HABITAT ASSOCIATIONS AND MOVEMENT TRACKING OF NORTH AMERICAN BLACK TERNS (*Chlidonias niger*)

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ABSTRACT:

Black Tern (*Chlidonias niger*) populations are declining across their range in North America, but it is unknown at what point during the annual cycle populations may be limited. Although causes of decline remain largely unknown, past studies showed that conditions on stop-over and over-wintering locations may be important factors. Little is known about the migration timing, routes, stop-over sites, or the range and environmental conditions of over-wintering Black Terns. Furthermore, it is unclear what habitat qualities and attributes influence Black Tern colony occurrence in the core of their breeding range in the Canadian prairies. Breeding habitat selection is increasingly important in the face of continuing and potentially damaging anthropogenic land uses and climate change. My objectives were to 1) examine the influence of various habitat, land use, and geographic covariates on Black Tern occupancy and abundance in the core of the species range in Saskatchewan; and 2) examine full annual cycle movements and potential differences in migratory stop-over and over-wintering locations from Black Terns breeding across their range in central (Saskatchewan, Canada) and eastern (Ontario, Canada and Michigan, USA) North America, while providing a preliminary assessment of migratory connectivity.

I assessed Black Tern occupancy and abundance at 68 wetlands compiled from historic waterbird databases and field surveys. I used aerial imagery to quantify four habitat covariates I predicted would influence Black Tern site suitability: total wetland area, the extent of emergent vegetation present at each wetland, wetland classification, and the degree of anthropogenic encroachment surrounding each wetland. I deployed 88 archival light-level geolocators on Black Terns across five colonies in Saskatchewan and Ontario, Canada, and Michigan, USA, during the

breeding seasons of 2016-2019 to track their migratory movements, stop-over, and over-wintering locations.

Habitat association results showed that colony occurrence was predicted by both geographic and habitat covariates, with wetlands at mid-latitudes and with more emergent vegetation associated with an increased likelihood of Black Tern colony occurrence. Abundance was best predicted by geographic patterns (latitude) alone. These results revealed that Black Terns are selecting breeding habitat at multiple scales primarily along a narrow latitudinal band across Saskatchewan. This suggests that individuals may first be locating breeding sites based on large-scale landscape features driven by latitude, and then selecting specific wetland locations for breeding based on small-scale features such as emergent aquatic vegetation. The highest abundances corresponded with the boreal transition zone between the prairies to the south and boreal forest to the north, an area that might be preferred by Black Terns due to its abundance of wetland habitat.

The migratory routes used by Black Terns varied among individuals, but some geographic patterns emerged; Black Terns from central and eastern regions used different migratory routes. All tagged individuals spent some or most of the wintering period at or off the coast of Panama, highlighting the importance of this location during the wintering period. These results suggest Panama might be a key location of population mixing on the wintering grounds. Additionally, migratory connectivity was stronger between breeding sites and the first migratory stopover location than it was between breeding sites and wintering locations, indicating that individuals from different breeding colonies generally remained more closely linked to other individuals from their same breeding colony during the fall migration, but that subsequent mixing of the populations occurred among individuals from multiple breeding locations on the wintering grounds. Some interesting patterns of Black Tern breeding dispersal were also uncovered based on long-distance breeding region switching of one individual tracked over multiple years. Furthermore, preliminary insights into colony abandonment and short-distance breeding dispersal of Black Terns in Saskatchewan were also revealed.

These results fill important data gaps that exist for the North American Black Tern. Although Black Tern populations are declining across their range, I demonstrate that colony occurrence and abundance can be predicted using both geographic and habitat models. These associations have revealed evidence that individuals are selecting habitat at multiple scales, both large and small. The quadratic relationship between the likelihood of colony occurrence and the latitude of a wetland suggests that large-scale landscape variables, such as variation in wetland density, may be driving this pattern. Very little was previously known about the Black Tern full annual cycle, and these migratory tracks are the first that have been collected for the species. Despite the use of different flyways across the breeding range, tracked individuals showed a high degree of mixing and weak migratory connectivity on the wintering grounds. A concentration of birds in Panama suggests that localized threats in this area could have an impact across the breeding range. In addition, evidence of long- and short-distance breeding dispersal suggest a lack of population structure and high levels of movement and gene flow. My results provide some of the first detailed migratory tracks for the Black Tern in North America, and reveal important habitat associations in the core of the species range, critical information that could benefit the conservation of the species.

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* One individual spent two stationary periods during the non-breeding season at this location.

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Spring staging may have occurred near the Gulf of California before travelling north through central North America and returning to Saskatchewan.

