hemisphere) ready to supply immigrants (Tibbitts & Moskoff 2020), population growth is dependent on successful reproduction.

These birds make epic hemisphere-spanning migrations twice yearly between their breeding and non-breeding ranges, annually covering an average of over 25,000 km (McDuffie et al. 2022). The majority of migrants funnel through North America's Prairie Pothole Region and refuel by foraging in shallow wetlands that were once historically plentiful (McDuffie et al. 2022).

Though adults exhibit high breeding site fidelity and use distinct migratory pathways, Lesser Yellowlegs do not have genetically distinct subpopulations since juveniles are less likely to return to their natal territory and may select different breeding grounds (Christie et al. 2023; Tibbitts & Moskoff 2020). This lack of natal philopatry increases genetic diversity within the species but also means that subpopulations are not necessarily insulated from the effects of regional threats because individuals may use multiple flyways and stopover sites during their lifetimes (Christie et al. 2023). Juveniles often spend their first full year in the non-breeding areas and then migrate to the breeding grounds in their second year (Tibbitts & Moskoff 2020).

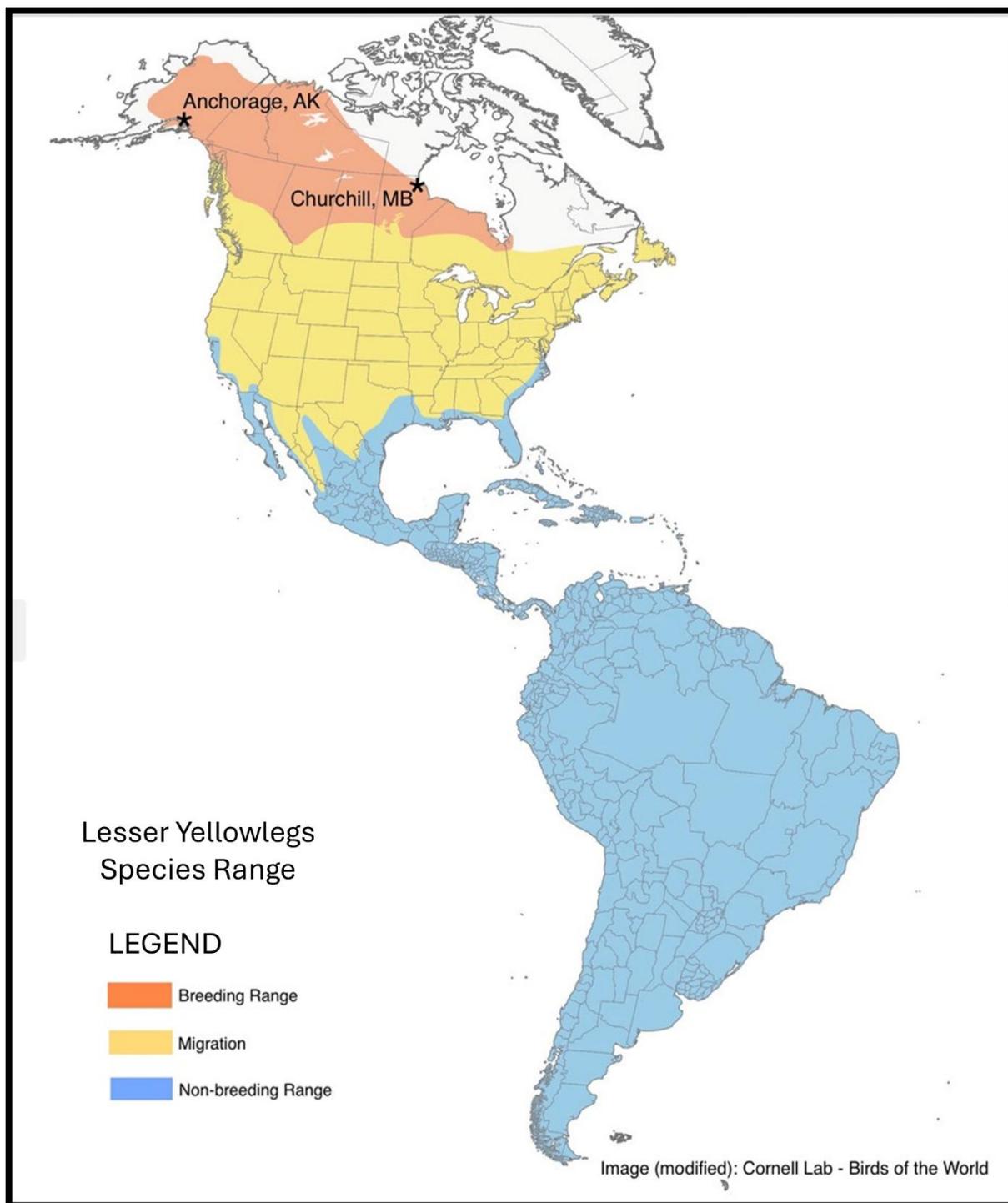
Lesser Yellowlegs tend to nest in relatively open areas with sparse small shrubs and often near the edges of boreal forest (Tibbitts & Moskoff 2020). But occasionally nests are placed on open ground, such as tundra or clearings, or well within the boreal forest. They are ground-nesting birds that lay their eggs in a shallow scrape, quite often beneath a small shrub (approximately 0.5 meters

tall) (Figure 1.2). The eggs are cryptic, having a light buff to sea green background and varying degrees of dark brown speckles and splotches concentrated more heavily at the blunt end of the egg. Egg laying begins 12–15 days after arrival on the breeding grounds (Tibbitts & Moskoff 2020). Complete clutches typically consist of four eggs but occasionally three (Tibbitts & Moskoff 2020). One egg is laid per day and incubation may begin with the second egg (Tibbitts & Moskoff 2020). Incubation lasts 22–23 days and eggs usually hatch within 2–12 hours of each other. Both parents incubate and switch incubation duties inconspicuously, traveling the several meters closest to the nest on foot (Tibbitts & Moskoff 2020, personal observation). Adults commonly engage in nest defense by alarm calling while perched but early in the nest season they may opt to quietly leave the nest or sit tightly, apparently relying on the camouflage provided by eggshell patterning or their own plumage. But they become more defensive as nests are closer to hatching, similar to the pattern observed in other shorebird species (Smith & Wilson 2010). If the threat continues, they may engage with fluttering fly-by maneuvers and hovering near the perceived threat while alarm calling loudly (Tibbitts & Moskoff 2020). As a relatively long-lived shorebird they likely weigh the risks of nest predation and benefits to lifetime fitness of favoring their own survival in a given season (Williams 1966; Colwell 2010).

In the following chapters I explore the breeding ecology of Lesser Yellowlegs. Chapter 2 is an examination of factors which may affect nest survival for two breeding populations: one in Churchill, Manitoba, Canada (58.77° N, -94.17° W)

and one in the Anchorage, Alaska, USA (61.22° N, -149.90° W) (Figure 1.3). My Churchill research provides a crucial missing perspective on Lesser Yellowlegs' population processes. Eighty percent of the species' global population breeds in Canada (COSEWIC 2020), yet prior to this work, no data were available on Lesser Yellowlegs' reproductive success in Canada (COSEWIC 2020). Research at these two study sites allowed us to sample the wide variety of habitats and weather conditions within the Lesser Yellowlegs' breeding range as well as to identify aspects that may be consistent between them, thus generating a more well-rounded view of population processes for the species. In Chapter 3 I study habitat selection for Lesser Yellowlegs nesting in the Churchill region. Nesting habitat features have not been formally quantified for the species. This information could help us to understand how breeding habitat features that are rapidly shifting due to climate change (e.g. vegetation cover and hydrology) might affect the species. In the final chapter I present my overall conclusions and suggestions for ongoing research.

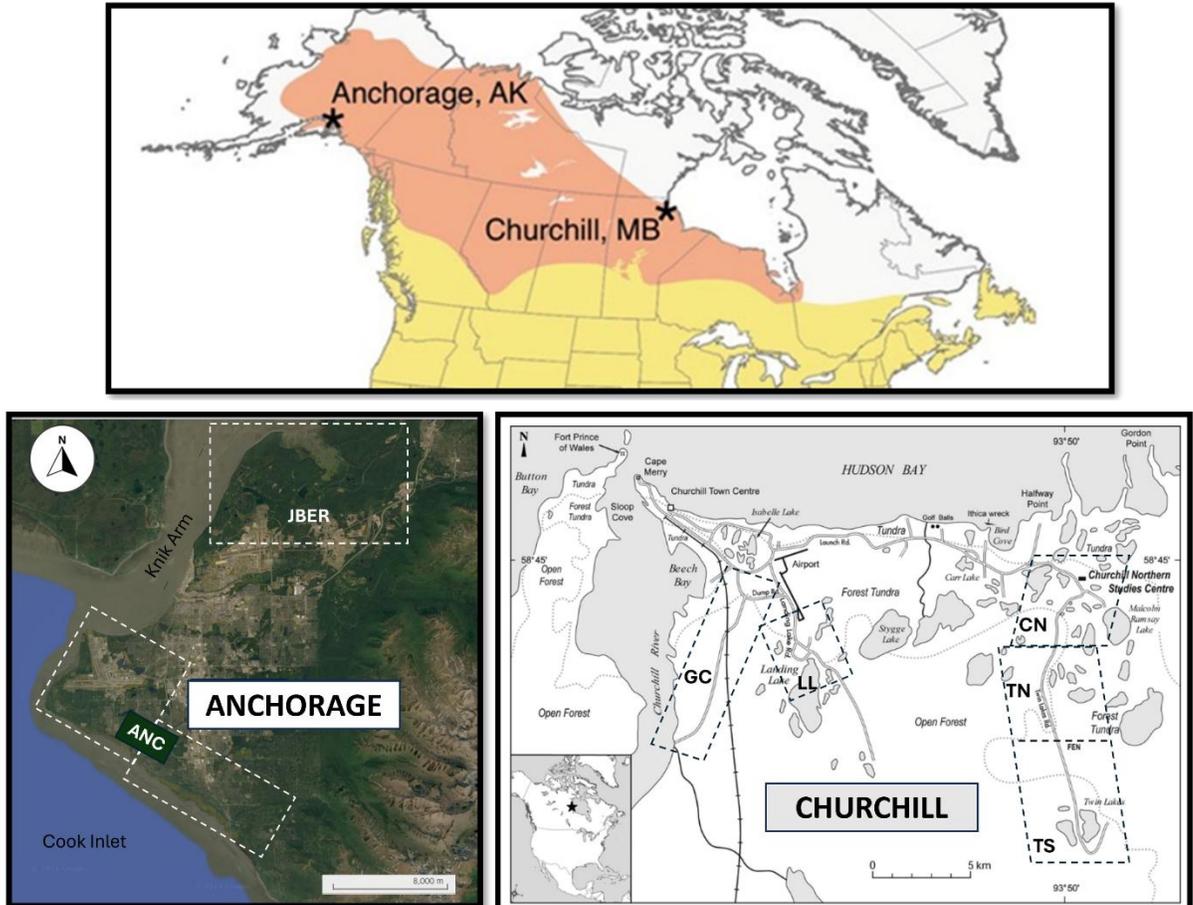
## Chapter 1 Figures:



**Figure 1.1** Species range map for the Lesser Yellowlegs. Data for this research were collected in Anchorage, Alaska USA and Churchill, Manitoba Canada. Map courtesy of Cornell Laboratory of Ornithology (Tibbitts & Moskoff 2020).



**Figure 1.2** Lesser Yellowlegs (indicated by the arrow) in Churchill Manitoba incubating a nest placed under a dwarf willow shrub.



**Figure 1.3** Study sites in Anchorage, Alaska, USA ( $61.22^{\circ}$  N,  $-149.90^{\circ}$  W)

and Churchill, Manitoba, Canada ( $58.77^{\circ}$  N,  $-94.17^{\circ}$  W). Image credits: top map (modified) courtesy of Cornell Laboratory of Ornithology, Birds of the World.

Anchorage map (modified) courtesy of Google Earth (*Google Earth* 2025),

Churchill map (modified) courtesy of Peter Kershaw.

## CHAPTER 2: Nest survival for the Lesser Yellowlegs

(*Tringa flavipes*): a comparison between Churchill,

Manitoba, Canada and Anchorage, Alaska, USA

### INTRODUCTION

One of the tenets of range limit theory is that organisms will have lower fitness at the edges of their range — this is what links ecological limits to evolutionary processes (Sexton et al. 2009). Broadly, species distributions in the northern hemisphere are limited north to south due to a gradient of environmental conditions which, at their extremes, can exceed species' tolerances for survival and successful reproduction (Hutchins 1947).

Populations of most North American shorebird species have been in decline over the past several decades (Smith et al. 2023). When searching for the causes of these declines we must consider reproductive success as part of demographic “accounting” (Norris 2004). Nest survival has important impacts on population dynamics as a primary means of recruitment of new individuals to the population (Colwell 2010).

Many factors may affect nest survival and there can be a complex relationship between abiotic (e.g., weather) and biotic factors (e.g., predation) (Smith et al. 2012; Smith & Wilson 2010; Weiser et al. 2018). Breeding birds must nest in a location and employ incubation behaviors that decrease the risk of predation on adults and eggs (Smith et al. 2012). They must also protect developing eggs

from weather extremes while taking foraging recesses often enough to meet their own metabolic demands for survival (Tulp et al. 2009). Since birds breeding at high latitudes face both a shorter breeding season and climatically more dynamic environments than those breeding in more temperate zones, these tradeoffs are magnified (Moltofte et al. 2007).

Because predation has the greatest impact on reproductive success for birds (Martin 1993; Smith et al. 2007) minimizing risk is paramount. Loss of nests, usually due to predation, is the most common cause of reproductive failure in birds (Colwell 2010; Martin & Geupel 1993). Nest site selection favoring higher or lower levels of nest concealment have each been found to be adaptive for different species of shorebirds (Colwell 2010; Laidlaw et al. 2020). The nest concealment hypothesis predicts that birds select sites that provide cover to reduce predation which then confers higher nest success (Martin 1988).

Alternatively, many species of shorebirds prefer more open habitats that allow the incubating adult to visually monitor the landscape and perceive danger early enough to leave the nest undetected if necessary (Amat & Masero 2004; Korne et al. 2020). Nest site concealment may protect against avian predators that use visual cues but may be less effective for mammalian predators that mostly use olfactory cues (Zhao et al. 2020)

Species breeding across a wide geographic range will contend with differing weather conditions. Egg production and incubation are energetically costly and since shorebirds are income breeders, they rely on adequate forage and environmental conditions on the breeding grounds to lay eggs (Klaassen et al.

2001; Tulp et al. 2009). Higher metabolic demands in challenging environments may lead to higher rates of nest abandonment (Weiser et al. 2018). Rates of abandonment can be difficult to quantify as eggs in an abandoned nest may be consumed by opportunistic nest predators and thus failures due to abandonment may be indistinguishable from predation on active nests. Nest sites may be selected based on favorable microclimates, which can ameliorate harsh environmental conditions by reducing convective heat loss for unattended eggs or for the incubating adult (Smith et al. 2007).

Timing of arrival for migrants and subsequent nest initiation can be factors influencing reproductive success and many studies of other species have shown that nests initiated early in a season have higher nest survival than those initiated later (Morrison et al. 2019; Weiser et al. 2018).

There can be a great deal of variation in predation pressure year to year depending on the numbers of alternate prey species (Sandercock 1998; Smith & Wilson 2010). Shorebird eggs can be valuable to nest predators but are likely secondary to other food sources (Mckinnon et al. 2013). For example, nest predation on shorebirds nesting on Bylot Island, Nunavut was much higher in years when lemming numbers were low (Mckinnon et al. 2013).

Many studies have found that nest survival rates vary temporally, meaning that they change over time during the nesting season (Smith & Wilson 2010; Weiser et al. 2018). This may occur for a variety of reasons, such as increased predation pressure due to phenology of co-occurring species or changes in environmental conditions (Smith & Wilson 2010; Weiser et al. 2018). Mountain Plover nests, for

example, failed at a predictably higher rate following heavy rain because bull snakes emerged after rain events (Dinsmore et al. 2002).

Variation in nest survival may also be related to nest age if parental behavior changes over the course of the incubation period. For example, research demonstrated that shorebirds at East Bay in Nunavut increased nest defense behaviors through the season and concluded that this likely increased survival rates as nests aged (Smith and Wilson 2010).

Subsequent developmental phases following survival of the eggs, such as survival and fledging of the young, are critical components of avian reproductive success (Cox et al. 2014; Pakanen et al. 2021). However, these are far more challenging to measure in precocial shorebird species and far fewer studies address this (Pakanen et al. 2021). Reproductive success for shorebirds is most commonly based on the egg stage since chicks are precocial and leave the nest soon after hatching and they are then very difficult to follow and monitor (Ricklefs 1969).

Most shorebird species are limited in reproductive capacity even under the best conditions because they are determinant layers, limited to a clutch of four eggs, and many produce only one clutch per season (Colwell 2010; Tibbitts & Moskoff 2020), so conditions affecting nest survival are critical.

Few studies have examined reproductive success for shorebird species at multiple and distant locations across the breeding range (but see Senner et al. 2017 and Weiser et al. 2018). Lesser Yellowlegs (*Tringa flavipes*) are an

excellent species for such a study since they have a wide and environmentally variable breeding range but are limited to North America (Tibbitts & Moskoff 2020).

My research examines nest survival for two breeding populations of Lesser Yellowlegs based on data collected in Anchorage, Alaska, USA (61.22° N, – 149.90° W) and Churchill, Manitoba, Canada (58.77° N, – 94.17° W). (Figure 1.3). The Churchill project, conducted during June and July of 2022 and 2023, was designed as a parallel study to an intensive demography project that began in Anchorage, Alaska in 2018 and spanned five full field seasons (Table 2.1). Anchorage nest data were collected during May and June of each year. Research at multiple sites over multiple years is enormously important to understanding complex factors that govern breeding biology for shorebirds (McGuire et al. 2020).

These two geographically distant sites vary in weather and vegetation characteristics and present an opportunity to explore the influence of multiple factors to determine whether these might contribute to expected differences in nest survival between these populations. Additionally, I tested whether capture of incubating birds on the nest affected nest success. While Lesser Yellowlegs in the Anchorage area have been under study since the 1990's (Tibbitts & Moskoff 2020), reproductive success for Lesser Yellowlegs breeding in Canada has not been documented (COSEWIC 2020). This window into population dynamics for Churchill breeding birds is valuable since Lesser Yellowlegs generally return to the same breeding areas (Tibbitts and Moskoff 2020). Therefore, collecting

demographic data in multiple regions of the range gives a more complete picture of the processes driving overall population trends.

## Study areas

Churchill and Anchorage both occur at the boundaries of North America's boreal forest such that Churchill grades into northern tundra, and Anchorage borders temperate rainforest to the south. The Churchill region is situated on the western shore of Hudson Bay and is characterized by its wide expanses of lichen-heath tundra, thermokarst wetlands, and open (<20% canopy closure) lowland and upland boreal forests (Kershaw & McCulloch 2007). Because of the cold air masses associated with Hudson Bay, which historically had sea ice that persisted typically until late July, permafrost stretches further south in this region than at similar latitudes to the east and west of the Bay (Dredge & Dyke 2020; Gagnon & Gough 2005). Because sea ice prevents a moderating effect of Hudson Bay's waters during much of the year, the Churchill region is characterized by continental weather patterns (Gagnon & Gough 2005) with very cold winters and periods of extreme heat in the summer. Quick and dramatic shifts in summer temperatures are common.

Anchorage is in Southcentral Alaska on Cook Inlet, a long narrow body of turbid brackish water that connects the region to the Pacific Ocean. Because of the moderating effect of Cook Inlet's waters, Anchorage is characterized by maritime weather patterns. This leads to a dampening of continental temperature extremes and creates a relatively mild climate compared to areas further inland. Anchorage nesting habitats investigated in this study occurred in black spruce

bogs and deciduous boreal forest typically within 5 km of the brackish coastal wetlands along Cook Inlet.

These sites represent two distinctly different environments with differing challenges for breeding birds. Since the Anchorage study site is situated toward a southern edge of the breeding range, Lesser Yellowlegs are likely to face more threats due to biotic factors (e.g., nest predators) according to classic range limit theory (Louthan et al. 2015). Weather conditions in Anchorage are moderate compared to more northern regions of the range. In contrast, Churchill breeding birds are at a northern edge of the breeding range. Temperatures are lower at the start of the breeding season, remain lower on average throughout incubation, and vary more widely during the nest season (Figure 2.1). As such, these individuals are challenged by abiotic factors as well as by nest predation.

Based on factors that influence nest survival in other bird species (e.g. initiation date, nest age), conditions that differ between the two study areas (e.g. temperature) and how abiotic conditions affect predation, I formed a series of hypotheses to explain expected differences in nest survival for Lesser Yellowlegs between the two sites. I predicted that Lesser Yellowlegs would have higher nest survival overall in Anchorage than in Churchill based on rationale that follows.

Very different summer temperature patterns between the two sites (Figure 2.1) may have affected pairs of incubating Lesser Yellowlegs. This species relies on resources on the breeding range to fuel the metabolic costs of egg production and both parents share incubation and territorial defense duties. I expected the lower average temperatures in Churchill coupled with an expected concomitant

early season reduction of invertebrate prey (compared to Anchorage) to negatively impact reproductive success by increasing the energetic costs for adults and possibly decreasing viability of eggs. Churchill birds, facing higher metabolic demands, likely have shorter incubation bouts and more activity at the nest as parents switch incubation duties, thus increasing the likelihood of predators finding nests there. Additionally, nest abandonment may be higher for Lesser Yellowlegs breeding in Churchill's harsher environment. In species having biparental care, if one partner abandons the nest or dies, the remaining adult normally abandons the nest too (Weiser et al. 2018). Higher variability in environmental conditions in Churchill may lead to more activity at nests if adults are adjusting to changing conditions. This restless behavior could increase likelihood of nest predation (Smith et al. 2012). Lesser Yellowlegs nests have varied levels of concealment. Greater concealment may help prevent detection by predators and the vegetation structure around the nest may improve the microclimate for eggs and for incubating adults. The Anchorage site was more vegetated overall than the Churchill site, which had wide expanses of tundra. Lesser Yellowlegs have initiated nests in Anchorage nearly two weeks earlier on average than in Churchill (L. McDuffie, unpublished data). Earlier initiation may confer an advantage on the Anchorage birds since they may be able to renest should nests fail early in the season (Gates et al. 2013) but Churchill's shorter summer, truncated by the "winterizing" effects of Hudson Bay, may not afford this opportunity to Lesser Yellowlegs breeding there. I test these hypotheses by exploring influences of a series of covariates including temperature, temperature

variability, concealment, and nest initiation date on nest survival for each study site.

## METHODS

### Churchill subsites

We worked at four subsites within the broader Churchill region accessed by the road system north of Churchill (Figure 2.2). These subsites ranged from 2 to 17 km away from Hudson Bay and were all associated with freshwater wetlands. Forests were composed primarily of spruce (*Picea sp.*), tamarack (*Larix laricina*), willows (*Salix sp.*), and birch (*Betula sp.*), occurring in differing relative abundances depending on local conditions.