CHAPTER 1:

FULL ANNUAL CYCLE DYNAMICS AND POPULATION DECLINES IN WATERBIRDS

1.1 Waterbird Declines

1.1.1 Waterbird Population Limitation

Waterbird species are in decline across the globe (Amano et al. 2010). Many historically abundant waterbirds are experiencing some of the fastest and most prolific declines of any species (Kirby et al. 2008). Global waterbird trends reveal that 40% of species with available trend data are decreasing, 34% are stable, and only 17% are increasing, with an additional 52 species already listed as extinct (Delany and Scott 2006). Rising global threats include the disturbance and destruction of sensitive aquatic environments, the prolific spread of invasive species, and increases in anthropogenic encroachment (Baldock 1984, Rashford et al. 2011, Matteson et al. 2012). Waterbirds depend on sensitive environments to breed, roost, and feed (Peron et al. 2013), and disturbances that threaten these habitats are in turn directly impacting waterbird populations (Amano et al. 2018). Wetland reliant species, such as the Rusty Blackbird (*Euphagus carolinus*), face risk of extinction due to severe destruction of wetland habitats (Greenberg et al. 2011). The often-cryptic nature of waterbirds, and resulting lack of survey and monitoring data, have resulted in a group of birds that is not only in decline but also understudied (Morris et al. 2017).

The North American Prairie Pothole Region is an area that is particularly important for colonial nesting waterbird species due to the high density of wetland habitat (Higgins et al. 2002) and because it encompasses the core of the breeding range for many of these species (Naugle et al. 2000). However, the Prairie Pothole region is projected to lose up to 97% of its wetland habitat by the year 2100 (Steen and Powell 2012). Habitat degradation in the form of agricultural conversion is already prolific in this region; land conversion for agriculture use, wetland drainage, and agrochemical runoff are all threats faced by wetland breeding waterbirds in the prairies (Rashford et al. 2011, Matteson et al. 2012).

Additionally, waterbirds face threats during the non-breeding season, such as on wintering grounds and during migration (Marra et al. 2015). Although pressures faced by waterbirds throughout their full annual cycle are less understood than those faced on breeding grounds, recent research has revealed that land-use changes, habitat conversion and destruction along key migratory flyways are among the greatest threats waterbirds face during their migration (Delany and Scott 2006, Stroud et al. 2008). Waterbirds face a suite of potential stressors at all stages of their annual cycle, including mortality caused by human artefacts (e.g., tall masts and other structures) (Newton 2007), unsustainable harvesting (Spray et al. 2004), human disturbance (Mainguy et al. 2002), and disease (Friend 2006). In order to fully understand these threats and how they might be impacting waterbird populations, it is imperative that we study waterbirds across their full annual cycle.

1.1.3a Full annual cycle tracking

Traditionally, the conservation of waterbirds, and migratory bird species as a whole, has focused on threats occurring during the breeding season (Knight et al. 2021). However, recent research has highlighted the complex pressures and stressors faced by migratory birds as they travel the globe, cross international borders, and occupy different habitats throughout their full annual cycle (Marra et al. 2015). Although events that occur during different phases of the annual cycle may be geographically separated, their effects carry over to influence subsequent phases of the annual cycle (Harrison et al. 2011). As a result, tracking full annual cycle movements of migratory species is critical for understanding species biology and informing proper conservation and management. New advances in technology have allowed for precise tracking of animal movements across long distances using devices and methods such as satellite and radio transmitters, light-level geolocators, stable isotope analysis, and genomics, many of which have only recently been refined and miniaturized enough for application on birds (Marra et al. 2015).

These tracking methods have been successfully applied to waterbirds: geolocators have been used to track Common Terns (*Sterna hirundo*) breeding in North America, uncovering patterns in migratory route and site use, as well as major stopover sites (Bracey et al. 2018). Stable isotopes have been used to understand the links between marine wintering grounds and freshwater breeding grounds in Caspian Terns (*Hydroprogne caspia*), Double crested Cormorants (*Phalacrocorax auratus*), and Herring Gulls (*Larus argentatus*) (Hobson et al. 1997). Recent satellite tracking of Bar-headed Geese (*Anser indicus*), Eurasian Spoonbills (*Platalea leucorodia*), and Oriental Storks (*Ciconia boyciana*) revealed stopover site locations used by species during migration, as well as important habitat type use, leading to suggestions for future land protection (Wang et al. 2020). As methods and technologies continue to improve, the ability to track the full annual cycles of waterbirds, and consequent understanding of what threats these migratory species face will ultimately result in better strategies for protection and conservation. These tracking technologies can not only reveal insights into full annual cycle movements, but also uncover how populations of a species are connected throughout migration.

1.1.3b Migratory connectivity

Migratory connectivity is the degree to which populations are linked in space and time across the annual cycle (Knight et al. 2021). A population has strong migratory connectivity when individuals in a population breed, migrate, and overwinter in the same areas, resulting in low mixing among populations. On the other hand, weak migratory connectivity exists when individuals of a population from one breeding area migrate and overwinter over a large area, resulting in high individual mixing with other populations (Webster et al. 2002). Knowledge of migratory connectivity is particularly important for waterbirds due to their tendency to congregate in specific locations, thus providing the ability to protect important habitats, predict the probability of local extinction, and develop strategies to address the causes of population declines (Cohen et al. 2014, Bracey et al. 2018). For example, tracking of Common Terns from breeding populations across North America revealed low connectivity among inland colonies as a result of high individual mixing at wintering locations, with the majority of tracked individuals congregating in Peru (Bracey et al. 2018). The authors noted that this accumulation of individuals may make large portions of the continental breeding population vulnerable to threats such as storm events that could impact this region. By understanding these patterns of migratory connectivity, researchers are better able to create conservation and protection strategies for waterbird species that can be applied at multiple stages of the annual cycle, in order to benefit large portions of the population.

1.1.3c Movement, dispersal, and genetic structure

Understanding the genetic structure of a species can inform conservation and management needs. Loss of genetic diversity, reduction of gene flow, and altered genetic structure can all impact waterbirds, and may lead to species declines. In addition to migratory movements throughout the full annual cycle, waterbirds are capable of dispersing over long distances, a behaviour that can influence the genetic structure of species (Reudink et al. 2011). However, a species' ability to migrate and disperse over long distances does not necessarily guarantee weak genetic structure, which would be expected if populations are mixing throughout the annual cycle. For example, Common Murres (*Uria aalge*) often disperse over thousands of kilometers, but genetic structure is maintained across ocean basins (Morris-Pocock et al. 2008). This retention of genetic structure despite high mobility may be due to behavioural phenomena such as philopatry (Friesen at al. 2007). Another migratory waterbird, the American White Pelican (*Pelecanus erythrorhynchos*), also disperses over large distances, but in this case genetic and isotopic data revealed that pelican populations showed no genetic differentiation and high population mixing across the entire breeding population (Oomen et al. 2011, Reudink et al. 2011). This is a phenomenon known as panmixia, something that only occurs in species where dispersal is high and gene flow is low (Reudink et al. 2016). Understanding movement and genetic structure can also inform my understanding of population processes. One study on the population genetics of North American Common Terns revealed evidence for biased movement (gene flow) from inland to coastal populations, potentially helping to explain population declines of inland populations. In this case, migration routes may help to explain the species' genetic structure, since inland birds pass over coastal areas, but the reverse is not true (Szczys et al. 2017a). Studying the links between movement, dispersal, and genetic structure can allow researchers to better understand how and why waterbirds occupy certain areas and are absent from others. Understanding waterbird movements will not only benefit species in decline, but may also benefit entire ecosystems, as waterbirds often act as important indicator species for ecosystem health.

1.1.2 Waterbirds as Indicator Species

The importance of waterbird conservation is evident given the value of waterbirds as indicators of change in environmental conditions (Amat and Green 2010). As ecosystems continue to be altered, degraded, and destroyed as a result of anthropogenic activity, the need to understand and assess this change grows, and using waterbirds as indicators of overall ecosystem health is a useful tool for doing so (Kushlan 2002). For example, the siltation of shallow lakes affects water levels causing declines in Red-knobbed Coot (*Fulica cristata*) populations, eutrophication can create an abundance of food supplies and increase Great-crested Grebe (*Podiceps cristatus*) populations, and periods of drought reduce wetland numbers leading to lower populations of Greater Flamingos (*Phoenicopterus roseus*) (Amat and Green 2010). Great-crested Grebes and Black-necked Grebes (*Podiceps nigricollis*) have been used as indicators for assessing the impacts of land-use changes on important coastal lagoons (Fernandez et al. 2005). Testing waterbird body tissues for accumulations of heavy metals can be used to gauge heavy metal pollution in wetlands (Zhang and Ma 2011). Eggshell thinning in some waterbird species led to the discovery of the insecticide DDT as a serious environmental contaminant, resulting in a ban of its use, a decision that benefited many bird species (Speich et al. 1992). Further study of waterbird species would not only benefit waterbirds specifically but could also have greater implications for the conservation of entire ecosystems.