The Churchill Northern (CN) subsite, furthest to the north, had wide open lichen-heath tundra and “forest-tundra” transitional zones with sparse individual trees and low shrubs and, in locations protected from the wind, small disjunct forest communities (Payette et al. 2001). CN had many thermokarst wetlands separated by expansive peat plateaus and a few large lakes. South of CN were the Twin Lakes north (TN), and Twin Lakes south (TS) subsites. These subsites were characterized by the ragged edge of the forest-tundra as it toothed into the boreal forest (Kershaw & McCulloch, 2007). Much of the northern end of TS was extensive fen which provided foraging sites, but we found no nests in the fen, despite considerable effort by the observers present during my study in 2022 and 2023. While researchers in 2024 did find one Lesser Yellowlegs nest in TS, they still found that the northern sites had much higher numbers of nests (L. Maskell,

unpublished data). Landing Lake (LL) subsite was not contiguous with the others. It had plentiful ponds and large wetlands interrupted by smaller peat plateaus than in CN or TN.

## Anchorage subsites

We had two subsites in Southcentral Alaska (Figure 2.3), one on Joint Base Elmendorf Richardson (JBER) and the other in west Anchorage; these each cover boreal forest, black spruce bogs and brackish wetlands along the margins of Cook Inlet. The JBER subsite covered an area of approximately 20 km<sup>2</sup> and stretched inland up to ~5 km from Cook Inlet while the west Anchorage subsite (ANC) covered approximately 16 km<sup>2</sup>. These subsites were coastal but included adjacent upland areas. The forest in these subsites is composed of deciduous species, including birch (*Betula sp.*), alder (*Alnus rugosa*), willows (*Salix sp.*), and balsam poplar (*Populus balsamifera*), as well as coniferous species (*Picea sp.*).

## Field Methods

### *Nest searching (Anchorage and Churchill Sites)*

We searched for Lesser Yellowlegs nests in Churchill during June and early July, and in Anchorage during May and June. We found nests based on observing bird behavior and visual searching of nesting habitat (Brown et al. 2014). Our goal was to maximize the number of nests found so we chose sites to search based on territorial behavior, knowledge of preferred nesting habitat and areas in proximity to known locations for nests found in prior years. End of season

protective behavior gave more cues to find nest sites and some nests were found in the process of hatching.

We estimated the nest initiation date by floating eggs to gauge developmental stage based on float height and angle and thereby determining age (Liebezeit et al. 2007). To reduce disturbance to the incubating pair, two eggs from the clutch were each floated in a container filled with lukewarm water from a thermos; the float angle was estimated based on angled lines marked on our translucent float container. If two eggs gave very different results, the rest of the clutch was floated to determine the average age.

If a nest was found prior to clutch completion, we determined the initiation date based on the number of eggs in the nest assuming one egg is laid per day (Smith & Wilson 2010; Tibbitts & Moskoff 2020). Occasionally a pair would lay an incomplete clutch (i.e., < 4 eggs); if we found three eggs on two consecutive visits we assumed that the clutch was limited to three eggs, and we floated the eggs on the second visit to the nest to estimate the initiation date. We recorded nest locations  $\pm$  3m using a handheld Global Positioning System (GPS) unit (Garmin Ltd., Kansas, U.S.A). We marked nest locations in the field using flagging tape tied to vegetation approximately 10m from the nest to prevent predators from cuing in on nest locations. No markers were placed immediately at the nests. The compass bearing and distance to the nest were recorded in our field books and on the flag to enable relocating the nest later. During nest checks we approached nests from different directions to avoid attracting predators or trampling vegetation.

### *Nest Monitoring*

We monitored nests at intervals of five to six days during the incubation period, since Lesser Yellowlegs are sensitive to more frequent disturbances which may increase rates of nest abandonment (K. Christie, pers. obs.). We revisited nests more frequently as the hatch date approached, to ensure precise recording of nest fate and the date of successful hatch or nest failure. We deemed a nest successful if at least one chick hatched. Nests were considered abandoned if found with cold eggs and no attending adult nearby on two consecutive visits. If a nest was suspected to have been abandoned, we turned one egg so that the narrow end faced out. If the nest was still being attended we would find that eggs were rearranged with the narrow ends returned to the center of the nest on the next visit. If all eggs were missing well before the hatch date we recorded the fate as failed and presumed predation as the cause (Weiser et al. 2018). We classified some nests that we did not directly observe hatching as successful based on evidence of small pip fragments in the nest lining (Mabee 1997) when hatch was possible based on the estimated hatch date (26 days after initiation). Adults remove eggshells once the chicks have hatched, and successful nests will typically only have small pip fragments remaining in the nest cup (Tibbitts & Moskoff 2020). Occasionally large pieces of shell from the final egg to hatch were left behind and we could infer that it had hatched successfully if the inner membrane was detached from the shell (Mabee 1997). Parental behavior also provided cues to determine whether a nest had hatched since adults are extremely protective of chicks and alarm call vigorously when they perceive

threats (Tibbitts & Moskoff 2020). Physical evidence that a nest had been depredated included shells of pecked out eggs in the case of avian predators or possibly fox urine or feces in the nest cup since foxes frequently scent mark depredated nests (Smith et al. 2012).

After nest fates were determined, we conducted habitat surveys at each Anchorage nest site to record broad habitat type, dominant vegetation surrounding the nest and, starting in 2020, the percentage of overhead concealment by vegetation. In Churchill we conducted more detailed habitat surveys (Chapter 3 methods), but the overhead concealment measurements were comparable between study sites. These concealment values serve more as relative indices of nest concealment since nests are initiated before leaf-out and much of early incubation takes place in very different vegetation conditions than the end of incubation and the period following departure from nest sites by Lesser Yellowlegs.

## Statistical methods

### *Daily nest survival*

I quantified reproductive success by calculating a daily nest survival rate—the probability that a nest will survive from one day to the next. Nest survival probability is expressed as a percentage and calculated as the daily survival rate raised to the power of the number of exposure days (26 days for Lesser Yellowlegs). Calculating a daily nest survival rate (hereafter “DSR”) based on exposure periods for nests addressed this bias (Mayfield 1961).

I used a maximum likelihood approach to model DSR in program RMARK (Dinsmore et al. 2002; Laake 2013; Cooch & White 2021; R Core Team 2024). Calculating DSR requires at least four data points for each nest: (1) the day of the nesting season on which the nest was found, (2) the last day the nest was active, (3) the last day the nest was checked, and (4) the fate of the nest (successful or failed) (Cooch & White 2021). Nests that hatched at least one egg were considered successful. In contrast to the Mayfield method, RMARK allows researchers to test the effects of covariates and of temporal factors (whether the DSR varies during the season) (Dinsmore et al. 2002).

I began with data collected at 100 nests (Anchorage n=70, Churchill n=30). I removed records that were not suitable for daily nest survival analysis in RMARK for the following reasons (Table 2.1). First, early in the Anchorage study, researchers captured Lesser Yellowlegs at the nest during the incubation using bownets as per common protocol in other studies (Gratto-Trevor 2018). However, due to a high incidence of nest abandonment they suspended this practice because of suspected impacts on nest success; captures of incubating adults were not conducted in subsequent field seasons. Since there was likely a capture effect, I removed 15 Anchorage nests where captures were conducted during the 2018 and 2019 field seasons. Second, I removed 10 nests that were found on hatch day (Churchill n=4, Anchorage n=6). These nests had insufficient monitoring history to calculate DSR although I do report apparent nest success while including these nests. I therefore conducted DSR analyses on a combined dataset of 75 nests (Anchorage n=49, Churchill n=26). To test percent nest

concealment as a covariate, a further subset of the data was required since early in the Anchorage study concealment data were not collected. This subset analysis used only data collected in 2020-2023 and resulted in removing the remaining nests from 2018 and 2019 (n=8) for a dataset of 67 nests (Anchorage n=41, Churchill n=26).

### *Covariates*

I modeled DSR using a selection of covariates (Table 2.2): site (Churchill and Anchorage), nest initiation date, nest age as a linear effect, broad habitat type (boreal forest, shrub-dominated wetland, or clearing), and percent overhead concealment of the nest cup. Additional covariates were ambient temperature, temperature variability, and temporal variables.

### *Temperature variables*

I compiled a dataset which describes average temperature, minimum and maximum temperatures for each day at each site during the nesting season. Weather data for Anchorage were collected at Ted Stevens International Airport adjacent to our study area and sourced from the National Oceanic and Atmospheric Administration (NOAA 2024). Churchill weather data were collected at the Churchill airport and sourced from Environment and Climate Change Canada (ECCC 2024).

To facilitate analysis of weather effects, I broke the nesting season into three periods that were based on the initiation date for each nest and thus the analysis considered temperatures experienced by the breeding pair during each stage of nesting. This allowed me to test whether nests at different development stages

responded differently to temperature changes. Making these periods specific to each nest allows for a finer examination of potential effects rather than considering every nest that season to have been exposed to the same conditions. While there is substantial overlap in these periods due to general synchronicity of nesting, this approach does differentiate conditions for earlier and later nesters within each season (Figures 2.4 and 2.5). The "early period" corresponds to a range of dates starting two days before our recorded initiation date for each nest and spans 12 days. This covered the period of nest selection, egg laying and the beginning of incubation. "Mid" corresponds to the range of dates beginning with the initiation date + 10; there are 10 days within the period, corresponding to the middle of incubation. The "late period" corresponds to the range of dates beginning with the initiation date + 20; there are 10 days within the period, corresponding to late incubation and hatch. While the biological time span from nest initiation to hatch for Lesser Yellowlegs is 26 days, I chose to cover 32 days to allow for the uncertainty of dates based on egg flotation (+/- 4 days). A record of the range of dates which bracketed each nesting season, including first and last estimated initiation and hatch dates, appears in Appendix 1.

Temperature was expressed as the average daily temperature experienced by each nest during the given period. I tested average daily minimum, average daily mean, and average daily maximum temperatures for each of the three nest periods. I also used the nest period structure to test a measure of the variability of temperatures using the standard deviation (sd) of average temperatures recorded during incubation for each nest. I chose standard deviation rather than

a simple range of highest and lowest temperatures because it gives a more accurate measure of variability over time than relying on the two most extreme data points that bound a range of temperatures (Figure 2.6).

#### Temporal variables

Since temporal trends have been found to be influential in many nest survival studies (Smith & Wilson 2010; Weiser et al. 2018), I tested these as linear and quadratic functions of “season day”. Season days are sequentially numbered each field season beginning with the day that the first nest was found (Table 2.3). This “season day 1” marks the beginning of data collection by nest monitoring; this is the measure of time that RMark uses to test temporal variables (Cooch & White, 2021).

#### Nest age

Nest age is an important factor that must be considered in nest survival studies since biases in DSR estimates are possible if an effect of age is not accounted for (Rotella et al. 2004; Weiser 2021). I tested a linear effect of nest age.

I tested covariates for collinearity in Program R using Pearson’s correlation coefficient. Highly correlated ( $r \geq |6.0|$ ) variables were not placed in the same models. As expected, the temperature variables were highly correlated with each other. Site was highly correlated with the temperature variables, temperature sd, and initiation date. I did not include different temperature variables in the same models or combine site and mean temperature or minimum temperature in models because of multicollinearity. However, I was able to combine site and

nest period maximum temperatures because these did not exceed my threshold correlation coefficients. Inclusion of both of these covariates in candidate models allowed me to test an effect of temperature while accounting for the potential of temperatures being confounded with site. To make valid comparisons using model results, covariates were scaled; all temperature variables, initiation and percent concealment data were centered on the mean and scaled by one standard deviation using the `scale()` function in program R prior to analysis.

I tested models using each variable separately and in combinations to test for additive effects, selecting the best models based on the Akaike information criterion adjusted for small sample size ( $AIC_c$ ) calculated in R. I did not test covariate interactions because of the small sample size. Currently there are no goodness-of-fit tests for nest survival models (Dinsmore et al. 2002; Rotella et al. 2004). In candidate model sets I included an intercept only (null) model to aid evaluation of model fit. Comparison of a candidate model with the null model indicates whether the covariate in the model has described more or less variation in nest survival than the constant survival rate.

Models that had the lowest  $\Delta AIC_c$  (0.00 to 2.00) were considered to best describe which factors most affected DSR for my datasets. Variables for which the 95% confidence intervals ("CI's") for the beta estimates did not include zero were considered to have a significant effect; however, results may be considered marginally significant when CI's include zero but at a small absolute value (Nakagawa & Cuthill 2007). Because of model uncertainty I report results from the top models and interpret results based on multiple high-ranking models. I

calculated importance values for variables that appeared in the top models to facilitate a quantification of the relative influence of that variable (Burnham & Anderson 2004). I based my ecological inferences on the variables that appeared in the highest ranked models and had confidence intervals that did not overlap zero.

I first ran a comprehensive set of models which tested each of my covariates including effects of temperature as a minimum, mean, and maximum at each of the three nest periods and an “all” variable for the combined periods that represented the overall time interval for each nest (Appendix 2). To reduce redundancies, I then tested a subset of the models with the most informative temperature variable.

I combined the Churchill nest data for 2022 and 2023 with a longer-term dataset (2018-2022) from Anchorage Alaska (n=75 total for combined data) to determine whether there was a significant difference in nest success in these different locations of the breeding range and whether any of the covariates were shown to have a significant effect on nest success across sites. To test whether concealment influenced nest survival I also completed the combined dataset analysis on a subset of data (n=67) for 2020-2023 since percent concealment data were not collected in Anchorage until 2020 and subsequent years of the study. I pooled the datasets to include both study sites due to small sample sizes and to allow direct comparison of potential effects. Because of low sample sizes in some field seasons (Table 2.1) I was not able to test for year effects.

## RESULTS

We found 30 Lesser Yellowlegs nests in Churchill in June and July of 2022 and 2023 and field crews in Anchorage found 70 Lesser Yellowlegs nests during May and June of 2018–2023 (Table 2.1).

### Combined Anchorage and Churchill dataset

When sites were combined ( $n=75$  nests), the highest ranked models included four covariates: site, initiation date, middle incubation period maximum temperatures, and temperature variability (Table 2.4).

For the same analysis on a subset of the site combined dataset ( $n=67$  nests) that included a covariate for “cover” (percent overhead concealment), cover appeared in the top models with site, initiation date, and middle incubation period maximum temperature (Table 2.6).

Site, initiation, temperature variability, and middle incubation period maximum temperatures were all significant single variable predictors in one or both analyses.

### *Site*

Site was the strongest predictor of nest survival; DSR was higher for Anchorage nests. As a single predictor, this was the second-best model in the  $n=75$  dataset ( $\Delta AIC_c = 0.42$ ) and yielded a DSR estimate for Anchorage = 0.983 ( $se=0.0048$ ,  $n=49$ ) and Churchill = 0.952 ( $se=0.0129$ ,  $n=26$ ) (Figure 2.7). Nest survival, derived from the  $DSR^{26}$ , was estimated at 63% for Anchorage ( $lcl-ucl = 45\%$ –

77%) and 28% for Churchill (lcl–ucl = 11%–48%). The much lower DSR for Churchill relative to the apparent nest survival estimate reflects both the more conservative estimates produced by the Mayfield method and the fact that apparent nest survival estimates (but not the DSR calculation) included four successful nests that were found on the day they hatched.

*Middle incubation period maximum temperature (“Midmax”)*

Maximum temperature variables were influential during the middle incubation period but not during early or late periods. Midmax appeared in three of the top models for the full dataset (n=75), including the top model. Parameter estimates were positive suggesting that DSR increased with higher mid-season temperatures (Figure 2.8); however, the top model estimates were equivocal ( $\beta$  estimate = 0.354, lcl–ucl = -0.063–0.077). Modeled as a single predictor ( $\Delta AIC_c$  = 1.41), estimates indicated a significant positive effect on daily nest survival ( $\beta$  estimate = 0.457, lcl–ucl = 0.021–0.893).

*Initiation date*

Initiation date appeared in four of the top nine models (Table 2.4). Parameter estimates indicated that DSR decreased as relative initiation dates advanced (Figure 2.8). The top model tested an additive effect of initiation date and midmax. The beta estimate of 95% confidence intervals included zero but both variables showed marginal significance (Table 2.5). Initiation date modeled as a single predictor indicated that earlier nest initiation significantly increased daily nest survival ( $\beta$  estimate = -0.468, 95% CI -0.880 – -0.057).

Nest initiation dates for each site reflected the expectation that Churchill Lesser Yellowlegs would begin nesting later in the year than Anchorage birds (Figure 2.9); while inclusion of initiation date strengthened top DSR models, it was one of the less influential covariates. My data revealed a similar span of days between the first and last estimated initiation date within a season for both sites, so Churchill birds did not appear to have a shorter nesting season than Anchorage birds (Table 2.9).

#### *Temperature variability (“sdAvg”)*

Temperature variability modeled as a single predictor ( $\Delta AICc = 1.87$ ), produced parameter estimates indicating a significant negative effect ( $\beta$  estimate =  $-0.412$ ,  $lcl-ucl = -0.805, -0.019$ ) (Figure 2.8).

#### Percent concealment

Percent concealment (“cover”) appeared in two of the top four models.

Parameter estimates were positive indicating that DSR increased with cover (Figure 2.8). The highest ranked model tested an effect of cover and middle period maximum temperatures, and cover was marginally significant (Table 2.6) but for other models, confidence intervals show that there was considerable model uncertainty.

#### *Uninformative Covariates*

Time trends, nest age and broad habitat categories were not significant covariates in these analyses.

### *Relative variable importance*

Based on importance values calculated from model weights for the n=75 (2018–2023) dataset, my results indicated that warmer mid-season ambient temperatures had the greatest influence on DSR. Initiation date was the next most influential factor, and site was third, followed by temperature variability (Table 2.9).

### *Capture effect*

An additional dataset of the Anchorage nests included records from 2018 and 2019 in which capture was conducted for incubating adults. These data demonstrated a significant capture effect which resulted in a DSR for disturbed nests = 0.946 (se=0.0199, n=15) and for undisturbed nests = 0.981 (se=0.005, n=53) (Figure 2.10). Period nest survival probability for disturbed nests was 21% (lcl–ucl 4%–46%) and for undisturbed nests, it was 64% (lcl–ucl 45%–77%).

## DISCUSSION

I found that daily nest survival rates for Lesser Yellowlegs in the Churchill Manitoba region were 35% lower than in Anchorage, Alaska. However, site alone is not informative regarding the biological mechanisms driving variation in nest survival. A few covariates were important predictors of nest survival in the best models. In summary, I found that the data indicate that higher ambient temperatures during the middle phase of the breeding season were linked with higher nest survival. Nests initiated earlier in the season had higher survival

rates. More variation in temperatures over the nesting season was linked with lower nest survival; however, temperature variability had low relative importance compared with mid-incubation temperatures and initiation date. I found that greater overhead concealment of nests was also correlated to higher nest survival, although with considerable model uncertainty.

Ambient temperatures have been found to be influential in other studies of avian reproductive success. A stable, moderate ambient temperature during incubation fosters embryo development (Ahmad & Li 2023) and, more importantly, reduces the metabolic needs of incubating adults (Moltofte et al. 2007; Tulp et al. 2009) . Other studies have demonstrated that shorebird reproductive success increased when temperatures were higher than average during the breeding season (Moltofte et al. 2007; Weiser et al. 2018). Conversely, low temperatures have been found to decrease reproductive success in Semipalmated Plovers (Nol et al., 1997). Demonstrating an effect of temperature can be challenging since air temperature effects should be attenuated when nest sites with favorable microclimates are selected and because nest initiation is adjusted according to the local climate (Moltofte et al. 2007).

Effects of ambient temperature in this study were only apparent during mid-season suggesting that this period coincided with other influential factors.

Seasonal patterns in daily nest survival can be driven by changes in predation pressure and availability of alternate prey (Smith et al. 2007; Weiser et al. 2018). For Lesser Yellowlegs at Churchill, I noted that the ravens' nests hatched midway through shorebird incubation, and I speculate that predation pressure increased

locally as ravens fed their chicks. Warmer temperatures mid-season may enable incubating adults to maintain longer incubation bouts, thereby reducing opportunities for predators to locate nests because of activity at the nest.

Another possibility is that nests are abandoned mid-season if the metabolic costs of incubation become too high (Meltofte et al. 2007; Weiser et al. 2018). When monitoring nests at 5–6-day intervals we may not detect abandonment of nests since unattended nests may be found and consumed, thus appearing to have failed because of predation. Higher ambient temperatures can decrease the energy demands of incubation (McKinnon et al. 2013) and potentially reduce rates of abandonment.

Data indicate that nests that were initiated earlier were more likely to be successful than later nests. This aligns with the common pattern for nest survival studies in shorebirds and other taxa (Kwon et al. 2018; Sandercock et al. 1999; Smith & Moore 2005). Higher nest survival for birds breeding in Anchorage may be related in part to the relative lag in initiation for Churchill Lesser Yellowlegs. However, my data showed that Churchill breeding birds had a similar span of initiation dates (an index of season length) to Anchorage birds, just shifted later.

Higher nest concealment appeared to have had a slightly positive effect on Lesser Yellowlegs nest survival since there was marginal model support.

However, if suitable nest sites are widely available, habitat selection may not result in higher hatching success (Smith et al. 2007). This does not imply that habitat is unimportant but that other factors (e.g., adult behavior influencing

predator detection of nest sites) are driving variation in predation (Smith et al. 2007).

Anchorage had moderate and more stable summer temperatures while Churchill had lower but also highly variable temperatures. While this may not indicate a direct causal relationship between temperature patterns and nest survival, many studies have found that low temperatures and shorebird behavioral responses to them can decrease reproductive success (Moltofte et al. 2007; Smith et al. 2007, 2012; Weiser et al. 2018). Lower daily nest survival in Churchill is likely driven by combinations of weather and predator effects. Other studies demonstrated that nest survival was inversely related to incubating adults' activity levels, such as restless movements and arrival to and exit from the nest (Smith et al. 2012). For Lesser Yellowlegs in Churchill, the need to meet higher energy demands due to lower ambient temperatures may have led to more frequent changeover of incubating adults and potentially more frequent short absences from the nest. Highly variable temperatures in Churchill may have also led to more adjustments and restlessness for the incubating adults. These would likely have increased the rates of nest predation as adult activity cued predators into the locations of nests. However, the relatively moderate and stable temperatures in Anchorage may have allowed these birds to have longer incubation bouts thus decreasing exposure to predation.