1.2 Wetland Conservation

1.2.1 Wetland Services

Wetlands are important landscape features that provide vital ecosystem services such as water quality improvement, flood prevention, and coastline preservation (Daily 1997, Gleason et al. 2008). Despite covering merely 1.5% of the Earth's surface, wetlands provide approximately 40% of global ecosystem services (Zedler and Kercher 2005). These services not only benefit waterbird populations, but also benefit many other species, as wetlands act as epicenters for biodiversity (Gibbs 2001). For example, when compared to unmanaged sites, conserved wetlands had significantly higher occupancy of waterfowl, marsh breeding birds, and frog species, including conservation-priority and at-risk species (Tozer et al. 2018). Wetlands improve water quality by storing nutrients and pollutants in their soil and vegetation and reducing concentrations of phosphorous and nitrogen often found in agricultural runoff and sewage (Clarkson et al. 2013). Wetlands are recognized for their key role in improving soil quality and reducing soil erosion (Knutsen and Euliss 2001), and wetland restoration research has provided evidence that improving wetland habitat can influence carbon sequestration, noting wetlands as important sinks of atmospheric carbon (Euliss et al. 2006). Wetlands also play a key role in reducing the impacts of extreme weather events and erosion on coastlines, as the roots of wetland vegetation consolidate and protect coastal substrates (Clarkson et al. 2013). There is a clear need to understand and protect wetlands, not just for waterbirds and other species that depend on them, but for broader ecosystem services and human well-being.

1.2.2 Linking Waterbird Habitat Associations to Wetland Protection

The restoration of wetlands has been a key management strategy for the protection and conservation of waterbird species (Vanausdall and Dinsmore 2019). Because many waterbird species are so dependent on wetlands, researching and understanding waterbird habitat needs has often resulted in the protection or restoration of wetland habitat. Increasing the density of marshes within a landscape, decreasing the presence of invasive plant species, and decreasing anthropogenic development and activity around wetland habitat are important for improving the occupancy and abundance of waterbird species in wetlands (Smith and Chow-Fraser 2010, Tozer 2016, Wyman and Cuthbert 2017). Through the process of understanding important wetland characteristics, research has shown that focusing on waterbird habitat associations can not only benefit waterbirds themselves, but entire wetland ecosystems. Specific management of habitat variables such as water depth and water level fluctuation, vegetation composition and structure, salinity, as well as wetland size and connectivity can help provide better habitat for a suite of waterbird species, and effectively restore wetland ecosystems (Ma et al. 2010).

Many wetland conservation studies have been conducted at the local scale (Flather and Sauer 1996); however, resource managers require large-scale studies in order to create conservation and management strategies that benefit entire landscapes (Haig et al. 1998). The use of remote sensing technology has been instrumental in developing conservation strategies that are useful at the landscape scale. For example, wetland inventories, based on remote sensing, allow for an understanding of how wetland loss has changed through time (Ozesmi and Bauer 2002) and have highlighted specific areas that may be most vulnerable to wetland loss (Doherty et al. 2015).

A number of tools, strategies, and policies have been put in place to help aid the conservation of wetland habitats. For example, the North American Waterfowl Management Plan (NAWMP) aims to conserve wetlands through water level manipulation, cattle exclusion, and the naturalization of uplands (NAWMP Canada 2013). Conservation agencies like Ducks Unlimited, Inc. have protected and restored wetlands across the continent in order to protect waterfowl populations (Vanausdall and Dinsmore 2019). Long-term inventory studies like Birds Canada's Great Lakes Marsh Monitoring Program (GLMMP) continue to inventory species use within wetlands, and have been useful in waterbird conservation by providing long-term abundance and occupancy data and informing patterns in species trends (Bird Studies Canada 2020). Programs such as these are imperative to the continued protection of important wetland habitats.

1.3 The Prairie Pothole Region (PPR) and Boreal Plains Ecozone (BPE)

1.3.1 Importance of the PPR and BPE to Waterbirds

The PPR is a landscape unique to North America, home to an approximate 5 to 8 million glacially formed wetlands (Millett et al. 2009) that exist within a mix of native grassland and agriculture (Johnson et al. 2005). Many of these wetlands are depressional and receive water by snowmelt or rain (Doherty et al. 2018). Covering approximately 800,000 square kilometers and spanning across southern Alberta, Saskatchewan, and Manitoba, as well as south into North Dakota, South Dakota, Minnesota, and Montana, the PPR with its abundance of wetland habitat is the most valuable and productive habitat in the world for waterfowl populations, hosting 50 to 80% of the North American duck population (Austin 2002, Johnson et al. 2005). The BPE is comprised of shallow lakes and ponds as well as wetland complexes characterized by peat deposits (Thompson et al. 2017). Covering approximately 740,632 square kilometers across areas of British Columbia, Alberta, Saskatchewan, and Manitoba, the BPE is dominated by coniferous forest, including black spruce, white spruce, jack pine, and tamarack (Smith et al. 2007).

Although many waterbird species are understudied compared to waterfowl, the importance of the PPR and BPE to waterbird populations remains clear. The PPR is a breeding stronghold for multiple families of waterbirds, including grebes, herons, rails, gulls, and terns (Steen et al. 2016). A large portion of many North American waterbird breeding populations are found in the PPR, with the landscape supporting over 60% of the Franklin's Gull (*Leucophaeus pipixcan*) population, and over 50% of Pied-billed Grebe (*Podilymbus Podiceps*), American Bittern (*Botaurus lentiginosus*), Sora (*Porzana Carolina*), American Coot (*Fulica americana*), and Black Tern populations (Niemuth and Solberg 2003). Further highlighting this importance, several endangered species and species of high conservation concern dependent on the PPR. Whooping crane (*Grus americana*) and Least Tern (*Sternula antillarum*), both listed as endangered species in the U.S. and Canada, as well as Western Grebe (*Aechmophorus occidentalis*), Franklin's Gull, Black Tern, Horned Grebe (*Podiceps auritus*), American Bittern, Yellow Rail (*Coturnicops noveboracensis*), and King Rail (*Rallus elegans*), species identified as of high concern by the Northern Prairie & Parkland Waterbird Conservation Plan, depend on wetland habitat provided by the PPR during breeding or migration (Prairie Pothole Joint Venture 2017). The BPE is also an important breeding area for many of North America's waterbird populations and contains some of the largest breeding populations of several colonial waterbird species, including cormorants, gulls, and terns (Wilson 2013). The southern portion of the BPE, in particular the boreal transition zone where wetland density is high, appears to be a hotspot for several marsh-nesting bird species (Prairie Habitat Joint Venture 2014). Despite the clear importance of the PPR and BPE for North American waterbird populations, this landscape is at risk, threatening the survival of waterbird species across the continent.

1.3.2 Wetland Loss in the PPR and BPE

Wetland loss in the PPR has already been significant, particularly in the U.S., with state wetland loss estimates during the 1980s of 89% in Iowa, 49% in North Dakota, 42% in Minnesota, 35% in South Dakota, and 27% in Montana (Dahl 1990). Less comprehensive data exist for Canada, but an estimated 40-70% of wetlands in the Canadian prairies have been lost since settlement (Dahl and Watmough 2007). The Prairie Habitat Joint Venture monitored wetland habitat change in the Canadian prairies, including areas in both the PPR and BPE, from 1985-2001 along 235,710 ha of study transects, finding gross wetland losses of 5%, and total net decline of individual wetlands equalling 5% (Watmough and Schmoll 2007). Overall, the authors estimated that annual rates of wetland loss were 0.31% in the Canadian prairies. Wetland degradation in the BPE has been extensive over the last 60 years, particularly along the region's southern edge (Bayley et al. 2013). Increased agricultural encroachment into the BPE has resulted in deforestation and land conversion for farming (Hobson et al. 2002). This process rapidly degraded wetlands through increases in agricultural runoff and nutrient accumulation, which can alter vegetation, biodiversity, and productivity of wetlands (Zedler and Kercher 2005).

The impact of agriculture has been and remains the most pervasive cause of wetland loss and degradation in this region (Doherty et al. 2018). A study of approximately 10,500 wetlands in the Canadian prairies examined the impact of agricultural activities on wetland habitat from 1985-2005 and found that recovery rates of wetlands were lower than rates of impact from agricultural activity, with shallow wetlands in areas of high agricultural activity experiencing higher impacts and lower recovery when compared to wetlands with higher water or in locations of lower agricultural intensity (Bartzen et al. 2010). Trends show that the percentage of wetland surface area loss is lower than the number of wetlands lost, as smaller more easily drained wetlands are typically converted first (Anteau 2012). This may be having disproportionate effects on waterbird species that depend on these smaller more ephemeral wetlands.

In addition to conversion and drainage, which in most cases completely destroy wetland habitats, agriculture can gradually degrade wetlands through wetland basin cultivation, a process that occurs during dry years. Prolonged cultivation and tillage of basins can destroy wetland plant community structure and composition and reduce wetland invertebrate populations, a key food source for many waterbird species (Prairie Pothole Joint Venture 2017). Furthermore, agricultural herbicides and pesticides can have direct and indirect effects on waterbirds and wetland ecosystem health. Pesticides such as carbofuran, chlorpyrifos, parathion, as well as increased use of neonicotinoids contaminate waterbird food sources, kill invertebrates that many waterbird species feed on, and can cause impaired migratory behaviour and direct mortality of avian species (Forsyth 1989, Gibbons et al. 2015, Eng et al. 2019). Wetland loss and degradation, particularly because of agricultural activity, is an ongoing issue in the PPR and BPE. Research on climate change impacts in the region has begun to reveal that wetland loss and impacts on waterbird species will continue to worsen in the future.

1.3.3 Climate Change Projections for Wetlands and Waterbirds in the PPR and BPE

Climate change research predicts that prairie pothole landscapes will be impacted by changes in temperature, alteration of wetland vegetation growing seasons, as well as variation in precipitation and snow cover levels and patterns. Climate change will likely speed the loss of wetlands through major reductions in water volume, shorter hydroperiods, and less diversity in wetland vegetation, resulting in even less habitat available for wetland-dependent species (Johnson et al. 2005, 2010). It is also possible that climate change will exacerbate the extreme wet-dry cycles that persist in the PPR, and threaten the unique and delicate hydrologic balance that exists within the BPE. This area is comprised of ecosystems that are particularly sensitive to changes in the timing and magnitude of precipitation, as well as increased evapotranspiration that may occur as a result of a longer and warmer growing season (Thompson et al. 2017).