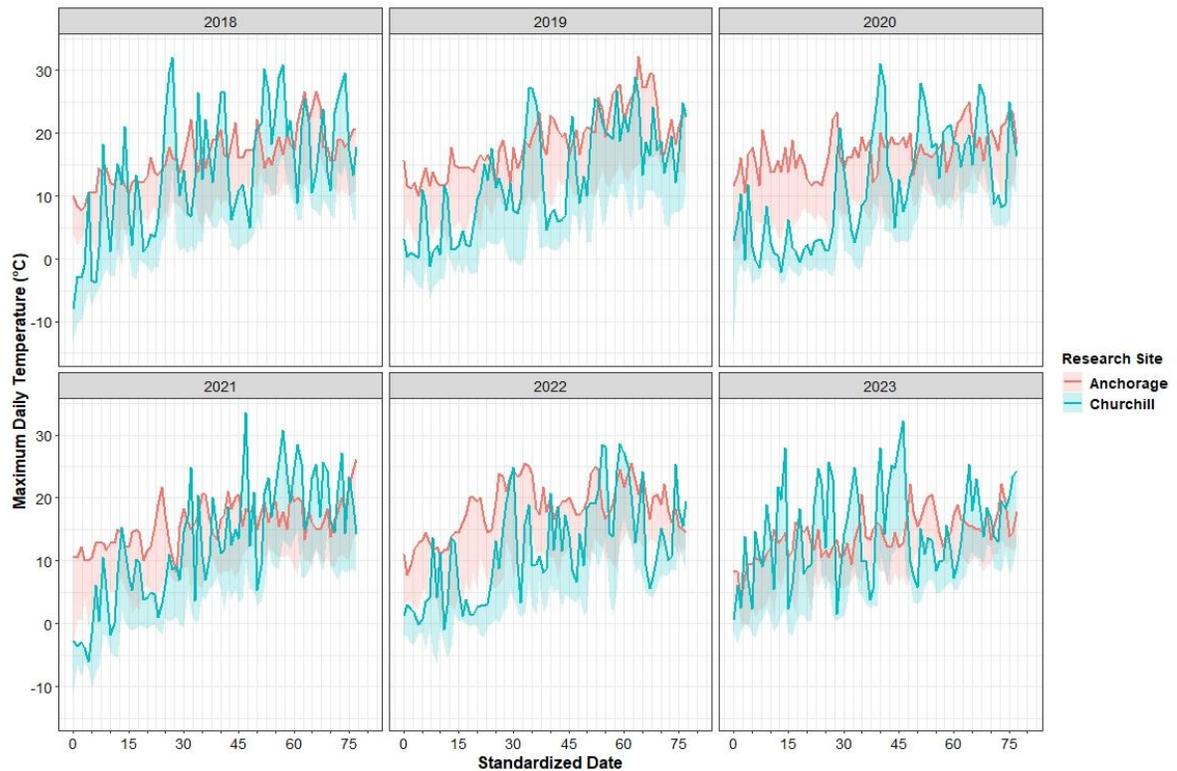
Because of evidence that increased temperatures can increase nest survival, some studies have concluded that warming trends in northern latitudes may confer at least short-term benefits to nesting birds (McKinnon et al. 2013; Weiser

et al. 2018). Additionally, warming trends leading to earlier spring conditions in parts of the range could be beneficial due to earlier nest initiation as has been demonstrated for many shorebird species (Liebezeit et al. 2014; Meltotte et al. 2007). A discussion of “warming trends” can invoke an impression of gentle increases in temperatures, but warming is frequently accompanied by extremes in early and late season conditions (McGuire et al. 2020; Thompson et al. 2013) which may counter the benefits of warming. For inland regions of the north with continental climate patterns, increased temperatures may include periods of extreme summer heat that counteract the benefits of warmer overall temperatures (O’Connor et al. 2022). Additionally, highly variable environmental conditions during the breeding season increase metabolic and behavioral costs of maintaining homeostasis which most likely affect reproductive success (Maresh Nelson et al. 2024). Most studies of the effects of climate change have focused on warming as measured by changes in mean temperatures; however, patterns that exhibit more extreme high temperatures accompanied by more extreme low temperatures will not be adequately captured by such measurements (Guo et al. 2021; Thompson et al. 2013). Thus, environmental variability is an important, but often overlooked, dimension influencing ecological systems (Maresh Nelson et al. 2024; Thompson et al. 2013).

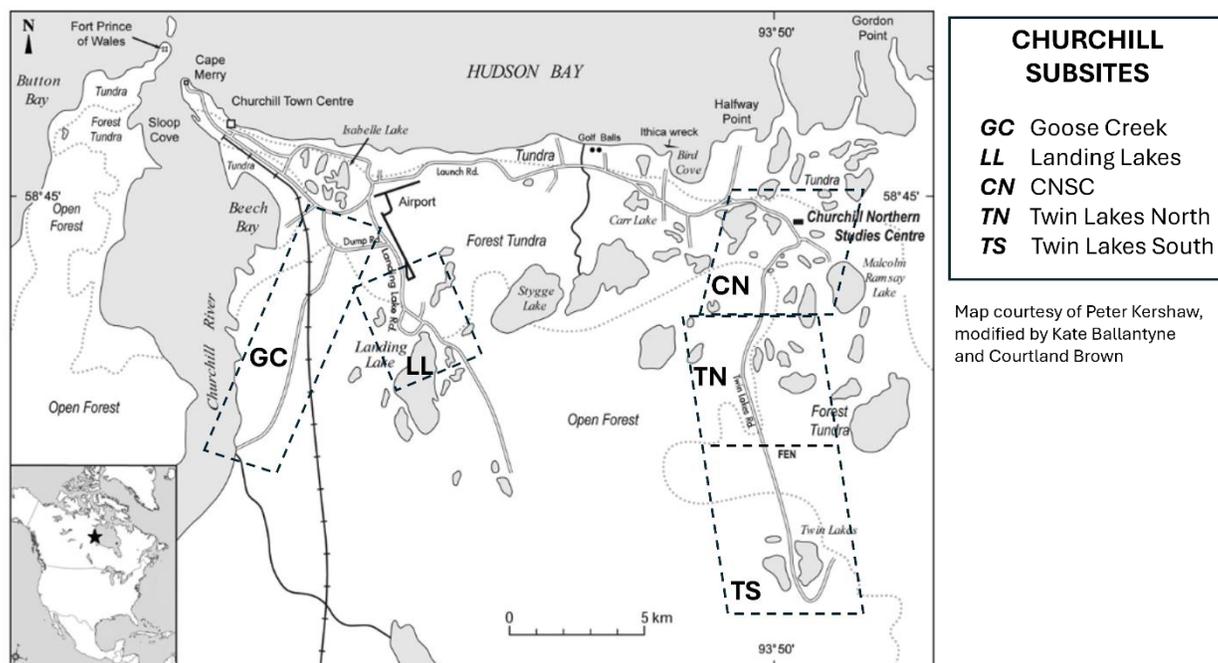
We found support for a benefit of higher temperatures in the Lesser Yellowlegs breeding range but also evidence of negative effects of high variability in ambient temperatures. Environmental conditions influence parental behavior which affects rates of predation (Smith et al. 2012). The effects of climate change on Lesser

Yellowlegs' reproductive success are likely to be a series of trade-offs having net outcomes dependent upon local abiotic and biotic conditions.

## Chapter 2 Figures and Tables



**Figure 2.1** Maximum daily temperatures (°C) for dates corresponding to the period spanning early nest initiation to late nest hatch for each study site. Dates are standardized (Anchorage May 1–July 17 and Churchill May 15–July 31) because Lesser Yellowlegs in Churchill typically initiate nests about two weeks later than Anchorage birds. Shaded areas indicate the range between maximum and minimum temperatures. 2018–2021 dates for Churchill are based on 2022 dates for the nest season, as an average year, rather than Lesser Yellowlegs nest data, since they were unavailable for those years.

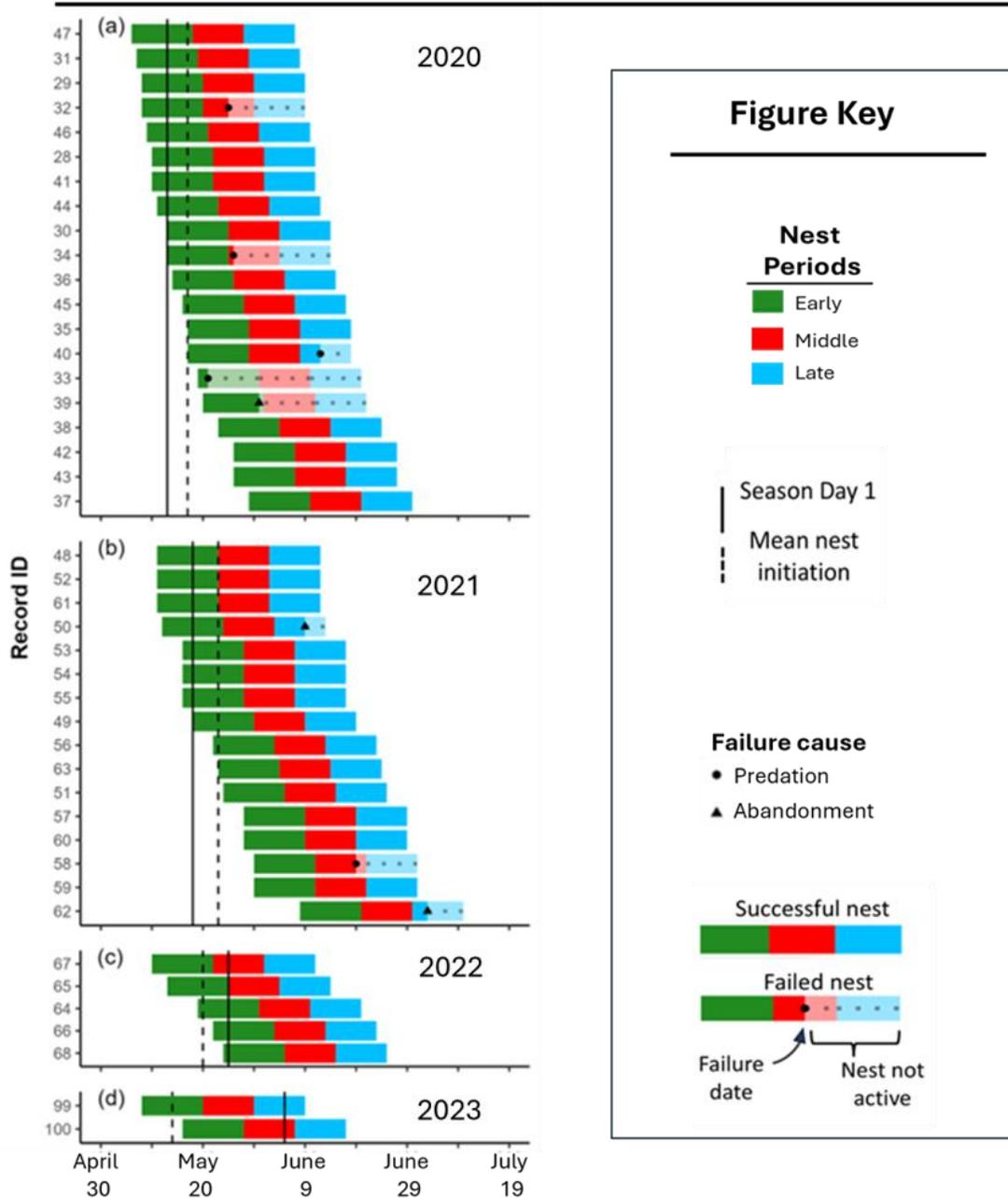


**Figure 2.2** Subsites in Churchill, Manitoba. Dashed outlines approximate the size and location of each subsite.



**Figure 2.3** Subsites in Anchorage Alaska. “ANC” is in the city of Anchorage and nest sites were within 3 km of Cook Inlet. “JBER” is on Joint Base Elmendorf Richardson north of Anchorage. Nest sites were mainly within 5 km of Knik Arm. Image credit Google Earth (*Google Earth 2025*).

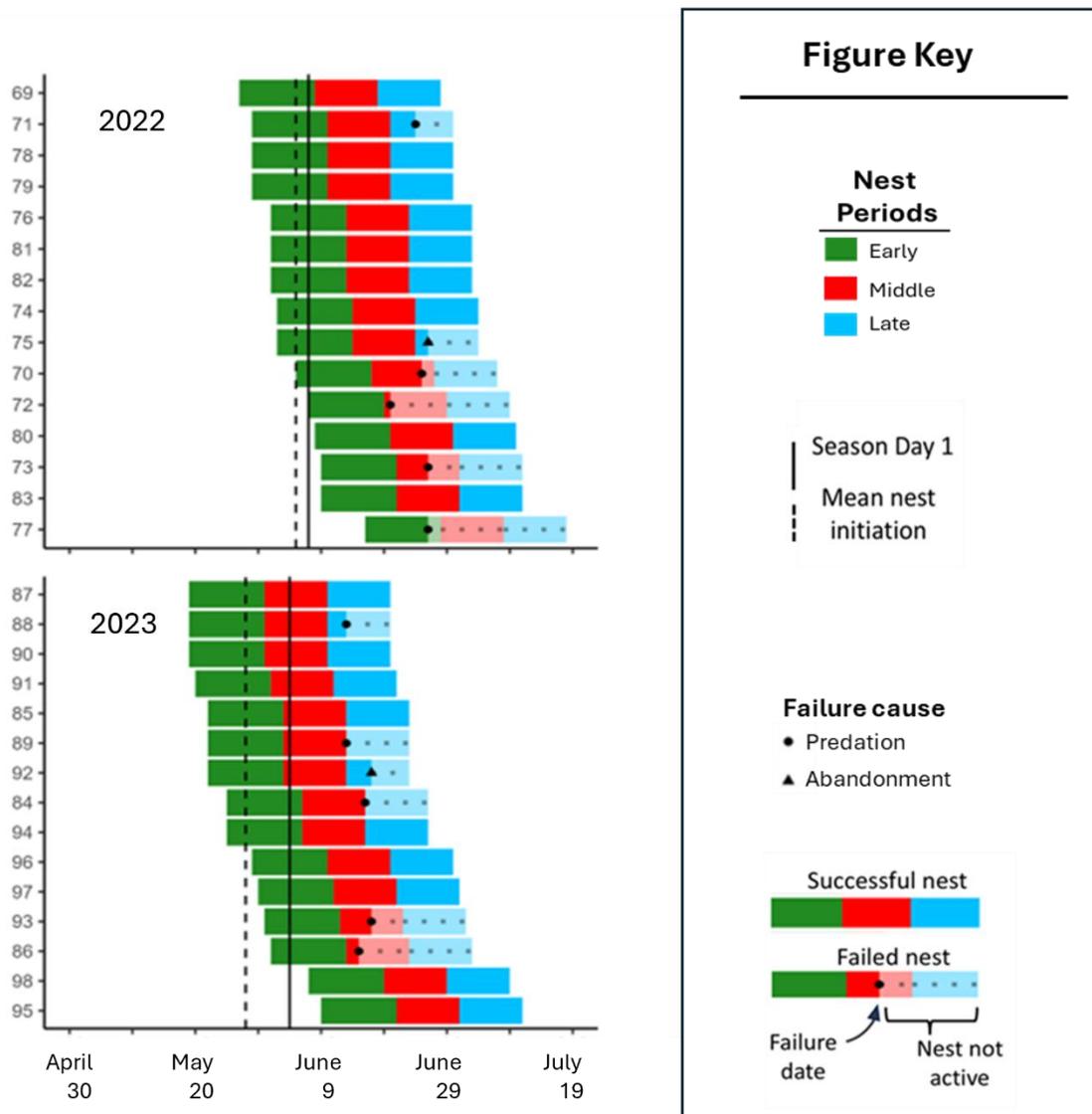
## Anchorage Lesser Yellowlegs nests



**Figure 2.4** Anchorage nest records for 2020-2023\*. The nest period dates highlight the degree of variability of nesting activity through the season and facilitate interannual comparison. Nests initiated late in the season are in the early incubation period while the nests initiated earliest are in the late period.

Each record ID represents one nest record for 2020-2023 displayed in sequence based on the initiation date. Dates and causes of failure for nests are indicated with a dot (predation) or a triangle (abandonment) and subsequent dates are shown lighter in color since these were no longer active nests that season. Season Day 1 was the first day of nest data collection. \*Data for 2018 and 2019 were not included because of the failures likely due to capture at the nests.

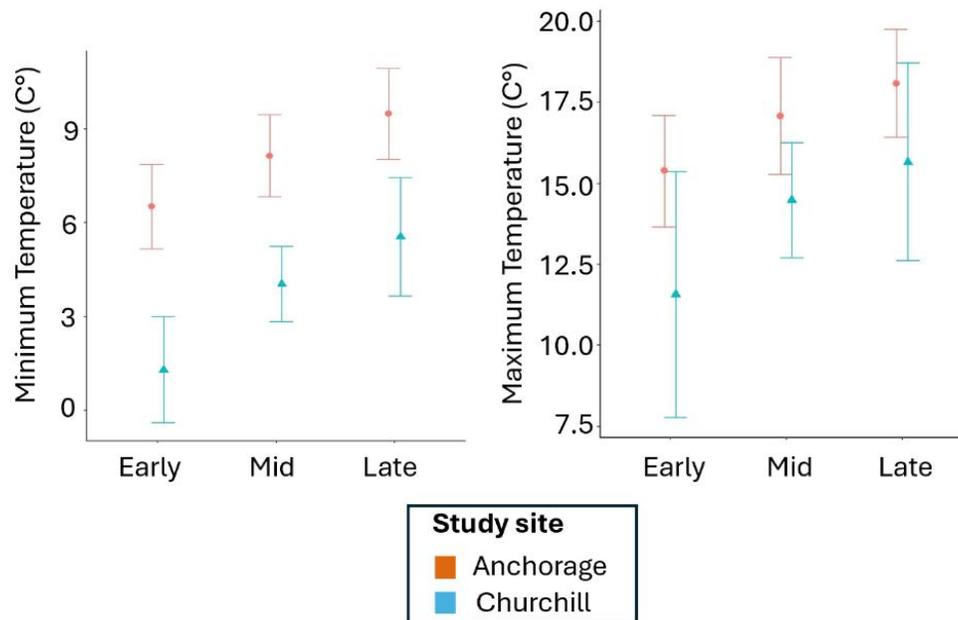
## Churchill Lesser Yellowlegs nests



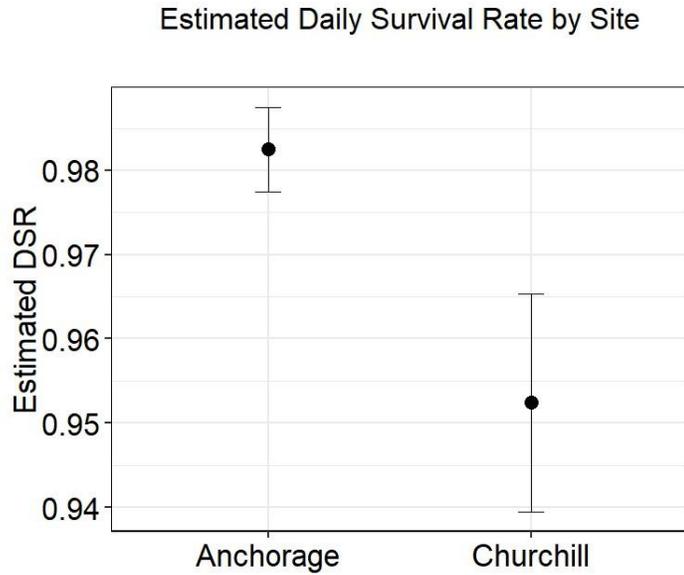
**Figure 2.5** Churchill nest records for 2022-2023. The nest period dates highlight the degree of variability of nesting activity through the season and facilitate interannual comparison. Clusters of mid-season failures are especially evident in the Churchill datasets.

The nests initiated late in the season are in the early incubation period while the nests initiated earliest are in the late period. Each record ID represents one nest

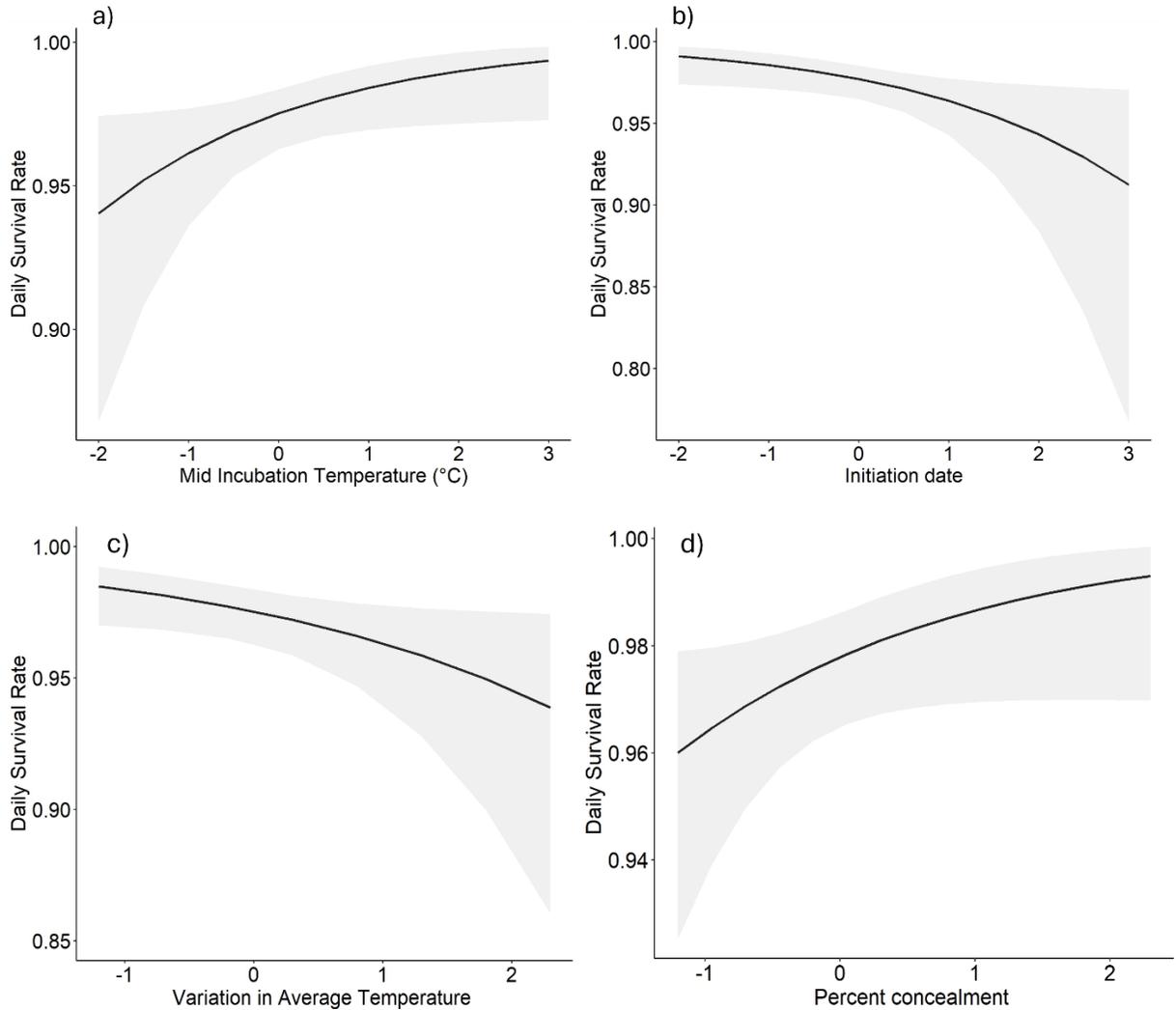
record for 2020–2023 displayed in sequence based on the initiation date. Dates and causes of failure for nests are indicated with a dot (predation) or a triangle (abandonment) and subsequent dates are shown lighter in color since these were no longer active nests that season. Season Day 1 was the first day of nest data collection.



**Figure 2.6** Temperature differences for nest periods. In the left plot, each bar represents the minimum temps (average over the period for all nests at that site) and the right plot gives the maximum temps for the periods at each site. Minimum temperature shows the differences between sites more clearly, but maximum temperatures capture more variation between periods.

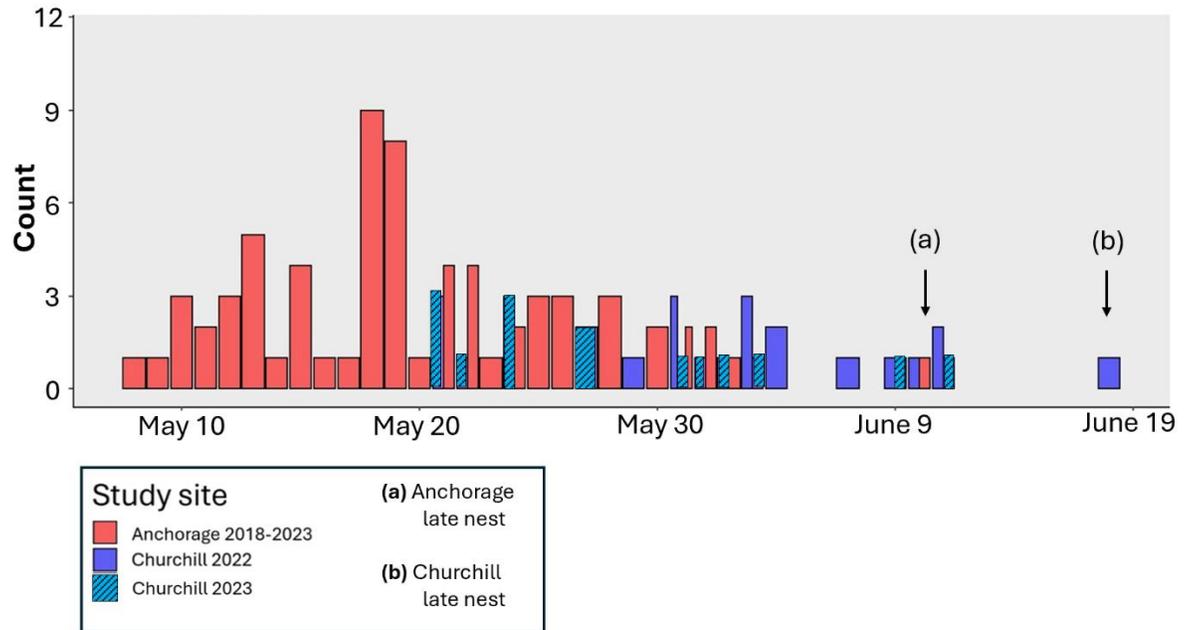


**Figure 2.7** Lesser Yellowlegs daily nest survival (DSR) estimates by site for Anchorage and Churchill 2018–2020 (n=75). Period nest survival probability for Anchorage was 63% (lcl–ucl = 0.450–0.773, n=49) and was 28% (lcl–ucl = 0.113–0.481, n=26) for Churchill. Error bars denote standard error.

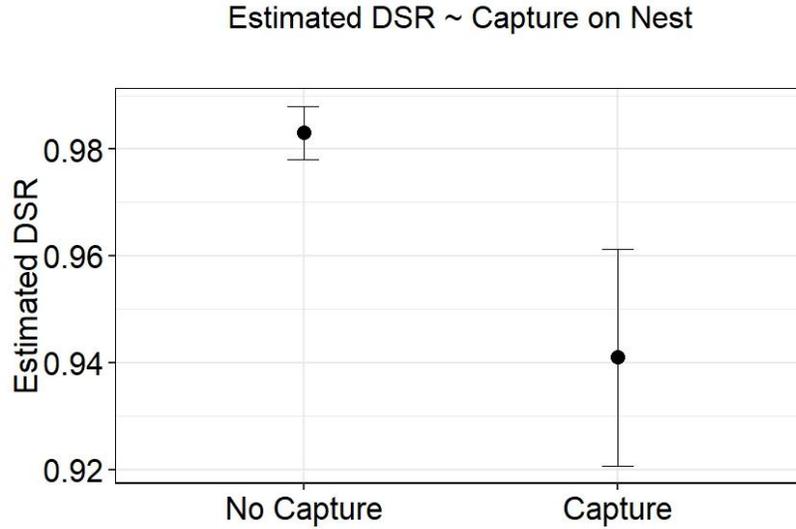


**Figure 2.8** Effects of predictor variables on daily nest survival from top models for combined datasets. These are each modeled as single predictors\*; beta estimates indicated significant effects for all but percent concealment which was marginally significant. Values on the horizontal axes are standardized by one standard deviation and centered on the variable mean to enable direct comparisons. Negative values are those that fall below the mean. Lower and upper 95% confidence intervals are indicated by the shaded ribbon.

\*Models used to create plots were: a) DSR~MidMax, b) DSR~Initiation, c) DSR~sdAvg, d) DSR~Cover.



**Figure 2.9** Nest initiation dates for Lesser Yellowlegs in Anchorage and in Churchill. Julian dates 128-170 span May 8 to June 19. Anchorage data 2018-2023 (n=70), Churchill data 2022-2023 (n=30). Churchill was unusually warm in 2023 and nests were initiated as much as 10 days earlier than in 2022. **(a)** denotes a possible re-nest attempt in Anchorage in 2021 and **(b)** denotes a possible re-nest attempt in Churchill in 2022.



**Figure 2.10** Capture of incubating adults had a significant effect on daily nest survival (DSR) for Anchorage Lesser Yellowlegs during the 2018–2019 field seasons. DSR was calculated using all Anchorage nests not found on hatch day 2018–2023 (n=64). Error bars denote standard error.

**Table 2.1** Left: Sample sizes for nests included in RMark analysis for each year and site. Right: Out of 100 nests found overall, (n=25) were removed from the dataset prior to the main DSR analysis. (n=15) Anchorage nests where captures were conducted in 2018 and 2019 were included in the analysis of the Anchorage dataset, that demonstrated a capture effect on DSR. (n=10) nests were found during hatch that lacked sufficient monitoring history to be included in RMark analysis.

Year	Anchorage	Churchill	Removed prior to main analysis
2018	3	--	(8) Anchorage, capture; (1) Anchorage, hatch day
2019	4	--	(7) Anchorage, capture; (4) Anchorage, hatch day
2020	20	--	none
2021	15	--	(1) Anchorage, hatch day
2022	5	12	(3) Churchill, hatch day
2023	2	14	(1) Churchill, hatch day
<b>Total</b>	49	26	(25) total nests not included in main DSR analysis

**Table 2.2** Covariates used for RMark daily nest survival analysis

<u>Variables for RMark DSR analysis</u>	<u>Description</u>	<u>Covariates</u>	<u>Description</u>	<u>Covariates</u>	<u>Description</u>
<b>First found</b> (Season day)	Standardized season day nest was found	<b>Cover:</b> <b>Continuous</b> (0-100)	Percent concealment of nest when viewed from above	<b>EarlyMinC/ MidMinC/ LateMinC</b>	Average of <i>minimum</i> temps for the specified period for that nest
<b>Last Present</b> (Season day)	Last season day nest was known to be active	<b>Habitat:</b> <b>Factor with 3 levels</b>	-Clearing -Shrub dominated wetland -Boreal Forest	<b>AllMinC</b>	Average of <i>minimum</i> temps for 32 days (combined periods) covering full nest-specific season
<b>Last Checked</b> (Season day)	Last day that nest was monitored, found either hatched or failed	<b>Site:</b> <b>Factor with 2 levels</b>	Anchorage or Churchill	<b>EarlyMeanC/ MidMeanC/ LateMeanC</b>	Average of <i>mean</i> temps for specified period
<b>Fate:</b> <b>Factor with 2 levels</b>	Hatch = 0 Fail = 1	<b>SubSite:</b> <b>Factor with 5 levels</b>	Study sites within larger Site	<b>AllMeanC</b>	Average of mean temps for full nest season
<b>Age Found</b>	How many days old the nest was when found	<b>Year:</b> <b>Factor with 6 levels</b>	What year nest was found	<b>EarlyMaxC / MidMaxC/ LateMaxC</b>	Average of maximum temps for specified period
<b>Initiation</b> (Julian day)	Julian date first egg was laid	<b>CapNest:</b> <b>Factor with 2 levels</b>	1 means capture at nest was conducted, 0 means it was not	<b>AllMaxC</b>	Average of <i>maximum</i> temps for full nest season
<b>Age Day 1</b> (relative to season day)	how many days old the nest is on standardized season Day 1	<b>HatchDay:</b> <b>Factor with 2 levels</b>	Indicates if nest was found when hatching, 1 means yes, 0 means no	<b>sdAvg</b>	Standard deviation of mean temps over full nest-specific season (all 3 periods)
<b>Early Period</b> Begins 2 days before initiation, spans 12 days		<b>Mid Period</b> Initiation date plus 10 days, spans 10 days		<b>Late Period</b> Initiation date plus 20 days, spans 10 days	

**Table 2.3** “Season Day 1” is the first day a nest was found each season and marks the start of nest monitoring data collection. “Season days” are numbered sequentially from this day (Julian date) each year. Field work for this study was not conducted in Churchill before 2022. During 2023 in Anchorage there was no systematic nest searching, but the research team did find two nests in the last week of incubation (June 5 and 10). Time trend models are based on Season Day.

Year	Anchorage		Churchill	
	Julian date	Calendar date	Julian date	Calendar date
2018	139	May 19	--	--
2019	136	May 16	--	--
2020	133	May 13	--	--
2021	138	May 18	--	--
2022	144	May 24	158	June 7
2023	156	June 5	155	June 4

**Table 2.4** Candidate models for daily survival estimates for Lesser Yellowlegs nests in Anchorage, Alaska, USA and Churchill, Manitoba, Canada 2018–2023 (n=75). Because of collinearity, site could not be combined with initiation date or sdAvg (temperature variability).

Akaike's Information Criterion for small sample sizes ( $\Delta AIC_c$ ), differences in  $AIC_c$  ( $\Delta AIC_c$ ) from the best fit model  $\Delta AIC_c$ , model weight ( $w_i$ ), deviance (relative fit of the model), and number of parameters (K) are provided.

<b>Model*</b>	<b>K</b>	<b>AIC<sub>c</sub></b>	<b><math>\Delta AIC_c</math></b>	<b><math>W_i</math></b>	<b>Deviance</b>
Initiation + MidMax	3	140.18	0.00	0.19	134.16
Site	2	140.60	0.42	0.15	136.59
Initiation	2	141.12	0.93	0.12	137.10
MidMax	2	141.59	1.41	0.09	137.58
Site + MidMax	3	141.68	1.50	0.09	135.65
Initiation + sdAvg	3	141.99	1.81	0.08	135.96
sdAvg	2	142.05	1.87	0.07	138.04
Time + Site + MidMax + NestAge	5	142.84	2.66	0.05	132.78
Time + MidMax	3	143.11	2.92	0.04	137.08
Null	1	144.02	3.84	0.03	142.02
Time + Initiation + MidMax + NestAge	5	144.14	3.95	0.03	134.07
Time2 + MidMax	4	144.78	4.59	0.02	136.73
Habitat	3	145.33	5.15	0.01	139.31
NestAge	2	145.96	5.77	0.01	141.94
Time	2	146.03	5.85	0.01	142.02
Time2	3	147.80	7.61	0.00	141.77

\*Covariates for top models: *Initiation*—initiation date, *MidMax*—mean maximum temperature for the middle incubation period, *Site*—(Anchorage or Churchill), *sdAvg*—standard deviation of mean temperatures over the full nest specific incubation period.

**Table 2.5** Covariate beta estimates from Program RMARK for substantially supported models ( $\Delta AIC_c < 2.0$ , Table 2.4) of daily survival rates for Lesser Yellowlegs nests in Anchorage, Alaska, USA and Churchill, Manitoba, Canada 2018–2023 (n=75). Results are listed in order of ranking according to  $\Delta AIC_c$ . The asterisk (\*) indicates covariates for which the 95% confidence intervals do not include zero; (~) denotes marginally significant results.

Parameter	estimate	se	lcl	ucl	
<b>1st Initiation + mid max</b> ( $\Delta AIC_c = 0.00$ )					
(Intercept)	3.731	0.224	3.292	4.170	
Initiation	-0.385	0.211	-0.798	0.028	~
MidMax	0.354	0.213	-0.063	0.77	
<b>2nd Site</b> ( $\Delta AIC_c = 0.42$ )					
(Intercept)	4.038	0.292	3.466	4.610	
Site (Churchill)	-0.986	0.416	-1.801	-0.171	*
<b>3rd Initiation</b> ( $\Delta AIC_c = 0.93$ )					
(Intercept)	3.747	0.224	3.309	4.186	
Initiation	-0.468	0.210	-0.880	-0.057	*
<b>4th MidMax</b> ( $\Delta AIC_c = 1.41$ )					
(Intercept)	3.673	0.213	3.255	4.091	
MidMax	0.457	0.222	0.021	0.893	*
<b>5th Site + MidMax</b> ( $\Delta AIC_c = 1.50$ )					
(Intercept)	3.938	0.305	3.341	4.535	

Site (Churchill)	-0.715	0.508	-1.711	0.281
MidMax	0.240	0.257	-0.263	0.743

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6th **Initiation + SdAvg** ( $\Delta AICc = 1.81$ )

(Intercept)	3.734	0.224	3.295	4.173
Initiation	-0.349	0.240	-0.819	0.122
SdAvg	-0.247	0.230	-0.698	0.219

---

7th **SdAvg** ( $\Delta AICc = 1.87$ )

(Intercept)	3.676	0.213	3.260	4.093
SdAvg	-0.412	0.200	-0.805	-0.019 *

**Table 2.6** Candidate models for daily survival estimates for Lesser Yellowlegs nests in Anchorage, Alaska, USA and Churchill, Manitoba, Canada 2020–2023 (n=67). Akaike's Information Criterion for small sample sizes ( $\Delta AIC_c$ ), differences in  $AIC_c$  ( $\Delta AIC_c$ ) from the best fit model  $\Delta AIC_c$ , model weight ( $w_i$ ), deviance (relative fit of the model), and number of parameters (K) are provided.

<b>Model</b>	<b>K</b>	<b><math>AIC_c</math></b>	<b><math>\Delta AIC_c</math></b>	<b>weight</b>	<b>Deviance</b>
<b>Cover + MidMax</b>	<b>3</b>	<b>120.71</b>	<b>0.00</b>	<b>0.21</b>	<b>114.68</b>
Initiation + MidMax	3	122.05	1.34	0.11	116.02
Cover + Site	3	122.08	1.37	0.11	116.05
MidMax	2	122.69	1.98	0.08	118.68
Site + MidMax	3	122.72	2.01	0.08	116.69
Site	2	122.90	2.19	0.07	118.88
Cover + sdAvg	3	123.47	2.76	0.06	117.30

\*Covariates for top models: *Site*—Anchorage or Churchill), *Cover*—percent concealment of a nest, *MidMax*—mean maximum temperature for the middle incubation period.

**Table 2.7** Covariate beta estimates from Program RMARK for substantially supported models ( $\Delta AIC_c < 2.0$ , Table 2.6) of daily survival rates for Lesser Yellowlegs nests in Anchorage, Alaska, USA and Churchill, Manitoba, Canada 2020–2023 (n=67). The asterisk (\*) indicates covariates for which the 95% confidence intervals do not include zero; (~) denotes marginally significant results.

Parameter	Estimate	se	lci	ucl	
<b>1<sup>st</sup> Cover + MidMax</b> ( $\Delta AIC_c = 0.00$ )					
(Intercept)	3.933	0.278	3.388	4.477	
Cover	0.538	0.296	-0.043	1.119	~
MidMax	0.688	0.268	0.163	1.213	*
<b>2<sup>nd</sup> Initiation + MidMax</b> ( $\Delta AIC_c = 1.34$ )					
(Intercept)	3.902	0.261	3.390	4.414	
Initiation	-0.361	0.225	-0.802	0.080	
MidMax	0.539	0.248	0.052	1.026	*
<b>3<sup>rd</sup> Cover + Site</b> ( $\Delta AIC_c = 1.37$ )					
(Intercept)	4.290	0.362	3.581	5.000	
Cover	0.446	0.290	-0.122	1.014	
Site (Churchill)	-1.130	0.466	-2.045	-0.216	*
<b>4<sup>th</sup> MidMax</b> ( $\Delta AIC_c = 1.98$ )					
(Intercept)	3.861	0.257	3.357	4.365	
MidMax	0.668	0.259	0.161	1.176	*

5 <sup>th</sup> <b>Site + MidMax</b> ( $\Delta AIC_c = 2.01$ )				
(Intercept)	4.163	0.360	3.458	4.869
Site (Churchill)	-0.794	0.562	-1.895	0.307
MidMax	0.413	0.297	-0.169	0.995
6 <sup>th</sup> <b>Site</b> ( $\Delta AIC_c = 2.19$ )				
(Intercept)	4.288	0.356	3.590	4.987
Site (Churchill)	-1.236	0.463	-2.144	-0.328 *
7 <sup>th</sup> <b>Cover + sdAvg</b> ( $\Delta AIC_c = 2.76$ )				
(Intercept)	3.858	0.257	3.355	4.361
Cover	0.450	0.285	-0.109	1.009
sdAvg	-0.468	0.216	-0.890	-0.045 *

**Table 2.8** Nest season length based on the range of initiation dates (Julian date) for each year and site (n=number of nests). The smaller range of dates for Anchorage in 2022 and 2023 are likely related to small sample sizes.

<b>Anchorage</b>				<b>Churchill</b>		
<b>Year</b>	<b>Dates</b>	<b>(n</b>	<b>Range</b>	<b>Dates</b>	<b>(n)</b>	<b>Range</b>
		)				
2018	130-148	12	18	--	0	--
2019	131-153	15	22	--	0	--

2020	128-151	20	23	--	0	--
2021	133-161	16	28	--	0	--
2022	132-146	5	14	149-169	15	20
2023	130-138	2	8	141-162	15	21

**Table 2.9** Relative importance values for variables in top models. Values were calculated by summing model weights for each model containing the variable for all models  $\Delta AIC_c < 4.0$ .

<b>Variable</b>	<b>2018-2023, n=75 nests</b>
Midmax	0.49
Initiation date	0.42
Site	0.29
sdAvg	0.15

# Chapter 3. Habitat selection for the Lesser Yellowlegs (*Tringa flavipes*) in Churchill Manitoba

## INTRODUCTION

Nest site selection in birds tends to be non-random, suggesting that selection evolved due to fitness consequences driving a preference for specific habitat features that are adaptive (Cody 1985; Walpole et al. 2008). Understanding habitat preferences for threatened species is a critical facet in conservation planning since it facilitates targeted management actions preserving important habitats and geographies for that species (Anteau et al. 2012). Climate change may dramatically alter and/or limit available habitat (Wauchope et al. 2017; Bateman et al. 2020). Indeed, this has already been observed as illustrated in a couple of studies; shrubs and graminoids doubled per decade in the western Canadian arctic (Myers-Smith et al. 2019) and a decline in Whimbrel (*Numenius phaeopus*) nesting densities was linked to shrub encroachment in a historically important breeding area (Ballantyne & Nol 2015). Nest site selection is complex and can be driven by several factors that may conflict (Mayer et al. 2009; Colwell 2010). A few of the main drivers of nest site selection are avoidance of predation (Smith & Edwards 2018), proximity to resources for adults and/or young (Lauro & Nol 1995), and a favorable microclimate (Amat & Masero 2004; Tulp et al. 2009). Since predation is the main cause of breeding failures for birds, selecting a nest site that minimizes risk of predation is crucial (Martin 1993). Nesting birds have evolved to generally be inconspicuous and crypsis may be accomplished through

concealment in vegetation and/or by plumage and egg coloration (Nguyen et al. 2003; Skrade & Dinsmore 2013). There can be a trade-off between vegetation concealment, which attenuates early detection of predators, and greater reliance on cryptic coloration while nesting in open habitats that afford a more clear view of the surrounding area (Gómez-Serrano & López-López 2014). When crypsis is an important strategy for a species, eggs are patterned to blend with substrates; consequently, certain substrates may be selected for by that species (Colwell 2010). Different species may find varying levels of vegetation advantageous depending on their predator avoidance strategy (Smith et al. 2007). A wide range of nest predator species may make a general strategy of nest concealment by vegetation challenging. Concealment from aerial predators (e.g. ravens) and terrestrial predators (e.g. foxes) requires different coverage (Clark & Nudds 1991) and too much vegetation may negatively impact adult survival if it interferes with early predator detection (Götmark et al. 1995). While predation is considered to have the greatest impact on nest success (Martin 1993), microclimate is also influential (Smith et al. 2007). Placing nests in a thermally favorable location may protect against harsh weather and decrease energy expenditure during incubation, presumably increasing nest survival (Amat & Masero 2004). Dunlin nest sites in Churchill, Manitoba, Canada had greater cover to the north than non-use sites; this may preserve a more favorable microclimate due to predominantly northwesterly winds there (Holmes et al. 2020). Birds may face a tradeoff between site features that are advantageous for predator avoidance versus those that provide the best protection from the weather (Amat & Masero

2004). Nest sites should be selected carefully since they must remain suitable throughout the laying, incubation and (for altricial species) the brood rearing period despite changes in vegetation phenology (Anteau et al. 2012).

The Lesser Yellowlegs (*Tringa flavipes*) is a ground nesting shorebird that breeds in the boreal region of North America (Figure 1.1) Lesser Yellowlegs use a variety of habitat types but are known to generally nest in relatively open areas often within ecotones (Street 1923; Tibbitts & Moskoff 2020) (Figure 3.1). "Sentry trees" from which an adult can watch and sound warnings of potential danger may be an important feature of a nest site. According to Street (1923) this was one of the only cues for researchers to locate a nest. Breeding Lesser Yellowlegs achieve crypsis through adult plumage and egg coloration which presumably help to protect adults and nests from predation (Tibbitts & Moskoff 2020). The species commonly nests beneath small shrubs or next to woody deadfall (Tibbitts & Moskoff 2020) which may aid nest concealment and/or improve microclimate. Chicks are highly mobile, typically leaving the nest within a day of hatching, and forage for themselves in shallow wetlands during a brooding period in which they travel with an adult (Tibbitts & Moskoff 2020).

Lesser Yellowlegs have experienced steep and accelerating population declines over the last 50 years (Smith et al. 2023). Among the identified threats to the species is a decrease in habitat quality due to projected effects of climate change on their breeding range (Clay et al. 2012). This species' breeding habitat has been changing rapidly in phenology (Gu et al. 2022), hydrology (Jones et al. 2022) and vegetation characteristics with climate change (Dial et al. 2022;

Walker et al. 2021). Wetland drying, a projected effect of climate change (Xu et al. 2024), will likely have a negative impact on Lesser Yellowlegs populations as it may limit suitable breeding habitat by reducing shallow ponds (Clay et al. 2012). Given the precipitous declines in Lesser Yellowlegs populations (Smith et al. 2023), it is important to understand and describe factors driving nest site selection. These have not yet been quantified in the literature.

## Hypotheses and predictions

I formed a series of *a priori* hypotheses based on other studies and prior knowledge of Lesser Yellowlegs behavior and ecology. I expected habitat selection to be hierarchical (Hutto 1985) such that arriving migrant Lesser Yellowlegs presumably first selected a territory within the broader landscape, and then chose a suitable nest site within a territory (Colwell 2010).

At the landscape-scale, I hypothesized that territories should be close to standing water to facilitate chick foraging (Tibbitts & Moskoff 2020), and I predicted that territories would be closer to water than fully random sites. I expected territories to be situated in more open areas than randomly available in the habitat (Tibbitts & Moskoff 2020) and predicted that nest sites should have lower percent shrub cover and fewer trees than random points to maximize viewshed for early detection of predators. Because many species of shorebirds choose nest sites on substrates that enhance crypsis due to plumage or egg patterns blending with surrounding features (Colwell 2010) I hypothesized that territories would be preferentially situated in high lichen areas. I expected lichen substrates might contribute to the camouflage of incubating adults and eggs, and I predicted that

territories would have higher lichen percentages than random points. I tested whether spruce dominated ecotypes or deciduous dominated areas were preferred.