Fluctuations in water levels drastically impact the landscape through the drying of wetlands and waterbodies. Waterbodies can fluctuate from open water lakes to dry marshes, and cycle durations can last anywhere from 5-35 years but more commonly occur every 10-20 years depending on drought (Weller and Spatcher 1965, Kantrud et al. 1989). This drastic annual change not only affects the water availability, but also the vegetation in a landscape (van der Valk 2005), and directly impacts the preferred breeding habitat for waterbirds. Although waterbirds are adapted to these wet-dry cycles, climate change could cause more extreme fluctuations to which birds are not adapted. Increased annual temperatures, altered precipitation and snowmelt, as well as increased evaporative demand are likely to reduce numbers of shallow wetlands in the PPR (Steen et al. 2016). Additionally, changes in wetland vegetation structure and composition may drastically reduce wetland functions if climate change induced temperature rise surpasses 1.5-2.0 degrees Celsius (Johnson et al. 2016). Furthermore, inundated wetland (when soil in the root zone is saturated with water) density is predicted to decline by 20-25% by mid-century based on projected future climactic conditions (Soafer et al. 2016). In the BPE, changes in climate may create conditions that result in the permanent drying of shallow lakes, ponds, and peatlands (Thompson et al. 2017). A warmer growing season and changes in precipitation (Thompson et al. 2017), as well as an increase in wildfire frequency (Flannigan et al. 2013) could permanently alter wetlands in the BPE (Alberta Dept. of Sustainable Resource Development 2009). Wetlands in the BPE, particularly peatlands, are important landscape features on both a regional and a global scale due to their carbon sequestration properties (Kleinen et al. 2012). Since 1948, annual temperatures across the BPE have risen between 1-3 degrees Celsius (Hengeveld et al. 2005). By the 2050s annual temperatures in the BPE may increase by another 2-5 degrees (Lemmen et al. 2008). These increased temperatures are likely to reduce the length of the snow-covered season, and overall snow cover levels, as well as reduce ground frost or frozen soil, resulting in greater changes in precipitation and evapotranspiration (Thompson et al. 2017).

As a result of these changes, waterbird species may lose important nesting and foraging areas, and may suffer from range contractions and/or changes to their migratory timing and duration. For example, it has been predicted that wetland dependant species in the PPR like Black Terns will lose up to 97% of suitable nesting sites by 2100 due to a decline in available wetlands caused by climate change (Steen and Powell 2012). Another study examined how wetland dependant waterbird, waterfowl, and shorebird species ranges in the PPR will change due to climate change and projected a decrease of -0.31 as a proportion of currently occupied range due to drying wetlands (Steen et al. 2016). Many long-distance migratory bird species, including waterbirds, depend on resources provided by the PPR and BPE in order to fuel migration (Skagen 2006). Fluctuations in wetland water levels may greatly reduce foraging opportunities (Skagen et al. 1999), and alteration to wetland vegetation may reduce the availability of foraging and nesting locations used by many waterbird species (Drilling 2007, Steen et al. 2016). In summary, climate change will drastically impact wetlands in this region, and as a result the waterbirds that depend on them.

My research focused on the North American Black Tern, a waterbird dependent on wetlands to breed, particularly those in the core of the range in the PPR (Steen et al. 2016). I aimed to understand both movements across the full annual cycle, and factors associated with breeding habitat. First, I used geolocators deployed at sites in the core of the Black Tern breeding range in Saskatchewan, and at sites on the periphery of the range in the Great Lakes Region, to uncover the first detailed migratory tracks of North American Black Terns and examine migratory connectivity across the range. Revealing the full annual cycle movements of Black Terns may provide insights into how populations are limited during migration, at migratory stopover sites, or at wintering locations. Second, I examined the influence of various habitat, land use, and geographic covariates on Black Tern breeding occupancy and abundance in Saskatchewan. Understanding breeding habitat associations can reveal the factors that influence the presence of a species across the landscape and begin to inform the most important areas and habitat features to protect in order to conserve the species.

1.4 Study Sites

Study sites included in the habitat association study focused on wetlands and waterbodies that fall within Saskatchewan, more specifically, Bird Conservation Region (BCR) 11, the Prairie Pothole Region and the Boreal Plains Ecozone portion of BCR 6, the Boreal Taiga Plains. The Canadian portion of BCR 11 extends from the Rocky Mountains in Alberta to the Red River Valley in Manitoba, and from the Canadian border to the southern edge of the boreal forest (ECCC 2013a), encompassing a significant portion of the species' breeding range (Heath et al. 2020). BCR 6 encompasses two ecozones, the Taiga Plains and the Boreal Plains, and extends from the Northwest Territories into Alberta, Saskatchewan, and Manitoba to the south, as well as slightly west into the eastern Yukon and British Columbia (ECCC 2013b). As a result of long-term declining population trends, Black Terns were listed as a priority species in both BCRs, with population objectives of "increase by 100%" (ECCC 2013a, 2013b).