At the microhabitat scale, I hypothesized that nests should be placed near tall shrubs that would help camouflage them and provide protection from the elements, and I predicted that nests would have taller point shrubs than paired random points. If nests were placed in vegetation that would help conceal them from aerial and terrestrial predators then nests should have higher vertical and lateral concealment values and higher percent shrub cover than paired random points. I hypothesized that dry nest sites would be chosen, with low susceptibility to flooding, thus nest plots should have lower percent water coverage than paired random points.

## Research questions

I asked two research questions regarding habitat selection in Lesser Yellowlegs at different scales: 1) how did Lesser Yellowlegs territories, represented by a paired random point associated with each nest, differ from fully random sites in the region, and 2) did microhabitat features at nest sites differ significantly from nearby paired random points that represented presumptive territory features? My overarching question asked which nest site characteristics were selected by Lesser Yellowlegs, and how does this align with predictions based on the biology of the species?

## Objectives

My objectives were to describe what combinations of vegetation species and structure, substrate features, and wetland proximity were preferred by Lesser Yellowlegs. Understanding habitat characteristics selected by Lesser Yellowlegs could help us to understand how changing conditions in the boreal forest might affect the species. For these analyses I used data collected on habitat features at Lesser Yellowlegs nests and at two types of random survey points representing presumed territories and widely available presumed non-use habitat in the boreal tundra ecotone around Churchill, Manitoba, Canada.

## METHODS

Data for this study were collected during July of 2022 and 2023 just north of Churchill, Manitoba, Canada (58.77° N, – 94.17° W). The region around Churchill is unique in that it has a mix of habitat types occurring together in an accessible landscape that offers a valuable opportunity to examine Lesser Yellowlegs' habitat preferences. The weather, ecological communities, indeed even the landscape itself, are shaped by the presence of Hudson Bay (Dredge & Dyke 2020). Its cooling sea ice brings both abiotic and biotic characteristics of the high subarctic south alongside fully developed boreal forests and there are extensive bands of transitional tundra-forest where they meet (Dredge & Dyke 2020). This region hosts the furthest southern extent of continuous permafrost in North America (Obu et al. 2019). Permafrost zones in the subarctic feature expansive

wetlands because of the impermeability of frozen soil (Dredge & Dyke 2020). Lesser Yellowlegs in Churchill select from a patchwork of highly variable and contrasting habitat types, whereas in other regions, habitat types are likely to be more continuous.

## Churchill Subsites

In Churchill, my subsites cover Lesser Yellowlegs nesting and foraging habitat and were accessed from Twin Lakes Road, Landing Lake Road, and the Churchill Northern Studies Centre (CNSC) (Chapter 2, Figure 2.2). There are broad differences between these subsites as the tundra grades into boreal forest roughly from north to south. They ranged from 2 to 17 km away from Hudson Bay and were all associated with freshwater wetlands. The Churchill Northern (CN) subsite, covering an area of approximately 20km<sup>2</sup>, was the furthest north of our subsites and was characterized by expanses of dry lichen covered peat plateaus and spruce forest with relatively open understory. In the transitional zones between the tundra and the boreal forest is “forest-tundra” (Payette et al. 2001), an ecotone comprised of tundra with scattered individual trees, sparse small shrubs and islands of forest communities confined to wind-protected well-watered areas. Twin Lakes road winds south from the Churchill Northern Studies Centre into the boreal forest. The Twin Lakes north (TN) subsite straddled the road and covered approximately 14km<sup>2</sup>. The eastern side of this subsite was forest-tundra and thermokarst wetlands and the western side was more characterized by boreal forest that varied from open understory to thick brush. The Twin Lakes south (TS) subsite covered approximately 20km<sup>2</sup> however much

of the northern end of the subsite was extensive fen. South of the fen TS covered mostly boreal forest and black spruce and tamarack (*Larix laricina*) bogs. The Landing Lake (LL) subsite covered approximately 10km<sup>2</sup> and was not contiguous with the other subsites. Located between the Churchill airport and Farnworth Lake, one of the largest lakes in the area, LL had extensive wetlands and large ponds and peat plateaus that are less expansive than those at the CN subsite. Tamarack was abundant in this subsite as it occupied wet habitats.

I conducted habitat surveys in all four subsites (Appendix 3). During the field seasons I chose to conduct habitat surveys in TS despite not having found nests there in 2022 with an expectation of finding them in 2023, however we did not find nests in that subsite in either year. Having no nest sites to survey within TS led to an unbalanced design across the four subsites. Therefore, my final analysis did not include the ten random points at the TS subsite. Nest sites and random points used in this analysis were surveyed in CN, TN and LL subsites.

### Habitat Survey Point types and point selection methods

Data collection followed protocols described by Miller et al. (2014) and Smith et al. (2007). I collected the same data at three different types of points, to represent three different spatial scales (Figure 3.2). The first was at each of the nests themselves (denoted as point type “N”) and a second set of random points (denoted as “PR”) were paired with each nest and located 15 m from the nest along a bearing that was selected using a random number generator (Karawita 2022). This point was presumed to fall within the territory of the Lesser Yellowlegs. The third point type was a set of five fully random points (denoted as

“R”) within each of four Churchill subsites. I established the fully random points by selecting random 100 m x 100 m grid intersections from a digital map of the study sites. Points that landed on roads or in lakes were discarded and points that were within 300m of a known nest of the season were also discarded. Since field observations of breeding bird behavior suggested that nest territories may have been approximately 500 m<sup>2</sup>, I chose 300 m as a conservative assumption of placement beyond a territorial boundary. Given the low number of nests in the study area each year, and the widely spaced nature of those nests, this point was unlikely to intersect with another Lesser Yellowlegs territory.

I tested hypotheses concerning territorial scale selection factors by comparing measurements taken at paired random points (non-use sites within Lesser Yellowlegs' territories) with the fully random points that represented presumed non-use sites within the wider available habitat. I tested hypotheses concerning nest site selection (microhabitat scale) by contrasting the characteristics of paired random points and nest points.

### Habitat characterization methods

All habitat surveys were conducted after nests had hatched and nest cups were no longer used by Lesser Yellowlegs. I surveyed plots surrounding each point, taking most measurements within a 5 m radius of the point and tree measurements within a 10 m radius of the point (Figure 3.3). I characterized Lesser Yellowlegs nesting habitat based on the following variables:

### *“Point shrub”*

I measured the features of the “point shrub” since a salient feature of most Lesser Yellowlegs nests was placement beneath or beside a small shrub. For random points, I placed the point marker beneath the nearest shrub within one meter of the gps coordinates for the point. I recorded the species and measured (cm) the tallest height, the widest width, the width along the north-south axis, and the width along the east-west axis.

### *Immediate vegetation*

The immediate vegetation variable includes the heights (cm) and the species of vegetation immediately adjacent to each point at each cardinal direction.

Most vegetation categories are self-evident but see Table 3.1 for complete details. For example, “graminoids” includes grasses (Poaceae) and sedges (Cyperaceae). “Ericaceae” includes Labrador Tea (*Rhododendron groenlandicum*), Lapland rosebay (*Rhododendron lapponicum*), *Vaccinium* species and *Myrica gale*. *M. gale*, a fragrant shrub, was low in representation; though it does not belong taxonomically, I added it to Ericaceae which contains other fragrant shrubs such as Labrador Tea. “Litter” refers to dead leaves, small sticks, and general detritus from the surrounding vegetation. This is distinct from exposed substrate since it is organic material. “Snag” refers to dead standing woody vegetation or deadfall trees.

### *Percent cover*

I recorded the percent cover (estimated proportions adding up to 100%) of vegetation types and substrates within a 5-meter radius of the point. These ground cover categories were shrub, graminoid (grasses and sedges), moss,

lichen, forbs (non-woody dicots), spruce, tamarack, exposed substrate (dirt, gravel, stone, and/or mud), and water.

### *Concealment*

I measured overhead and lateral nest concealment following Smith et al. (2007). These included percent overhead concealment of the point (as an aerial predator might see it), measured from human eye level, and percent lateral concealment measured from each of the cardinal directions 5 meters away from the point when viewed from approximately 40cm above ground level (as a fox might see it). Estimates of percent concealment were standardized by placing a 10cm<sup>2</sup> marker cube at the point. The marker was gridded with one hundred 1cm x 1cm squares on each side which were counted to indicate how much of the marker was not obscured by vegetation. The number of visible squares was subtracted from 100 to record the value that was obscured. For example, a value of 100 would indicate that the point was completely concealed.

### *Distance to water*

Distance to water was measured as the distance in meters (accuracy to 0.1 m) to the nearest persistent water at least 3 cm deep at the time of surveys. Ephemeral wet areas that had dried to mud by the time of surveys were not included.

### *Trees*

I recorded tree species, heights in meters (accuracy to 0.1 m), and the distance from the point (m, accuracy to 0.1) of all woody vegetation at least one meter tall within a 10-meter radius of the point. The same data were collected at all the points surveyed.

## Statistical Analyses

I began with 39 variables (Appendix 4). Since variables were measured using different units I centered and scaled the data (to the mean and 1 standard deviation) and conducted analyses only on the standardized data. I adjusted these data by manually imputing missing values (1.3% of total data points) with mean values from the same point type and subsite for some variables for five surveys out of the 91 total surveys in the analysis (Appendix 5.)

I built models based on my hypotheses and predictions. The variables I tested at the territorial scale were distance to water, percent shrub cover, total number of trees in plot, percent lichen cover, and a binary variable—“spruce dominated”, or not—to differentiate habitat ecotypes (Table 3.2).

At the microhabitat scale, that differentiated nest sites from the surrounding presumptive territory, the variables I tested were point shrub height, lateral concealment, vertical concealment, percent water cover, and a binary variable—“willow dominated”, or not—for vegetation immediately surrounding the point (Table 3.3).

### Regression procedure and model averaging:

I conducted the analysis in two steps. First, I compared paired random point data with fully random point data to test selection at the presumptive territorial scale. Second, I compared nest points with paired random points within the presumptive territories to test selection at the microhabitat scale. I conducted a separate regression analysis for each habitat scale following the general procedure described below.

I tested covariates for collinearity in Program R using Pearson's correlation coefficient. Highly correlated ( $r \geq |0.6|$ ) variables were not placed in the same models or in the same candidate model set. For each scale I built and tested a candidate set of generalized linear models using *a priori* predictor variables in all additive combinations of these variables; I also included single predictor variable models in the candidate model set. I used a mixed effects model framework with subsite as a random effect because of broad habitat differences between subsites. I also tested year as a random effect since phenology was very different between field seasons. However, including a random effect did not improve model fit (AIC scores were higher for the equivalent models and model weights were lower) and the random effects had 0 variance indicating no influence of the random effect variables. Therefore, I concluded that including random effects was not necessary for these data.

I evaluated model support and model fit using  $\Delta AIC_c$  scores (Akaike information criterion adjusted for small sample size) and model weights (Burnham 2002). The top models were closely ranked with  $\Delta AIC_c < 2.0$  and similar weights. I used covariate beta estimates to make inferences about how related, and in which direction, the variables were to selection criteria for Lesser Yellowlegs. I calculated a relative importance value for each variable by summing the Akaike weights for each model that the variable appears in the full candidate set (Burnham 2002). A higher value for a variable indicates greater importance. At the territorial scale I used an unconditional generalized linear model with a binomial distribution using the lme4 package (version 1.1-35.3) in R to compare

characteristics of fully random presumed non-use points to the paired random points which represented Lesser Yellowlegs territories. The response variable was a binary outcome "Territory" to indicate whether the point was in a presumptive territory versus a fully random point. I tested all possible additive combinations of five explanatory covariates, for a total of 32 models. At the microhabitat scale I compared nests to paired random points using conditional (paired) logistic regression since the points chosen randomly around the nests were not independent of the nest points. The response variable was a binary outcome of "Nest" (1 = yes, 0 = no). The strata() function identified the matched variable of Point\_ID which provided the link between a nest and its paired random point. These conditional logistic models analyzed the data separately, automatically adjusting for the matches. In addition to the pairing built into the study design, I had three instances where a nest cup was re-used by Lesser Yellowlegs in subsequent field seasons. I surveyed these reuse sites both seasons since they were selected again by Lesser Yellowlegs each year. In these cases, the Point\_ID linked the surveys for both seasons because there were two surveys of the area around the same nest point and two paired random surveys each at a different location (for example, Figure 3.4). With five explanatory variables in all additive combinations, I tested 31 models total in the candidate set for the microhabitat scale. A constant (intercept only) model cannot be fit using conditional logistic regression. Model output for conditional logistic regression provides odds ratios which are a measure of how strongly "nest" occurs with exposure to each of the variables. Odds ratios greater than 1.0

indicate a positive relationship (potential selection), less than 1.0 a negative relationship (potential deterrence), and 1.0 being neutral (no influence). If the confidence intervals include one, then the variable was not considered to be significantly related to nest site selection.

## RESULTS

In total our crew found and surveyed 30 nests in Churchill during 2022 and 2023. Most nests were found in the study area surrounding the Churchill Northern Studies Centre although territorial behavior and consistent presence of Lesser Yellowlegs during the breeding season indicated that all four subsites were nesting areas. During each of the 2022 and 2023 seasons I surveyed 15 nest sites, 15 non-use sites and 20 fully random sites. There were five fully random surveys completed each year in each of the CN, TN, TS and LL subsites. My full dataset had a total of 30 nests, 30 paired random points, and 41 fully random points since we had an “extra” survey in the CNSC subsite in 2023. TS included random points in the fen which had high overall graminoid percentages. This site and LL were wetter on average than the others. The habitat surveys used in this analysis included 30 nest sites, 30 paired random points, and 31 fully random points (Table 3.4).

### Field observations

In Churchill Manitoba, Lesser Yellowlegs nested mainly in the tundra/boreal ecotone in areas that are typically open tundra to sparse boreal forest understory. Nest sites were often placed in patches that were more vegetatively open (i.e.,

with low tree canopy cover or lower shrub density) than the surrounding area. Nests were nearly always at the base of a low shrub (~ 50 cm tall). Most nests were placed next to willow (n=13), followed by birch (n=6). By contrast, territory points and random points were more likely to occur near Ericaceae shrubs. All other nests occurred next to a variety of vegetation types but with no strong differences compared to territory and random points (Figure 3.5).

### Territorial scale analysis

At the territorial scale, the only variable that reliably explained selection was distance to water. Territories were further from water than fully random points (Table 3.5). Results provide tentative support (marginally significant positive effect in three top models) for Lesser Yellowlegs favoring spruce dominated habitats. The tree number variable also strengthened top models (Table 3.6), and coefficient estimates suggested a negative relationship with the probability of territory selection (Table 3.7), but it was not a significant variable in any model. All top models ( $\Delta AIC_c \leq 2.0$ ) included distance to water. The strongest model, according to  $\Delta AIC_c$  and model weight, was the additive model with distance to water, tree number and spruce dominated (Table 3.6). However, distance to water was the only variable that had a significant effect. The third ranked model ( $\Delta AIC_c = 0.29$ ) tested an additive effect of distance to water and spruce dominated habitat and had the least model uncertainty of the top three models (Table 3.7, Figure 3.6). Importance values calculated from model weights indicated that distance to water was the most influential variable followed by

spruce dominated, tree number, and percent shrub cover respectively (Table 3.8).

### Microhabitat scale analysis

At the microhabitat scale, testing for differences in characteristics of paired random points and nest sites, eight top models described selection factors with little difference in model weights for the highest ranked models (Table 3.9). In two individual models, point shrub height had a clear positive effect (i.e. taller shrubs increased the likelihood of nest site selection). Positive parameter coefficients suggested that higher lateral concealment values and more willow vegetation at survey points were linked to nest sites while a negative coefficient for percent water cover suggested that nest sites may be drier than at paired random points. However, there is considerable overlap in the value ranges for these variables and model uncertainty precludes drawing conclusions from these results (Table 3.10). The most important variables were point shrub height followed by willow dominated, lateral concealment and percent water cover respectively (Table 3.11).

## DISCUSSION

Lesser Yellowlegs in Churchill nested in a wide variety of habitats, although they selected certain habitat features at the landscape and micro-scale. Lesser Yellowlegs territories were further from standing water than randomly available sites. This finding was counter to my prediction that they would select territories near water. However, given the abundance of wetlands in the Churchill region,

nesting pairs were likely not limited in wetland accessibility. Results also suggested that territories were more often spruce-dominated than randomly available habitat. Predictions that points within territories would have fewer trees and lower percent shrub cover than the randomly available habitat were not supported, nor were territories more likely to have high lichen cover than the randomly selected points.

The data on microhabitat nest site selection provided some support for a prediction that nests would be placed in areas with taller than random shrubs, although evidence was weak. Contrary to my predictions, nest sites were not significantly more concealed, nor did they have a lower percent coverage of water than non-use points within the territory. If territory selection factors included the features most important to nest sites then there may not be strong selection at the microhabitat level. For example, since territories were already selected to be in drier locations it is reasonable to expect that there would be little difference in water coverage at the microhabitat scale.

Lesser Yellowlegs in Churchill appeared to be breeding habitat generalists occupying a wide range of habitat types. The strongest selection factor identified in this study showed a preference for drier territories. Site selection takes place under conditions that normally change dramatically later in the season during nest incubation. Lesser Yellowlegs likely selected drier sites to avoid nest inundation as weather warmed into summer, or these sites were snow free, and therefore available, early in the season. Migrating Lesser Yellowlegs typically

arrive in Churchill while the landscape is still largely covered in snow as has been observed by long-term researchers working in the region.

Through the breeding season, as the snow melts, many sites remain wet due to permafrost influence. A multispecies study of nest site selection on the Arctic coastal plain of Alaska also found that shorebirds preferred drier sites (Cunningham et al. 2016). Given that the Hudson Bay region features the third largest wetland on earth (Rouse 1991), foraging ponds are currently plentiful. However, the hydrology of this region is likely to shift as climate patterns change. Ultimately, climate models project draining and drying of wetlands as permafrost thaws (Woo et al. 2008) but local effects are difficult to predict. As hydrology shifts, permafrost thawing may lead to a local increase in thermokarst bogs and fens as peat plateaus collapse and become dominated by sphagnum mosses and graminoids (Spiller et al. 2024). The Churchill region has been described as a sensitive ecosystem because the permafrost was at 0°C according to Dredge and Dyke (2020) at the time of authorship. This means that even small changes in air and ground temperature could lead to large changes in the peatlands as permafrost either builds or melts over a given season. Rapid shifts to either wetter or drier habitats as areas that were historically characterized by permafrost are changing will require species to adapt or shift breeding ranges (Bateman et al. 2020). Indeed, it appears that Lesser Yellowlegs in the Hudson Bay region may be shifting their range since eBird trends modeled for 2012-2022 indicate increases in abundance south of Churchill to the west side of James Bay (*Lesser Yellowlegs - Trends Map - eBird Status and Trends, 2025*) (Figure 3.7).

While my study did not show a clear influence of tree density or shrub cover on nest site selection, it may not mean that these factors are unimportant to Lesser Yellowlegs. It is possible that the degree of variability in vegetation characteristics in my study sites was too wide to capture a measure of preference. Equally, they may find a variety of microhabitat types suitable. Selection by Lesser Yellowlegs of relatively open sites such as clearings, powerline cuts and forest burns has been documented in the literature (Street 1923; Tibbitts & Moskoff 2020) and corroborated by field observations. But in the absence of clear quantitative support, discussion of potential impacts of changing vegetation characteristics remains speculative.

Lesser Yellowlegs displayed an apparent preference for relatively tall shrubs at nest sites in Churchill, but few nests were in densely vegetated areas. A lower density of shrubs and trees may facilitate early predator detection as has been hypothesized for other shorebirds (Dorsey et al. 2025; Smith et al. 2012).

Vegetative shifts due to climate change have been documented across the boreal regions of North America (Nill et al. 2022; Tape et al. 2006). Projected losses of wetlands in the Hudson Plains region (Nelson et al. 2014) may exacerbate the effects of tree encroachment. But local vegetative responses to climate change can vary depending on complex factors including landscape and soil. One long-term monitoring study in Northwest Territories, Canada did not find evidence of a northward shift of the treeline (Timoney 2023).

Lesser Yellowlegs are known to use clearings and forest burns for nesting habitat (Street 1923; Tibbitts & Moskoff 2020) and may adapt to moderate disturbance in

the boreal forest. Wildfire and logging are both forces shaping North America's boreal forests, creating openings and shifting species compositions in different ways (Boucher et al. 2017; Carleton & MacLellan 1994). Areas that have been completely clear-cut may be less suitable than burns given the widely observed use of "sentinel trees". The somewhat greater propensity for Lesser Yellowlegs to nest in spruce dominated areas may be a byproduct of more subtle conditions associated with spruce rather than site selection based directly on the presence of spruce.

Lichen substrates were not found to have a significant effect on site selection. However, it is interesting that lichens in sub-arctic Norway were found to create a more stable microclimate than dwarf birch (*Betula nana*) which is rapidly expanding with climate change (Mallen-Cooper et al. 2021). Their study was interested in microclimate as it relates to soil warming and permafrost melt, but substrate microclimate properties would be important to ground-nesting birds as well.

### Caveats and data limitations

These analyses were conducted based on a limited sample of 30 nests. Statistical power to detect selection would have increased with a larger sample of nests. Additionally, my two field seasons had very different weather conditions and phenology. The first field season in 2022 was more typical of prior years with substantial snow cover in early June and sea ice on Hudson Bay well after summer solstice. However, 2023 was historically atypical in that there was no

snow cover or sea ice at the start of field work on June 1 and green-up of vegetation was well advanced. Mean nest initiation for Lesser Yellowlegs in 2023 was advanced by ~8 days relative to 2022. Other studies have found a year effect in habitat selection factors; Walpole et al. (2008) found differences in mesohabitat selection by Red-necked Phalaropes (*Phalaropus lobatus*) in study seasons having very different weather conditions. However, I feel confident that this difference did not affect my analyses since the random effects showed 0 variance and did not increase model weights. The difference in the temperatures and timing of snow melt between field seasons was stark and noteworthy but given the lack of a year effect in my models, I suspect that Lesser Yellowlegs likely had similar selection criteria year to year. It is possible, of course, that selection was based on factors that I did not measure.

## Conclusions

Lesser Yellowlegs used a variety of breeding habitats, as evidenced by the high variability around the means for the variables that I measured (Tables 3.5 and 3.12). While this made it challenging to clearly describe selection factors, it may be a beneficial trait for the species as climate change continues to affect habitat characteristics over the breeding range. Since Lesser Yellowlegs use highly variable habitats, they may be able to adapt to conditions brought about by climate change more readily than species with more rigid habitat requirements. Many species are expected to shift their breeding ranges if they are unable to adapt to the rapidly changing high latitudes (Callaghan et al. 2004). Unlike many shorebird species that breed in the high arctic and are already “squeezed in” at a

northern limit (Meltotte et al. 2007), Lesser Yellowlegs may adapt to shifting boreal vegetation patterns.

## Chapter 3 Figures and Tables



north



south

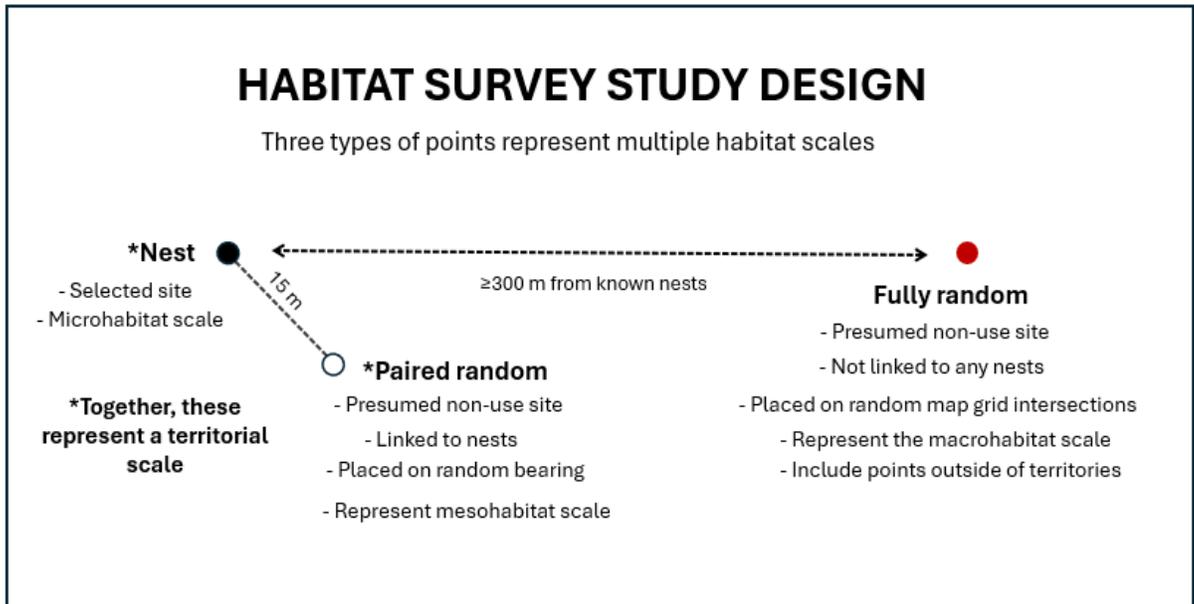


east

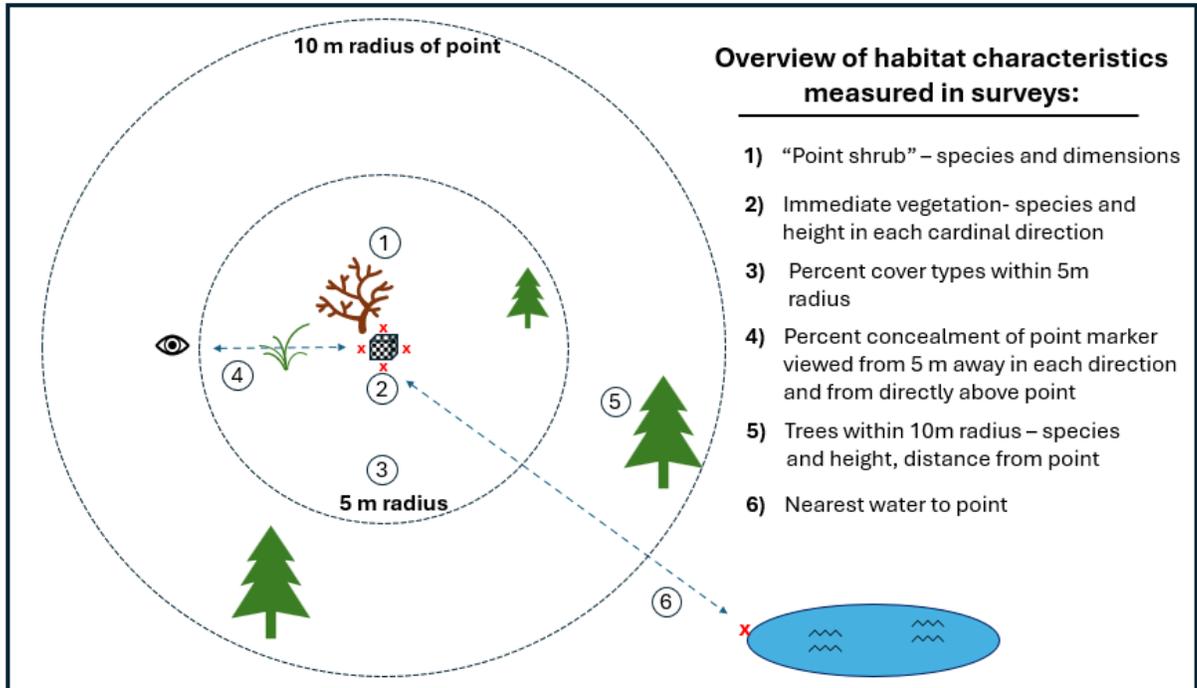


west

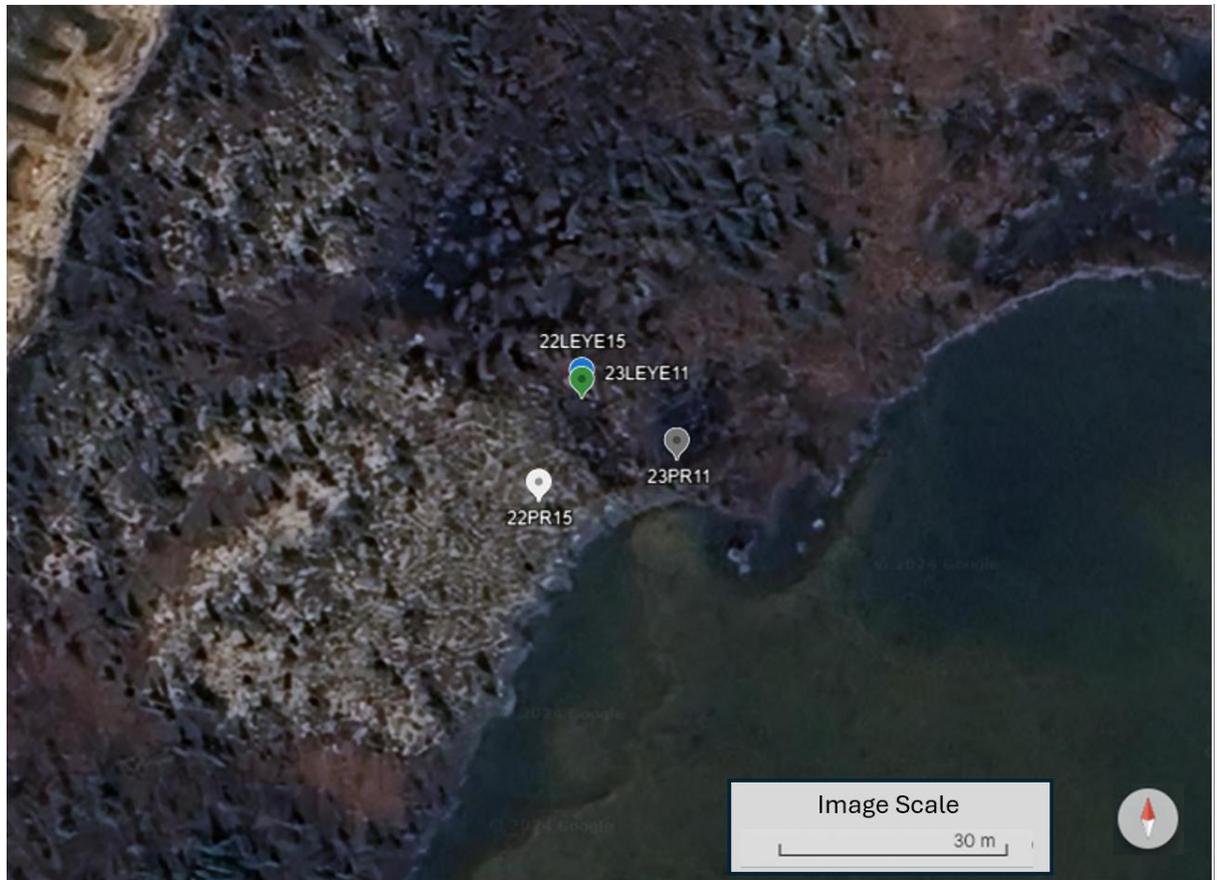
**Figure 3.1** Directional photos taken at a single nest point (mapped in Figure 3.4) showing the variety of vegetation and habitat features nearby. The nest was placed in the transitional zone between open habitat to the south and west and shrubbier habitat to the north and east.



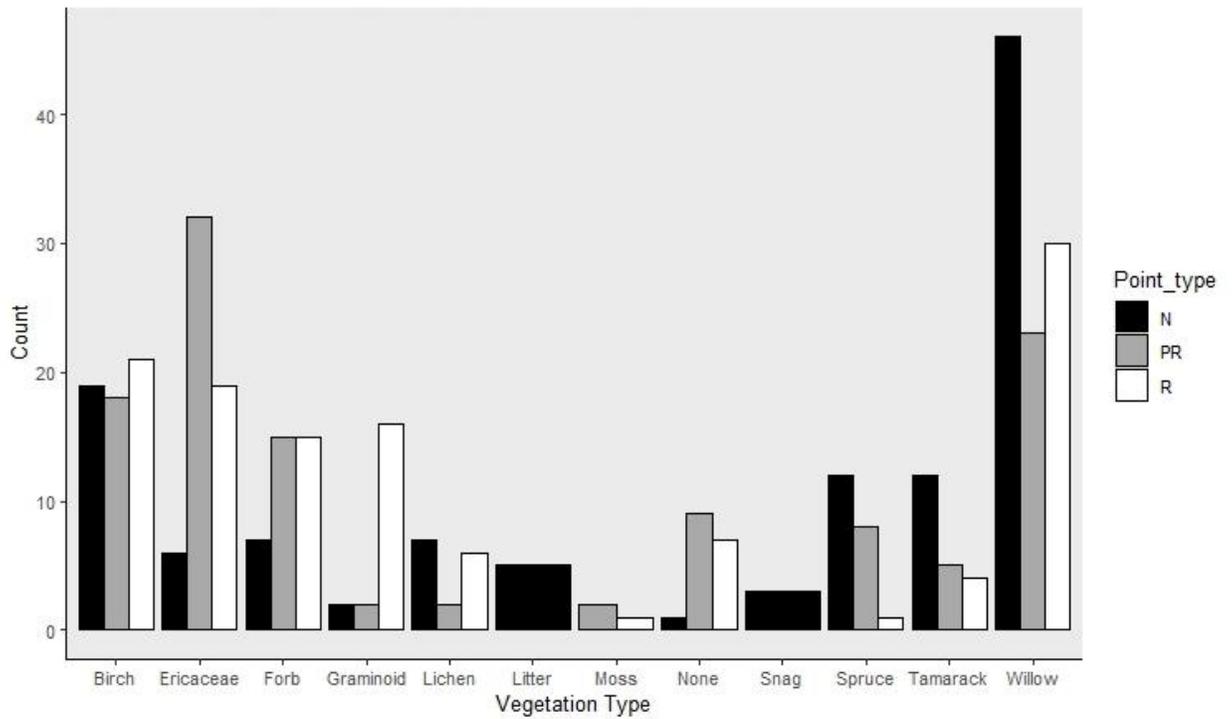
**Figure 3.2** Habitat surveys were conducted at three different types of points which represented microhabitat, mesohabitat, and the widely available macrohabitat in the Churchill, Manitoba region.



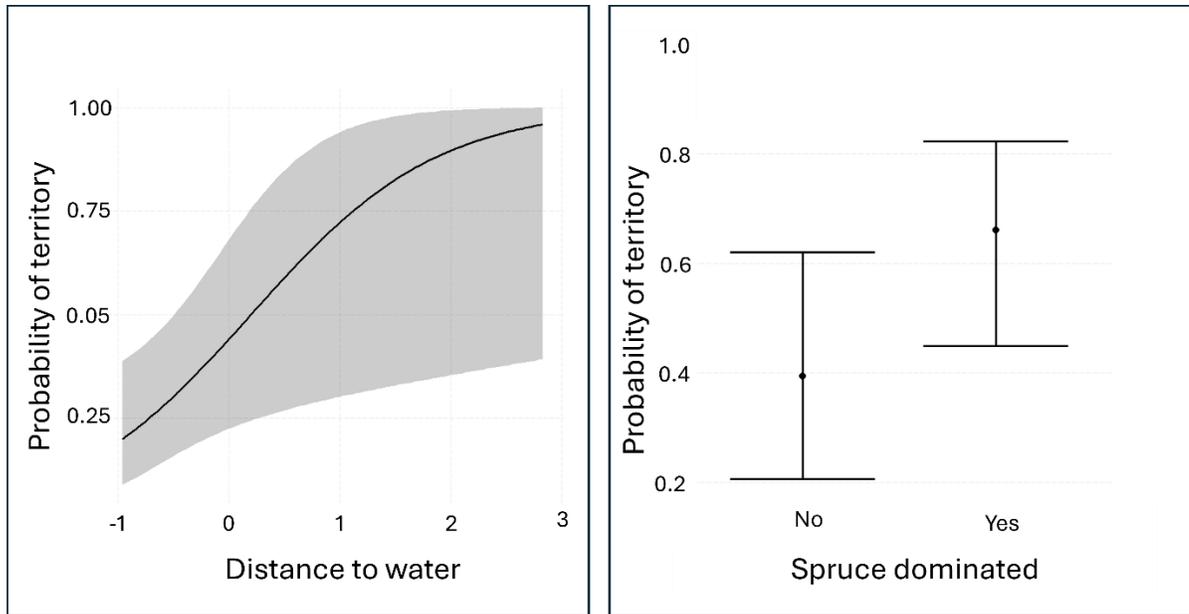
**Figure 3.3** Overview of plot design and habitat parameters measured in surveys.



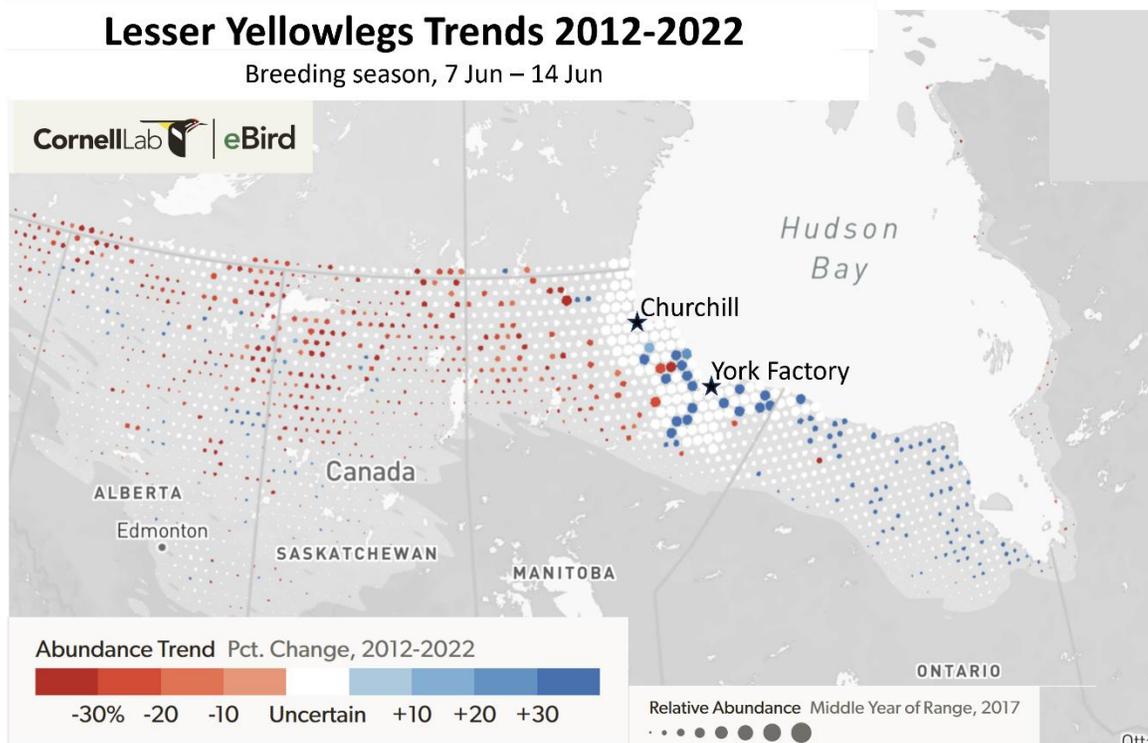
**Figure 3.4** One of the nest sites, precisely the same nest cup, found in 2022 was reused in 2023. The paired random points landed on either side of a change in the vegetation features.



**Figure 3.5** Vegetation types immediately surrounding each point type. It is interesting that litter and snag only appeared at nests and only one count of “none” appeared at a nest.



**Figure 3.6** Predicted probability of territory selection based on a model of distance to water and an additive effect of a spruce dominated habitat type. Distance to water consistently had a significant effect in models and spruce dominated had marginally significant effects in top models. Values on the horizontal axis are scaled and centered to the mean; negative values are those that fall below the mean. Shaded ribbon indicates 95% CI's.



**Figure 3.7** Modeled eBird trends (80% confidence interval) for the eastern part of the breeding range suggest that Lesser Yellowlegs numbers are increasing south of Churchill and to the west side of James Bay while decreasing through Central Canada. This may represent a range shift.

Circles represent 27km x 27km regions, darker circles indicate a stronger trend, larger circles indicate higher relative abundance in the middle of the time period modeled (2017). Blue indicates increased abundance while red indicates decreased abundance; white circles indicate that the trends are uncertain. (<https://science.ebird.org/en/status-and-trends/species/lesyel/trends-map>)

**Table 3.1** Vegetation species categories used in Churchill Lesser Yellowlegs habitat surveys.

<b>Vegetation category</b>	<b>Description</b>	<b>Comments</b>
Birch	<i>Betula sp.</i>	na
Ericaceae	Members of family Ericaceae	Present at my sites: <i>Rhododendron groenlandicum</i> , <i>Rhododendron lapponicum</i> , <i>Vaccinium spp.</i> , <i>Myrica gale*</i>
Forb	Non-woody dicots	A general category
Graminoid	Sedges and grasses	All monocots placed in this category
Lichen	Cladoniaceae	Usually reindeer lichen ( <i>Cladonia rangiferina</i> )
Litter	Dead organic material	dead leaves, small sticks, and general detritus from the surrounding vegetation
Moss	Bryophyta	na
None	Exposed substrate	Category used when there were no organic materials at point
Snag	Dead woody vegetation	Standing or deadfall
Spruce	<i>Picea sp.</i>	na

Tamarack	<i>Larix laricina</i>	na
Willow	<i>Salix sp.</i>	na

\**Myrica gale* is not in Ericaceae but was low in representation, I added it to the fragrant shrubs category.

**Table 3.2** Variables used to test Lesser Yellowlegs territory selection

<b>Variable Code</b>	<b>Variable name</b>	<b>Description and ecological meaning</b>
Dist.wtr	Distance to water (accuracy within 10 cm)	Distance to nearest persistent water at least 3 cm deep. Provides foraging for precocial chicks.
Shrub	Shrub % cover	Proportion of 5m radius plot covered with shrubs. Selection may depend on an optimal level of shrub cover to provide protection without hampering predator detection.
Lich	Lichen % cover	Proportion of 5m radius plot covered with lichens. Lichen substrates may enhance crypsis of incubating adults and unattended nests.
TrNum	Tree number	Total number of trees within a 10 m radius of point. Selection may depend on tree density.
SprDom	Spruce dominated	More than half of the trees in a plot are spruce. Certain ecotypes may be preferred.

**Table 3.3** Variables used to test Lesser Yellowlegs nest site selection

<b>Variable Code</b>	<b>Variable name</b>	<b>Description and ecological meaning</b>
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TopCnc	Vertical concealment (%)	Percentage of the point concealed by vegetation when viewed from directly above. More vertical concealment may protect against aerial predators.
LatCnc	Lateral concealment (%)	Average of concealment values of point taken from all four cardinal directions from 5 m away. Higher lateral concealment may protect against terrestrial predators.
PS.ht	Point shrub height (cm)	Tallest vegetation of the shrub immediately over or next to point. Selection may favor taller shrubs for concealment or microclimate benefits.
Wtr	Water % cover	Proportion of 5m radius plot covered with water. Birds may select sites based on how wet the area is.
WillDom	Willow dominated	Most of the vegetation immediately adjacent to the point was willow. Willow may be a preferred species.

**Table 3.4** Distribution of point types within the four Churchill subsites. Most nests were found in the study area surrounding the Churchill Northern Studies Centre (CN). Twin Lakes north (TN) and Landing Lakes study areas were used for nesting, but we found far fewer nests there. Twin Lakes south (TS) was most likely used for nesting based on behavior and seeing adults with chicks late in the season, but we did not find any nests in this area.

Study area	Study area code	Nest points (n)	Paired randoms (n)	Random (n)
CNSC	(CN)	21	21	10
Twin Lakes North	(TN)	5	5	10
Landing Lakes	(LL)	4	4	10
Twin Lakes South	(TS)	0	0	10

**Table 3.5** Summary statistics for the variables used to explain territory selection factors.

Variable	Paired random point (n=30)		Fully random point (n=31)	
	Mean (se)	Median	Mean (se)	Median
Distance to water (m)	36.5 (5.60)	27	11.1 (3.43)	6
Shrub percent cover (%)	18.13 (2.99)	12	14.76 (2.09)	14

Lichen percent cover (%)	23.13 (3.53)	17	14.16 (3.41)	2
Tree number (count)	10.76 (2.09)	8	22.23 (6.19)	5
Spruce dominated (a binary variable)	Yes for 70% (21/30) No for 30% (9/30)		Yes for 29% (9/31) No for 71% (22/31)	

**Table 3.6** Model selection sorted by  $\Delta AIC_c$ : the best models ( $\Delta AIC_c \leq 2.0$ )

describing territory selection factors for Lesser Yellowlegs in Churchill MB.

Variables: *Dist.wtr*—distance to water, *TrNum*—tree number, *SprDom*—spruce dominated, *Shrub*—shrub percent cover.

Model	K	$AIC_c$	$\Delta AIC_c$	$W_i$	Cum.Wt	LL
Dist.wtr+TrNum+SprDom	4	72.21	0.00	0.14	0.14	-31.75
Dist.wtr+TrNum	3	72.49	0.28	0.12	0.26	-33.03
Dist.wtr+SprDom	3	72.50	0.29	0.12	0.37	-33.04
Dist.wtr+TrNum+SprDom+ Shrub	5	72.91	0.70	0.10	0.47	-30.91
Dist.wtr	2	73.45	1.24	0.07	0.55	-34.62
Dist.wtr+SprDom+Shrub	4	73.68	1.47	0.07	0.61	-32.49
Dist.wtr+TrNum+Shrub	4	73.90	1.69	0.06	0.67	-32.59

$K$ —number of parameters,  $AIC_c$ —corrected AIC criterion,  $\Delta AIC_c$ —difference in  $AIC_c$  between the best model in the candidate set and the model listed,  $W_i$ — $AIC_c$  model weight, *Cum.Wt*—cumulative model weight, *LL*—model log-likelihood

**Table 3.7** Beta estimates and test statistics for top models testing territory

selection factors. Lcl and ucl indicate beta results 95% confidence intervals.

Significant (\*) and marginally significant (~) results based on confidence intervals and/or p-value (alpha level = 0.05) are bolded.