Geolocator deployment sites consisted of five Black Tern breeding colonies in lakes and wetlands located in central and eastern North America. Colonies were located in Saskatchewan and Ontario, Canada, and Michigan, USA. From west to east, study sites included a stretch (~750 m) of marsh-fringed shoreline in Jackfish Lake, a large recreational lake located in south-western Saskatchewan (53.132391, -108.426024), Bricksaw Marsh, a (~15 ha) semi-permanent wetland located on private land near Foam Lake in south-eastern Saskatchewan (51.779793, -103.585164), a (~4 ha) section of hemi-marsh in Good Spirit Lake, a large recreational lake located in south-eastern Saskatchewan (51.551698, -102.629302), St Claire Flats, the world's largest freshwater delta (~25000 ha) located in eastern Michigan (42.585636, -82.639688), and Tiny Marsh a (~600 ha) managed wetland within a provincial wildlife area located in southern Ontario (44.60666 , -79.93516).

1.5 Study Species

Black Terns (*Chlidonias niger*) belong to the order Charadriiformes, family Laridae (gulls and terns), and subfamily Sterninae. There are two recognized subspecies: *Chlidonias niger surinamensis,* found in North America and *C. niger niger*, found in Eurasia (Kudell-Ekstrum 2004). Approximately 23-28 cm in size and 50-60 g in weight, with a wingspan of 57-65 cm, the Black Tern is distinctive with a black bill, head, neck, and breast; grey back, belly, upperwing and tail; white vent and undertail-coverts; and legs blackish red (Heath et al. 2020). The North American Black Tern subspecies is a localized breeder, mostly between latitudes 40–

60°N, from the northern U.S. through south and central Canada (Heath et al. 2020). They breed in all provinces of Canada except Prince Edward Island and Newfoundland, and from southwestern and east-central British Columbia and south-central Mackenzie to southern Quebec and southern New Brunswick (Kudell-Ekstrum 2004). In the U.S. they breed from south-central California and northern Utah, Wyoming, Nebraska, Kansas, south-central Illinois, Indiana, Ohio, Pennsylvania to northern New York, northern New England, and Maine (Kudell-Ekstrum 2004). During the winter, Black Terns are most commonly found in marine and coastal marine areas of Central and South America, on both the Pacific and Caribbean seas (Heath et al. 2020). Black Terns overwinter along the south Pacific coast to Panama, and south of the Gulf coast through Central America to northern South America (Kudell-Ekstrum 2004). General breeding habitat consists of freshwater marshes with emergent vegetation such as sloughs and lake margins, as well as river or island edges (Greenberg 1972). Diet on the breeding grounds consists mainly of insects such as dragonflies, mayflies, and caddisflies. During the non-breeding season, Black Terns feed on insects while occupying coastal or inland habitats, but mainly feed on small fish such as sardines and anchovies while occupying pelagic habitats (Heath et al. 2020).

The genetic structure and gene flow of the North American Black Tern population remains unknown, although recent genetic analysis suggest that the North American population displays a lack of genetic structure. In contrast, a genetic analysis of Black Terns across Eurasia showed that they exhibited strong genetic and morphological differentiation likely due to the use of discrete staging sites along distinct migratory flyways on the way to a widely dispersed wintering distribution along the west coast of Africa (Szczys et al. 2017b). Given the continuous though patchy distribution of Black Terns across the continents and the high mobility of the species, gene flow must have been restricted outside of the breeding season.

The Black Tern is a declining species with little information on its ecology, which is key to understanding causes of population decline and to identify priorities for conserving and protecting the North American population. I chose the Black Tern as my focal study species because it is a priority species in Saskatchewan. With a declining annual population trend of -2.96%/year (CI: -1.32 – -4.49, 1970-2019) across the breeding range (Smith et al. 2020) and a population that is approximately one-third the size of what it was in the 1960s (Stephens et al. 2015), the Black Tern is a species of high conservation interest. The Black Tern is an understudied species with little information regarding the full annual cycle, where population limitation is occurring, and how populations are connected across North America. With virtually no band-resighting data and little information on migration timing, routes, stop-over sites, or the range and environmental conditions of over-wintering locations, it is possible that preferred habitats are being lost or degraded and/or threats to Black Tern populations are occurring outside of the breeding season across the range. My research will aim to fill these gaps in data regarding the Black Tern full annual cycle by tracking the migratory movements of individuals from across the breeding range, and examining breeding habitat associations in the core of the range. Finally, the Black Tern can be considered a potential indicator of prairie ecosystem health, as changes in Black Tern populations may provide insight into the health of wetlands in the prairies (Amat and Green 2010). Further understanding Black Tern habitat associations may benefit the large numbers of waterbirds, waterfowl, and shorebirds that also utilize these habitats and resources, or are impacted by similar threats (Steen et al. 2016).