<b>1<sup>st</sup></b>	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
<b>Dist.wtr+TrNum+</b>							
<b>SprDom</b>							
$\Delta AICc = 0.00,$							
$W_i = 0.14$							
(Intercept)	-0.256	0.509	-0.504	0.6145	-1.254	0.741	
Distance to water	1.171	0.502	2.335	<b>0.0196</b>	<b>0.188</b>	<b>2.154</b>	*
Tree number	-0.576	0.436	-1.321	0.1865	-1.430	0.278	
Spruce-dominated	1.024	0.640	1.600	0.1096	-0.230	2.278	
<b>2<sup>nd</sup></b>							
<b>Dist.wtr+TrNum</b>							
$\Delta AICc = 0.28,$							
$W_i = 0.12$							
(Intercept)	0.330	0.361	0.915	0.360	-0.377	1.037	
Distance to water	1.447	0.494	2.930	<b>0.003</b>	<b>0.479</b>	<b>2.416</b>	*
Tree number	-0.619	0.430	-1.441	0.150	-1.461	0.223	

**3<sup>rd</sup>** Estimate Std. Error z value Pr(>|z|) LL UL

**Dist.wtr+SprDom**

$\Delta AICc = 0.29,$

$W_i = 0.12$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
(Intercept)	-0.241	0.499	-0.483	0.629	-1.218	0.737	
Distance to water	1.197	0.517	2.315	<b>0.021</b>	<b>0.184</b>	<b>2.211</b>	*
Spruce-dominated	1.097	0.619	1.771	<b>0.077</b>	-0.117	2.311	~

**4<sup>th</sup>** Estimate Std. Error z value Pr(>|z|) LL UL

**Dist.wtr+TrNum+**

**SprDom+Shrub**

$\Delta AICc = 0.70,$

$W_i = 0.10$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
(Intercept)	-0.338	0.517	-0.653	0.514	-1.351	0.676	
Distance to water	1.127	0.496	2.273	<b>0.023</b>	<b>0.155</b>	<b>2.099</b>	*
Tree number	-0.665	0.464	-1.435	0.151	-1.574	0.243	
Spruce-dominated	1.213	0.667	1.818	<b>0.069</b>	-0.095	2.520	~
Shrub	0.408	0.331	1.232	0.22	-0.241	1.057	

**5<sup>th</sup> Dist.wtr** Estimate Std. Error z value Pr(>|z|) LL UL

$\Delta AICc = 1.24,$

$W_i = 0.07$

(Intercept)	0.388	0.362	1.070	0.285	-0.322	1.098	
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Distance	1.487	0.515	2.891	<b>0.004</b>	<b>0.479</b>	<b>2.496</b>	*
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<b>6<sup>th</sup></b>	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
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**Dist.wtr+SprDom**

**+Shrub**

$\Delta AICc = 1.47,$

$W_i = 0.07$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
(Intercept)	-0.315	0.508	-0.620	0.535	-1.311	0.681	
Distance to water	1.143	0.517	2.209	<b>0.027</b>	<b>0.129</b>	<b>2.157</b>	*
Spruce-dominated	1.256	0.645	1.947	<b>0.052</b>	<b>-0.008</b>	<b>2.520</b>	~
Shrub	0.329	0.324	1.016	0.310	-0.306	0.964	

<b>7<sup>th</sup></b>	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
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**Dist.wtr+TrNum+**

**Shrub**

$\Delta AICc = 1.69,$

$W_i = 0.06$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
(Intercept)	0.347	0.364	0.954	0.340	-0.366	1.060	
Distance to water	1.441	0.493	2.923	<b>0.003</b>	<b>0.475</b>	<b>2.407</b>	*
Tree number	-0.689	0.451	-1.529	0.126	-1.573	0.194	
Shrub	0.292	0.323	0.904	0.366	-0.341	0.924	

**Table 3.8** Importance values for variables appearing in the highest-ranking models ( $\Delta AIC_c \leq 2.0$ ) describing territory (mesohabitat) selection factors for Lesser Yellowlegs in Churchill MB. The full 32 model candidate set was used to calculate values based on model weights. A higher importance value indicates relatively higher importance of the variable.

<b>Variable</b>	<b>Importance Value †</b>
Distance to water	0.97
Spruce dominated	0.63
Tree number	0.59
Shrub percent cover	0.41

† Importance values for variables were calculated as the summed Akaike weights ( $w_i$ ) for each model in the candidate set that the variable appeared in.

**Table 3.9** Model selection results sorted by  $\Delta AIC_c$  including highly supported models ( $\Delta AIC_c \leq 2.0$ ) of nest site (microhabitat) selection by Lesser Yellowlegs in Churchill MB.

Variables: *LatCnc*—Lateral concealment, *PS.ht*—Point shrub height, *Wtr*—water percent cover, *WillDom*—willow dominated

<b>Model</b>	<b>K</b>	<b>AIC<sub>c</sub></b>	<b><math>\Delta AIC_c</math></b>	<b><math>W_i</math></b>	<b>Cum.Wt</b>	<b>LL</b>
LatCnc + PS.ht + WillDom	3	36.13	0.00	0.13	0.13	-14.85
LatCnc + PS.ht + Wtr + WillDom	4	36.39	0.26	0.11	0.24	-13.83
PS.ht + Wtr + WillDom	3	36.74	0.61	0.09	0.33	-15.16
PS.ht + WillDom	2	37.02	0.89	0.08	0.41	-16.41
LatCnc + PS.ht + Wtr	3	37.15	1.02	0.08	0.49	-15.36
PS.ht + Wtr	2	37.29	1.15	0.07	0.56	-16.54
LatCnc + WillDom	2	37.90	1.76	0.05	0.61	-16.84
LatCnc + PS.ht	2	38.12	1.99	0.05	0.66	-16.96

*K*—number of parameters, *AIC<sub>c</sub>*—corrected AIC criterion,  $\Delta AIC_c$ —difference in *AIC<sub>c</sub>* between the best model in the candidate set and the model listed,  $W_i$ —*AIC<sub>c</sub>* model weight, *Cum.Wt*—cumulative model weight, *LL*—model log-likelihood

**Table 3.10** Coefficient estimates and test statistics for top models testing microhabitat selection factors. LL and UL indicate 95% confidence intervals for the odds ratio; results are considered statistically significant if these do not

overlap 1. Significant (\*) and marginally significant (~) results based on confidence intervals and/or p-value (alpha level = 0.05) are bolded.

Variables: *LatCnc*—Lateral concealment, *PS.ht*—Point shrub height, *Wtr*—water percent cover, *WillDom*—willow dominated

<b>1<sup>st</sup></b>	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
<b>LatCnc+PS.ht+Wi</b>							
<b>IIDom</b>							
$\Delta AICc = 0.00,$							
$W_i = 0.13$							
Lateral	0.616	0.371	1.659	<b>0.0971</b>	0.894	3.830	~
Concealment							
Point shrub height	0.744	0.488	1.524	0.1275	0.808	5.483	
Willow-dominated	1.912	1.107	1.726	0.0843	0.772	59.241	
<b>2<sup>nd</sup></b>							
	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
<b>LatCnc+PS.ht+Wt</b>							
<b>r+WillDom</b>							
$\Delta AICc = 0.26,$							
$W_i = 0.12$							
Lateral	0.611	0.398	1.535	0.1248	0.844	4.017	
Concealment							
Point shrub height	1.190	0.637	1.869	<b>0.0617</b>	0.944	11.441	~
Percent water	-2.061	1.658	-1.243	0.2140	0.0049	3.286	

Willow-dominated	1.727	1.137	1.520	0.1285	0.606	52.199
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<b>3rd</b>	Estimate	Std. Error	z value	Pr(> z )	LL	UL
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**PS.ht+Wtr+WillD**

**om**

$\Delta AICc = 0.61,$

$W_i = 0.10$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
Point shrub height	1.323	0.682	1.939	<b>0.0525</b>	0.986	14.31	~
Percent water	-2.568	2.090	-1.229	0.2192	0.0013	4.610	
Willow-dominated	1.614	1.117	1.446	0.1482	0.563	44.84	

<b>4th PS.ht</b>	Estimate	Std. Error	z value	Pr(> z )	LL	UL
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**+WillDom**

$\Delta AICc = 0.89,$

$W_i = 0.09$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
Point shrub height	0.905	0.590	1.534	0.1250	0.778	7.851	
Willow-dominated	1.965	1.100	1.785	<b>0.0743</b>	0.824	61.70	~

**5th** Estimate Std. Error z value Pr(>|z|) LL UL

**LatCnc+PS.ht**

**+Wtr**

$\Delta AICc = 1.02,$

$W_i = 0.08$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL
Lateral concealment	0.570	0.388	1.470	0.1416	0.827	3.780
Point shrub height	1.429	0.664	2.152	<b>0.0314</b>	1.136	15.333 *
Percent water	-2.585	1.810	-1.428	0.1533	0.002	2.619

**6th PS.ht +Wtr** Estimate Std. Error z value Pr(>|z|) LL UL

$\Delta AICc = 1.15,$

$W_i = 0.08$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL
Point shrub height	1.623	0.701	2.317	<b>0.0205</b>	1.284	20.032 *
Percent water	-3.414	2.201	-1.551	0.1209	0.0004	2.461

**7th** Estimate Std. Error z value Pr(>|z|) LL UL

**LatCnc+WillDom**

$\Delta AICc = 1.76,$

$W_i = 0.06$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL
Lateral concealment	1.843	0.338	1.813	<b>0.0699</b>	0.952	3.568 ~
Willow dominated	2.128	1.087	1.958	<b>0.0503</b>	0.998	70.738 ~

**8th**                      Estimate   Std. Error   z value   Pr(>|z|)   LL   UL

**LatCnc+PS.ht**

$\Delta AIC_c = 1.99,$

$W_i = 0.05$

	Estimate	Std. Error	z value	Pr(> z )	LL	UL	
Lateral concealment	0.616	0.353	1.744	<b>0.0811</b>	0.927	3.699	~
Point shrub height	0.875	0.504	1.735	<b>0.0828</b>	0.893	6.445	~

**Table 3.11** Importance values for variables in best models describing nest selection factors for Lesser Yellowlegs in Churchill MB. A higher importance value indicates relatively higher importance of the variable.

<b>Variable</b>	<b>Importance value †</b>
Point shrub height	1.09
Willow dominated	0.68
Lateral concealment	0.62
Percent water	0.35

† Importance values for variables were calculated as the summed Akaike weights ( $w_i$ ) for each model in the candidate set that the variable appeared in.

## Chapter 4. General Discussion

### *Findings, Limitations, Future Research, and Conservation*

Shorebird populations in North America have been in steep decline (Smith et al. 2023). Discerning the causes for declines, and thus potential conservation actions to reverse them, depends on understanding what drives changes in vital rates. For shorebirds with extensive geographic ranges, multi-site studies are necessary for making general inferences regarding demographic rates (Weiser et al. 2018). My study found that Lesser Yellowlegs in Churchill, Manitoba had significantly lower nest survival than Lesser Yellowlegs in Anchorage, Alaska.

This study faced some important constraints. Given the challenges in finding Lesser Yellowlegs nests and only two field seasons in Churchill, my sample size is limited. This decreased statistical power to detect effects of covariates. While remote field work is costly and requires great effort, collecting additional data would enable more refined inferences. Studies in other parts of the breeding range may help determine whether our low daily nest survival rates may have resulted from conditions specific to the northern limit of the Lesser Yellowlegs range or if they are representative of a broader region. Comparing Churchill conditions with weather data elsewhere in the eastern breeding range may also be informative. Additionally, since interannual nest survival rates can vary widely depending on local conditions and predator-prey cycles (Smith et al. 2012), a two-year survey of nest survival may not capture the true range of nest survival rates for the Churchill region.

Temperature differences between Anchorage and Churchill were significant and my results suggested an effect of lower temperatures to decrease DSR. My two field seasons in Churchill were very different from each other yet the nest survival rate was very similar for Churchill in each season. That was an unexpected result since I would have expected 2023, as a warmer than average year for Churchill and phenologically advanced relative to 2022, to have had higher nest survival.

Future studies testing the effects of temperature on nest survival would benefit from placement of temperature data loggers at nests. Directly measuring temperature at the nest cup, rather than reliance on ambient temperature measures, would account for microclimate effects and greatly increase precision. It would also enable comparison to ambient temperatures thereby opening lines of inquiry into microhabitat effects. Additional important benefits of this type of automated nest monitoring would come from obtaining precise timing for the failures of nests as well as less disturbance to incubating birds and freeing up more time for researchers to search for nests (Stephenson et al. 2021).

While there was considerable model uncertainty as to the mechanisms driving differences in DSR for Lesser Yellowlegs the disparity between estimates at each site is striking. Discerning factors that caused differences in nest survival between sites is difficult. A wide-ranging study by Weiser et al. (2018) of 17 taxa of arctic breeding shorebirds at 16 sites over 7 years did not find effects of environmental or predator related covariates in 12 taxa studied despite high variability of conditions. Smith et al. (2007) conducted a three-season study of nest survival for five species of shorebirds at East Bay in Nunavut, Canada in

which they tested covariates that included habitat type, overhead and lateral nest concealment, predator abundance, rodent abundance and parental behavior. They concluded that the factor with the greatest influence on nest success was the yearly fluctuation in predation pressure. In years when lemmings were at a low point in their population cycle, predators that normally consumed rodents switched to predation of birds' eggs. It is possible that my study corresponded with a peak in predator abundance at Churchill that covered both years, resulting in the observed low nest survival rates.

Given well documented habitat shifts in the boreal region (Dial et al. 2022; Serreze et al. 2000; but see Timoney 2023), assessing habitat requirements for threatened and declining species is critical (Bateman et al. 2020; Wauchope et al. 2017). The broad expanse of the Lesser Yellowlegs breeding range contains a variety of habitats in which territory and nest site selection can be further investigated. Future work might include nest habitat selection studies at additional sites in other parts of the range to provide a more rounded view of Lesser Yellowlegs nest site preferences. It would be informative to see what habitats are selected in breeding areas that are not at a northern limit of the species' range. Perhaps a contrast with Churchill, which is at a northern limit, would reveal differences between factors selected in a more moderate climate versus those at the edges of suitability. Modeled eBird trends indicate that Lesser Yellowlegs numbers may be increasing along the southwestern shores of Hudson Bay (*Lesser Yellowlegs - Trends Map - eBird Status and Trends*, 2025). A study of nest survival and habitat features in these more recently occupied areas would

be of interest. Additionally, a more detailed survey of Anchorage nest sites or another site where there are known populations of LEYE (e.g., Yellowknife, Northwest Territories, Canada) may provide counterpoint data.

As expected, my habitat selection results indicated more variability between fully random points and territory points, but the finer details of microhabitat selection were difficult to distinguish. At the territorial scale there may be benefits in future research that takes advantage of satellite imagery to examine sites based on GPS points for Lesser Yellowlegs nests recorded in Churchill and in Anchorage. A combination of image analysis and ground truthing of known nest sites may provide a useful means to extend inferences to areas where we have not conducted on-the-ground research. Methods for linking Landsat imagery or other remote-sensing to habitat characteristics may be valuable for evaluating habitat availability in remote and less accessible areas (Gottschalk et al. 2005; Toral et al. 2011; Le Tallec et al. 2025) that encompass much of the Lesser Yellowlegs breeding range. These further studies could help elucidate how climate change may affect conditions on the breeding range.

Other than a nest concealment variable, my study did not attempt to link detailed habitat survey data to nest success. A standard hypothetical assumption is that selected features are adaptive (Cody 1985) but there is much in the literature that indicates this cannot always be assumed. For example, some areas may function as ecological traps if the habitat changes but cues that had been previously advantageous lead birds to use currently unsuitable habitat (Swift et al. 2017). Or there may be a time lag between decreases in habitat quality and response by

birds (Swift et al. 2017). Whether certain selection factors are adaptive is an important question, but my sample size for Churchill Lesser Yellowlegs ( $n=26$ ) was too limited to adequately test this.

My nest survival models indicated that more overhead concealment may have been linked with higher success. I was unable to test lateral concealment with nest survival for my full dataset since these data were not collected during the Anchorage study and sample size was too small for Churchill data alone. My habitat selection analysis for Churchill Lesser Yellowlegs indicated that lateral concealment was weighted higher in models than overhead concealment. Lateral concealment is thought to protect against mammalian predators, for which anti-predator actions taken by incubating adults were less effective than for avian predators (Larsen et al. 1996); perhaps lateral concealment is a more important factor and should be measured in future nest survival studies.

Understanding effects of weather, temperature and habitat on the breeding biology of birds is critical given the rapid shifts that are occurring at high latitudes due to climate change. Relationships among abiotic and biotic factors that drive nest survival and shape habitat characteristics are complex and they are subject to local conditions and temporal variation. The costs and benefits of future changes for breeding birds will likely accrue differently depending on a suite of factors. There may be a possible short-term benefit of warming as it can decrease energetic costs to birds breeding in high latitudes (McKinnon et al. 2013; Weiser et al. 2018). Additionally, earlier onset of spring has led to earlier nest initiation for many species (Liebezeit et al. 2014) and earlier laying often

increases nest survival (McGuire et al. 2020). However, these benefits are likely to be outweighed by negative impacts of weather extremes (Delfino 2024). Extreme events have become more common, and these can have locally devastating consequences such as the nearly complete reproductive failure of the terrestrial ecosystem of northeast Greenland in the summer of 2018 due to abundant late melting snow (Schmidt et al. 2019). Changes in climate are also likely to exacerbate a disconnect between conditions at stopover sites and breeding areas leading to phenological mismatch and consequently lower reproductive success (Senner et al. 2012). While broad changes in temperature regimes have been well documented, local effects can vary; spring temperatures in Churchill, for example, have demonstrated a cooling trend (Senner et al. 2017).

Based on this study, breeding Lesser Yellowlegs appear to be habitat generalists that likely have a wide range of preferred habitat characteristics. Under projected climate change scenarios, requirements for suitable breeding conditions for many other shorebird species are expected to shift beyond species' capacities to adapt (Wauchope et al. 2017). Vegetative changes, for example, can impact distributions of nesting shorebirds—shrub encroachment in Churchill likely led to lower densities of nesting Whimbrel (Ballantyne & Nol 2015).

I found that higher overhead concealment of nests was linked with higher nest survival and an apparent preference for relatively tall shrubs to nest beneath, thus increased shrub cover at the tundra edge due to climate change may be neutral or beneficial at moderate vegetation density. Lesser Yellowlegs may be

better equipped than many shorebird species to adapt to changing vegetative conditions induced by a warming climate. My results indicated that higher temperatures, particularly in mid incubation, were predictive of higher nest survival for Lesser Yellowlegs. This suggests that this species may benefit from increased temperatures on the breeding range. However, climate change is not characterized by warming alone and weather conditions will likely become more extreme (IPCC 2023). I also found support for a detrimental effect of high variability in temperatures over the incubation period. Churchill's dynamic summer weather delivers both hypothermic and hyperthermic conditions over a nesting season but also within much shorter timeframes. Thermoregulation in such an environment is energetically costly (Stager et al. 2016) and, compounding the issue, conditions that lead to restlessness for incubating birds increase the risk of nest predation (Smith et al. 2012). High variability in ambient conditions over the nesting season likely has a negative impact on avian reproductive success even in the absence of the dramatic weather anomalies that are now becoming ever more common.

Habitat characteristics are shifting in response to climate change. In short, "global weirding", a term coined to capture the variety of extreme phenomena (beyond simply warming) that are occurring due to climate change, is projected to be highly disruptive to ecosystems generally (Bunnell et al. 2011). Each study increasing our knowledge of biological systems makes it more likely that we can respond to the enormous challenges of our times with targeted management actions to preserve declining species.

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## Appendices:

### Appendix 1. Nesting season dates of first and last estimated initiation and hatch dates and mean nest initiation

Dates for Anchorage and Churchill study areas (Julian dates appear in parentheses).

	<b>Anchorage</b>	<b>Churchill</b>
<b>2018</b>		
Season length	May 10-June 23 (130-174) 45 days	na
<i>Mean nest initiation</i>	<i>May 20 (140)</i>	
<b>2019</b>		
Season length	May 11-June 28 (131-179) 49 days	na
<i>Mean nest initiation</i>	<i>May 20 (140)</i>	
<b>2020</b>		
Season length	May 11-June 28 (131-179) 49 days	na
<i>Mean nest initiation</i>	<i>May 17 (137)</i>	
<b>2021</b>		
Season length	May 13- July 6 (133-187) 55 days	na
<i>Mean nest initiation</i>	<i>May 23 (143)</i>	
<b>2022</b>		
Season length	May 12-June 21 (132-172) 41 days	May 29-July 14 (149-195) 47 days
<i>Mean nest initiation</i>	<i>May 20 (140)</i>	<i>June 5 (156)</i>
<b>2023</b>		
Season length	May 10-June 13* (130-164) 35 days	May 21-July 7 (141-188) 48 days
<i>Mean nest initiation</i>	<i>May 14 (134)*</i> *n=2	<i>May 28 (148)</i>
<b>Site mean nest season dates</b>	May 11-June 25 (131-176)	May 25-July 11 (145-192)
Mean Season length	46 days	48 days
<i>Site mean nest initiation</i>	<i>May 20 (140)</i>	<i>June 1 (152)</i>

## Appendix 2. Candidate model list for initial analysis including all covariates for the site combined dataset of 75 nests.

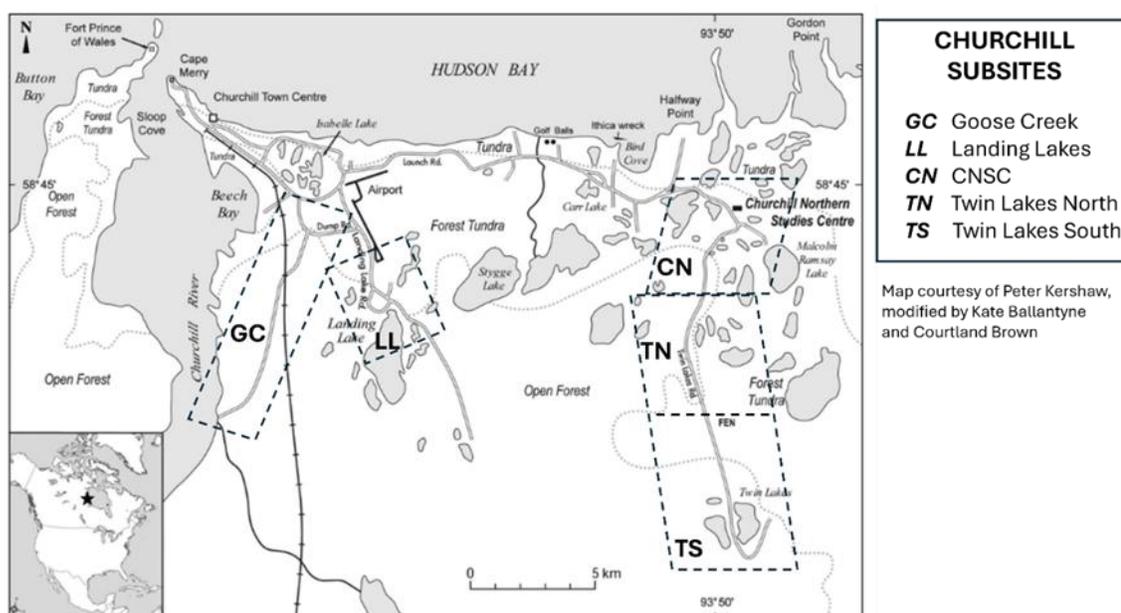
I first tested all the nest period temperature variables and found that the middle period maximum temperature appeared most often in the substantially supported models. The models using middle period temperature measures were most highly weighted and the models of the midmax variable had the greatest certainty based on the beta estimate confidence intervals. Middle period mean and middle period minimum temperature appeared to be second and third best respectively.

<b>Model list: Full dataset (n=75)</b>	<b>K</b>	<b>AICc</b>	<b>ΔAICc</b>	<b>weight</b>	<b>Deviance</b>
<b>all vars</b>					
S(~Init + MidMax)	3	140.18	0.00	0.09	134.16
S(~Site)	2	140.60	0.42	0.08	136.59
S(~Init + MidMean)	3	140.81	0.62	0.07	134.78
S(~Init)	2	141.12	0.93	0.06	137.10
S(~Init + MidMin)	3	141.55	1.37	0.05	135.52
S(~MidMax)	2	141.59	1.41	0.05	137.58
S(~Site + MidMax)	3	141.68	1.50	0.04	135.65
S(~Init + sdAvg)	3	141.99	1.81	0.04	135.96
S(~sdAvg)	2	142.05	1.87	0.04	138.04
S(~Site + AllMax)	3	142.17	1.98	0.03	136.14
S(~Init + AllMin)	3	142.18	1.99	0.03	136.15
S(~MidMean)	2	142.34	2.15	0.03	138.32
S(~Init + EarlyMin)	3	142.36	2.17	0.03	136.33
S(~Site + EarlyMax)	3	142.41	2.23	0.03	136.38

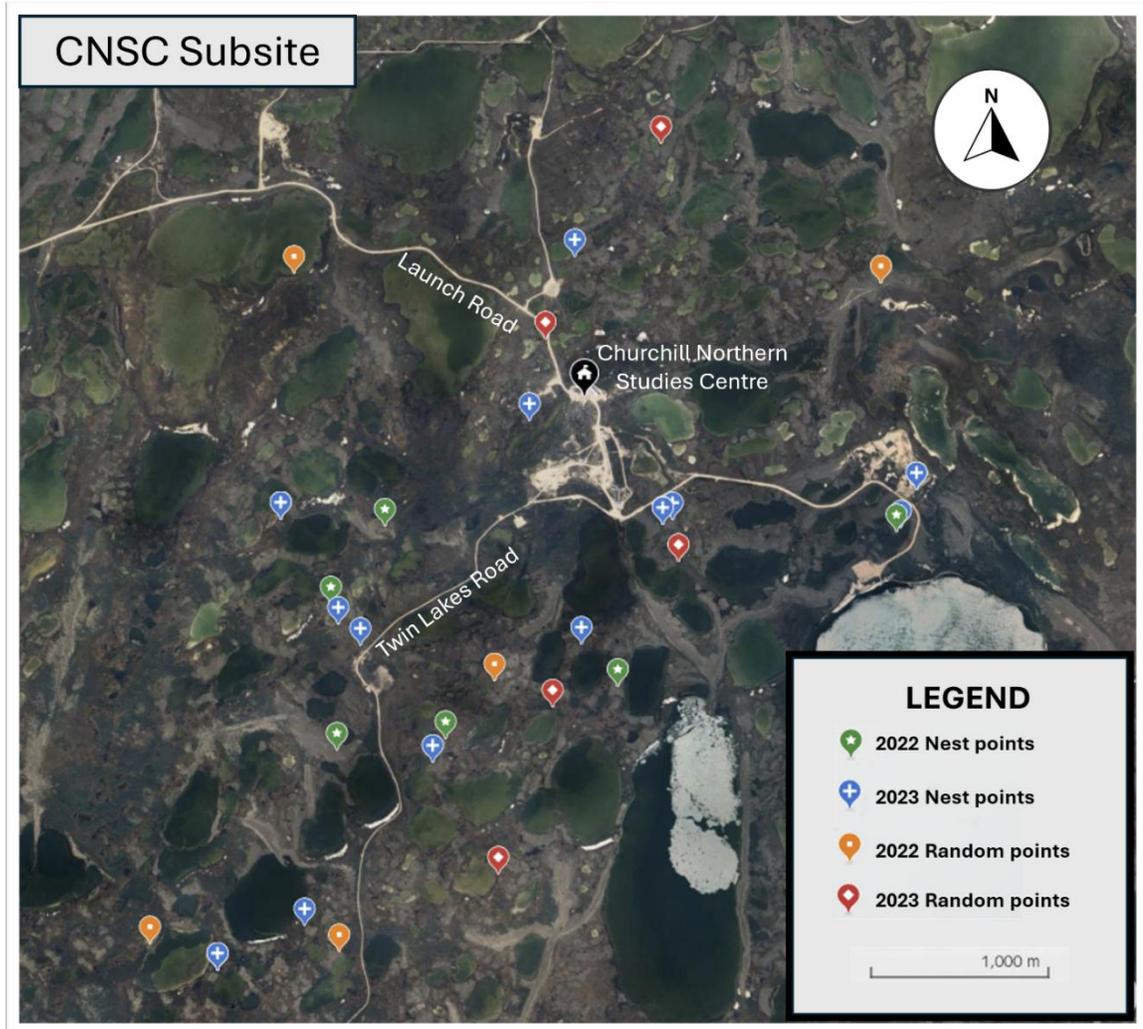
S(~Init + AllMean)	3	142.48	2.29	0.03	136.45
S(~Init + EarlyMax)	3	142.68	2.49	0.03	136.65
S(~Init + AllMax)	3	142.79	2.60	0.03	136.76
S(~Time + Site + MidMax + NestAge)	5	142.84	2.66	0.02	132.78
S(~Time + MidMax)	3	143.11	2.92	0.02	137.08
S(~MidMin)	2	143.12	2.94	0.02	139.11
S(~1)	1	144.02	3.84	0.01	142.02
S(~AllMin)	2	144.11	3.93	0.01	140.10
S(~Time + Init + MidMax + NestAge)	5	144.14	3.95	0.01	134.07
S(~Time + Site + MidMin + NestAge)	5	144.20	4.01	0.01	134.13
S(~EarlyMin)	2	144.35	4.17	0.01	140.34
S(~Time + MidMin)	3	144.43	4.25	0.01	138.41
S(~AllMean)	2	144.54	4.35	0.01	140.52
S(~EarlyMean)	2	144.56	4.38	0.01	140.55
S(~Time + I(Time^2) + MidMax)	4	144.78	4.59	0.01	136.73
S(~AllMax)	2	144.90	4.72	0.01	140.89
S(~LateMin)	2	144.95	4.76	0.01	140.93
S(~EarlyMax)	2	144.95	4.77	0.01	140.94
S(~Habitat)	3	145.33	5.15	0.01	139.31
S(~Time + Init + MidMin + NestAge)	5	145.37	5.18	0.01	135.30
S(~LateMax)	2	145.74	5.56	0.01	141.73

S(~NestAge)	2	145.96	5.77	0.01	141.94
S(~LateMean)	2	145.99	5.80	0.01	141.97
S(~Time)	2	146.03	5.85	0.01	142.02
S(~Time + I(Time^2) + MidMin)	4	146.19	6.00	0.00	138.14
S(~Time + I(Time^2))	3	147.80	7.61	0.00	141.77

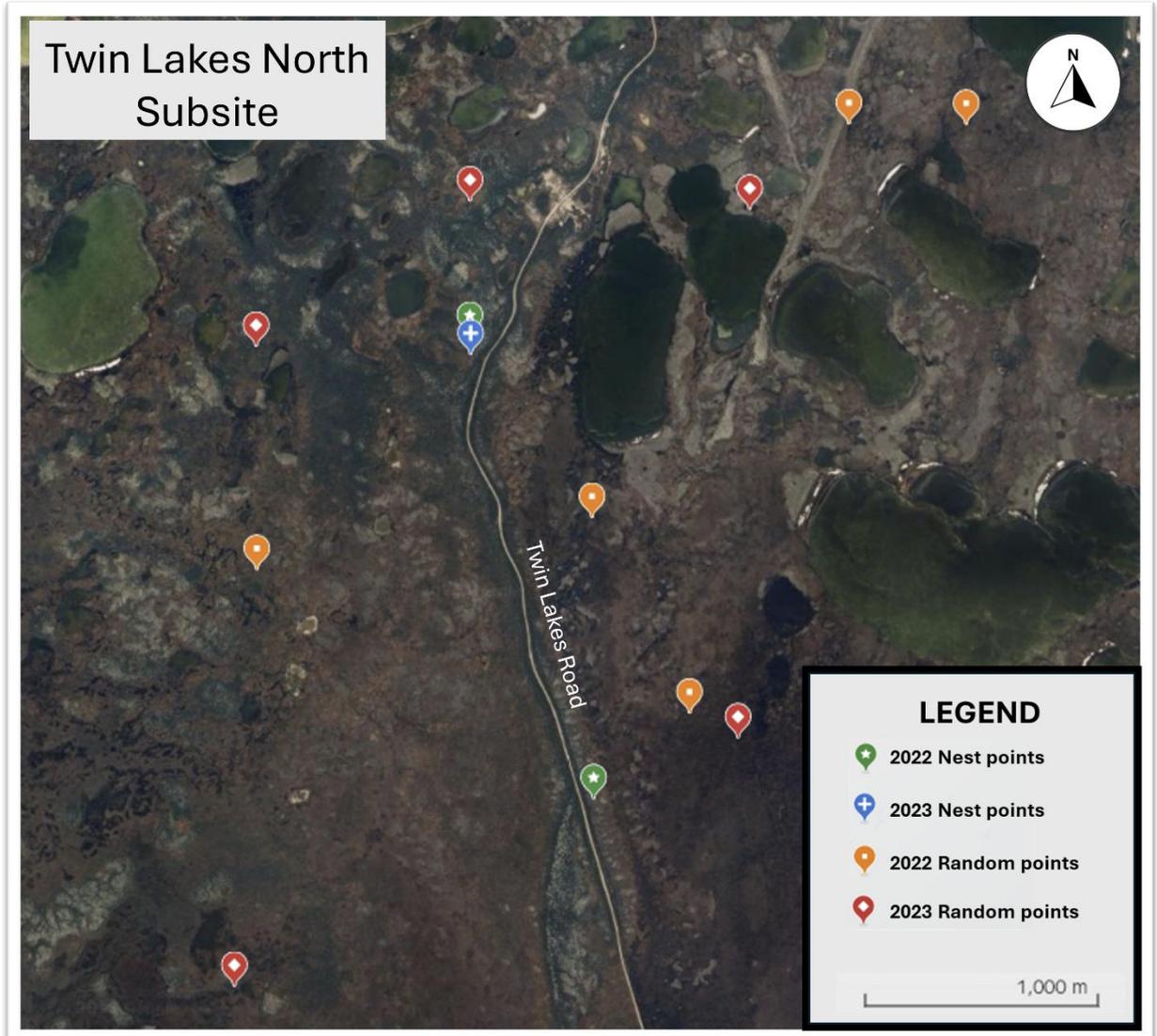
### Appendix 3. Habitat survey locations for Churchill subsites



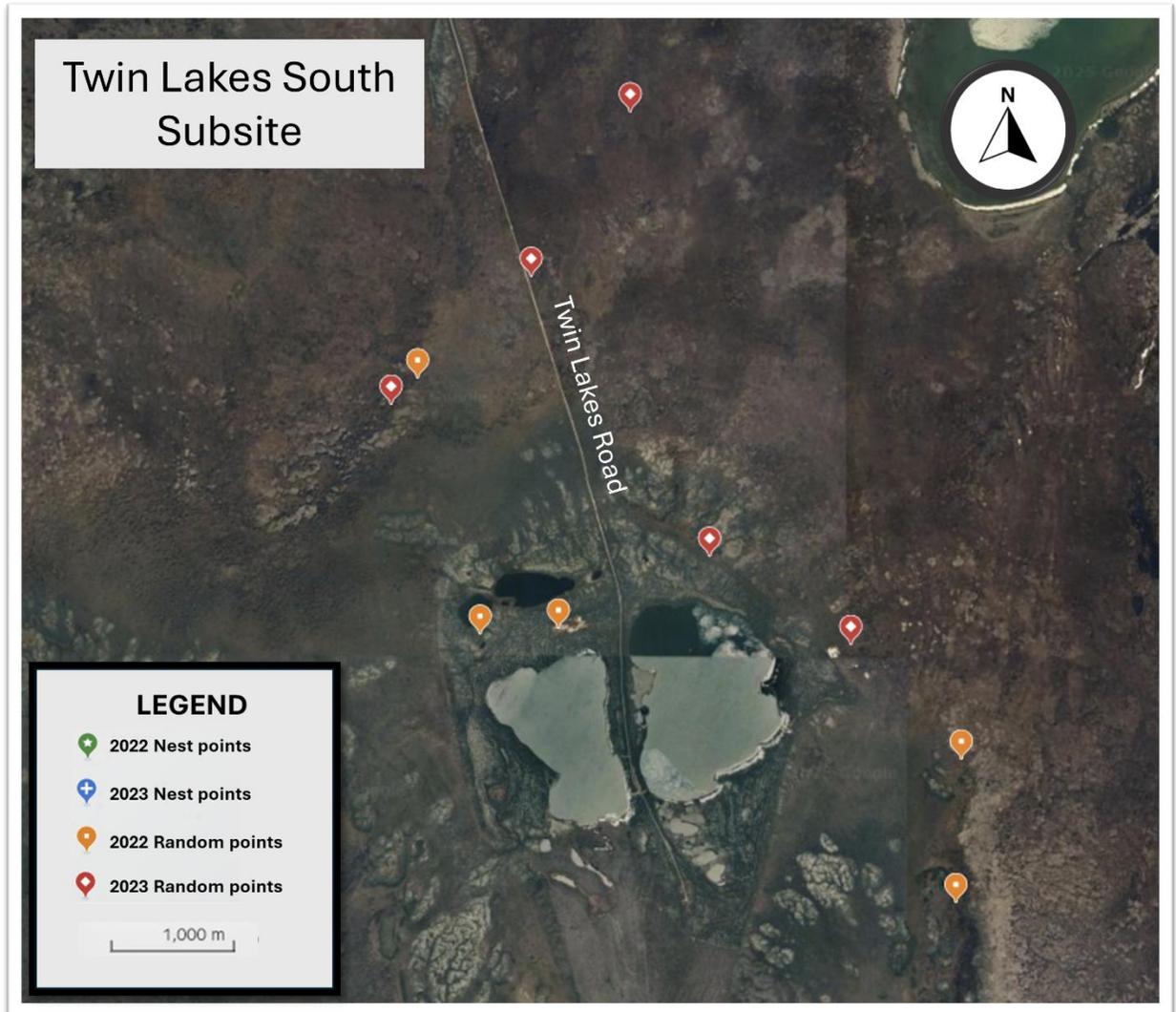
**Appendix 3a.** Overview map of Churchill study area



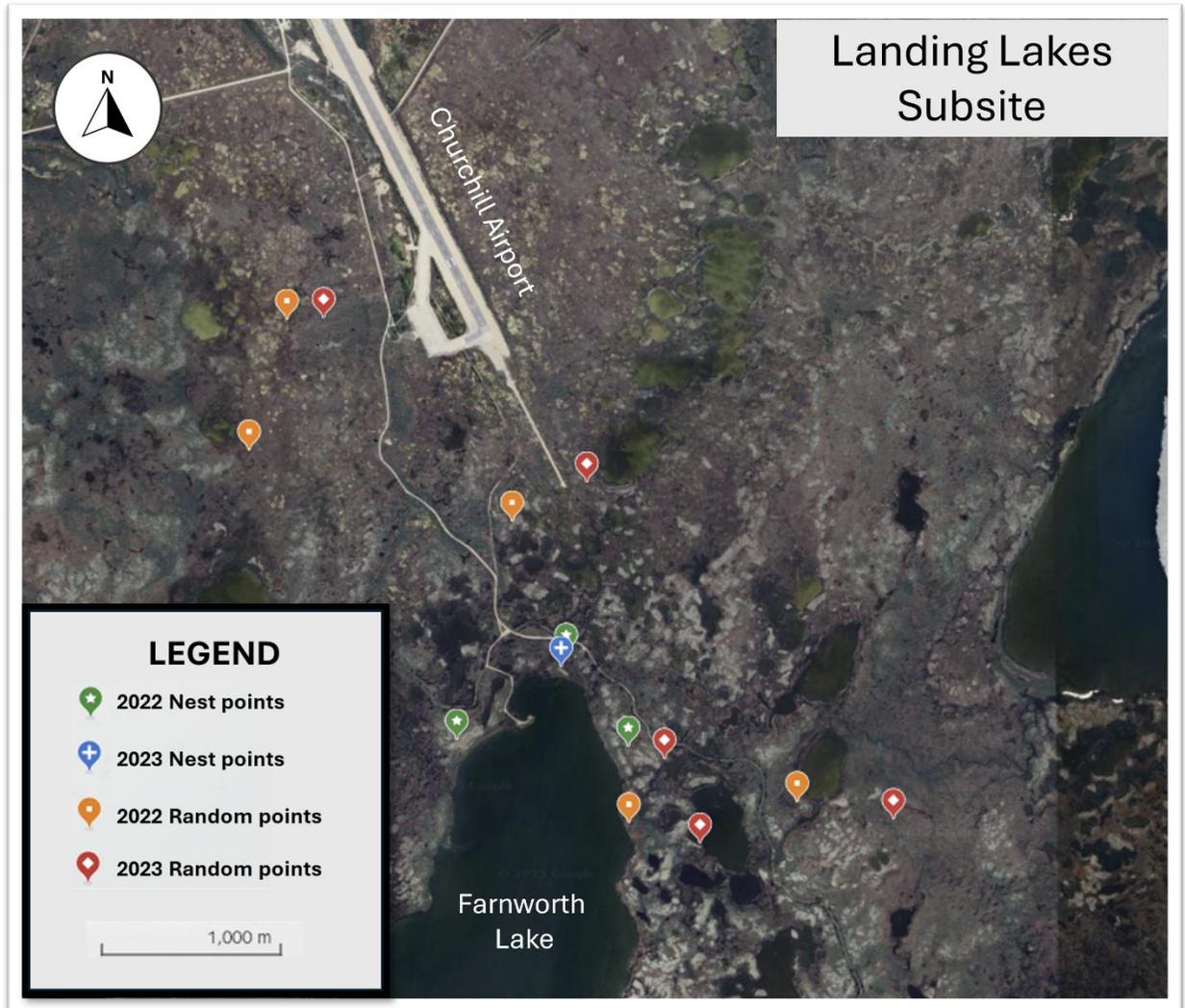
**Appendix 3b.** CNSC subsite showing nest locations and fully random points. Paired random points are not shown since they overlap with nest points at this scale. Each nest had a paired random point surveyed with it.



**Appendix 3c.** Twin Lakes North subsite showing nest locations and fully random points. Paired random points are not shown since they overlap with nest points at this scale. Each nest had a paired random point surveyed with it.



**Appendix 3d.** Twin Lakes South subsite showing fully random points. Since I did not find any nests in this area there were no nest points or paired random points in this subsite.



**Appendix 3e.** Landing Lakes subsite showing fully random points and three nests found in 2022 and one nest in 2023. Paired randoms are not shown since they overlap with nest points at this scale.

## Appendix 4. Habitat analysis variables list, descriptions and rationale

	Variable	Description	Rationale
	Nearest water	Closest persistent water at least 3 cm deep	Precocial chicks need to forage shortly after hatching
Vegetation immediately next to point	NVeg_height	Immediate vegetation height at north side of point	Vegetation dimensions at nests may vary according to cardinal direction (e.g. to provide greater protection from prevailing winds)
	SVeg_height	Immediate vegetation height at south side of point	
	EVeg_height	Immediate vegetation height at east side of point	
	WVeg_height	Immediate vegetation height at west side of point	
	AvgVeg_height	The mean of immediate vegetation heights for the four cardinal directions	

	Immediate veg species (four records per point)	Species recorded at each cardinal direction	Certain species may be favored at nests
	Willow dominated	Binary variable indicating whether willow was most highly represented immediately next to point	Willow may be preferred at nest sites
Point shrub characteristics	PointShrub_tallest	Tallest veg of shrub at survey point	Selection may depend on shrub dimensions
	PointShrub_widest	Widest dimension of shrub at survey point	
	PointShrub_NSwidth	Width of shrub along north-south axis	Vegetation dimensions at nests may vary according to cardinal direction
	PointShrub_EWwidth	Width of shrub along east-west axis	
	PointShrubSp	Species of point shrub	Some species may be favored over others
values	Concealment	Percentage of point obscured by vegetation when	

		viewed from north side	Concealment values may vary by cardinal direction
	SPercConc	Percentage of point obscured at south side	
	EPercConc	Percentage of point obscured at east side	
	WPercConc	Percentage of point obscured at west side	
	AvgLatPercConc	Mean of four percent concealment values for each cardinal direction	Nest concealment overall may vary from random but not directionally
Percentages of different ground cover types	Lichen_perc	Lichen cover percentage within 5m radius of point	Selection may depend on types of cover
	Graminoid_perc	Graminoid cover percentage within 5m radius of point	
	Forb_perc	Forb cover percentage within 5m radius of point	

	ExpSubstrate_perc	Exposed dirt, rock, or gravel percentage of cover within 5m radius of point	
	Spruce_perc	Spruce cover percentage within 5m radius of point	
	Tamarack_perc	Tamarack cover percentage within 5m radius of point	
	Shrub_perc	Shrub cover percentage within 5m radius of point	
	Water_perc	Standing water percentage of cover within 5m radius of point	
Tree characteristics	Average tree height	Overall average for trees within 10 meters of point	Trees of certain heights may be preferred, or avoided
	AvgHt_InTrees	average height of trees within 2 meters of the point	Sites may show selection based on

			heights of trees nearest to point
AvgHt_MidTrees	average height of trees between 2-5 meters of the point		Sites may show selection based on heights of trees near, but not immediately next to, point
AvgHt_OutTrees	average height of trees between 5-10 meters of the point		Taller "sentry trees" may be 5-10 meters from nest sites
Total number trees	Overall number of trees within 10 meters of point		If nest sites were in more open habitats total tree numbers should vary non-randomly
n_InTrees	Number of trees within 2 meters of the point		If proximity of trees to nest sites was selected for, that may be reflected by the number of trees within various distances to point
n_MidTrees	Number of trees between 2-5 meters of the point		
n_OutTrees	Number of trees between 5-10 meters of the point		

	Perc_TreesOver3m	Percentage of trees exceeding 3 m tall	Observations in the field suggested that “sentry trees” were usually taller than 3 m
	AvgDistFromPt	Average distance from point for all trees within 10 m of point	If tree proximity to nest is selected for this may be reflected in average distance variable
	Spruce dominated	Binary variable indicating whether more than half of the trees within 10 m of the point were spruces	Selection may depend on an area having mostly spruce trees

## Appendix 5. Imputation details for missing survey parameters

The six incomplete survey records were imputed as follows:

- Record number 56, Paired random (23LEYE13PR) percent cover data filled in using mean for the variables for PR points both seasons for CN study area
- Record number 60, Paired random (23LEYE15PR) filled in immediate veg average height using mean for the PR points for both seasons for CN study area
- Record number 85, Fully random (23LLRR05) Concealment values and immediate veg average height filled in using mean from both season's R points for LL study area
- Record number 90, Fully random (23CNSR05) used point shrub dimensions mean for both seasons for R points for CN study area
- Record number 91, Fully random (23CNSR06) mean for percent cover variables from both season's R points for CN study area
- Record number 94, Fully random (23TLNR03) mean for percent cover variables from both season's R points for TN study area