1.6 Research Objectives

My thesis evaluates Black Tern colony habitat features and migratory movement patterns during the full annual cycle for birds breeding in Saskatchewan, Ontario, and Michigan. My specific thesis objectives were to:

1) Use wetland survey data and aerial imagery to examine the influence of various habitat, land use, and geographic covariates on Black Tern occupancy and abundance in Saskatchewan (chapter 2).
2) Examine full annual cycle movements and potential differences in migratory stop-over and over-wintering locations from Black Terns breeding across their range at three colonies in central (Saskatchewan, Canada) and eastern (Ontario, Canada and Michigan, USA) North America using light-level geolocators (chapter 3).

CHAPTER 2

ASSESSING BLACK TERN HABITAT ASSOCIATIONS IN SASKATCHEWAN USING AERIAL IMAGERY

2.1 Introduction

Waterbird populations are declining across the globe (Wendt et al. 2006, Wetlands International 2010). Major factors contributing to waterbird population declines include habitat loss and alteration due to agriculture, biological resource use such as overfishing, and natural system modification through wetland drainage (Kirby et al. 2008). These factors could be especially acute for marsh-obligate waterbird species, as specific habitat traits such as sensitive marsh vegetation and wet-dry cycles result in vulnerable ecosystems that are highly susceptible to changes in water levels and surrounding landscape uses (Tozer et al. 2020).

Anthropogenic disturbance to wetland habitats, including marshes, is especially pronounced in the North American Prairies, an area that has experienced decades of land conversion for agriculture use, wetland drainage, and agrochemical runoff. This area is also home to a majority of the continental population of many waterbird species which rely on these wetland habitats (Rashford et al. 2011, Matteson et al. 2012, Doherty et al. 2018). Wetlands in the Prairie Pothole Region (PPR) have already experienced substantial declines, with wetland loss estimates throughout the 1980s of 89% in Iowa, 49% in North Dakota, 42% in Minnesota, 35% in South Dakota, and 27% in Montana (Dahl 1990). Areas of the northern prairies, known as the Boreal Plains Ecozone (BPE) have also experience significant wetland degradation over the past 60 years, with annual rates of land conversion for agriculture ranging from 0.87% to 1.76% per year over the past three decades (Hobson et al. 2002, Bayley et al. 2013). The Prairie

Habitat Joint Venture monitored wetland habitat change in the Canadian PPR and BPE from 1985-2001 along 235,710 ha of study transects and found gross wetland losses of 5%, as well as a total net decline of individual wetlands equalling 5% (Watmough and Schmoll 2007). A study of approximately 10,500 wetlands in the Canadian PPR and BPE examined the impact of agricultural activities on wetland habitat from 1985-2005, finding that recovery rates of wetlands were lower than rates of impact from agricultural activity. Furthermore, shallow wetlands in areas of high agricultural activity experienced higher impacts and lower recovery when compared to wetlands with higher water or in locations of lower agricultural intensity (Bartzen et al. 2010). Finally, it is expected that climate change will likely speed the loss of wetlands through major reductions in water volume, shorter hydroperiods, and less diversity in wetland vegetation, resulting in even less habitat available for wetland-dependent species (Johnson et al. 2005, 2010).

Largely as a result of this wetland habitat loss, over a dozen marsh-obligate bird species of the Canadian PPR and BPE are considered priorities for conservation, including several species listed federally as Species at Risk and others with declining population trends (ECCC 2013a, 2013b). As threats to wetlands become increasingly pervasive, understanding associations between waterbirds and their wetland and marsh habitats can help inform sites of conservation priority. Increasing marsh density within a landscape, decreasing anthropogenic development and activity around wetland habitat, and decreasing presence of invasive plant species are among the most important factors impacting the occupancy and abundance of different waterbird species within wetland habitats (Smith and Chow-Fraser 2010, Tozer 2016, Wyman and Cuthbert 2017). The availability of food resources at wetlands may also be an important factor impacting waterbird populations. A review of global insect declines predicted the extinction of 40% of the world’s insect species over the next few decades, including many generalist species such as dragonflies (Sánchez-Bayo and Wyckhuys 2019). These insect declines are largely a result of habitat loss due to intensive agriculture and urbanization as well as pesticide and fertilizer use, stressors that are common in the prairies. Recent study has noted the decrease of available insect food for chicks, specifically dragonflies, and this is hypothesized as a major cause for Black Tern declines in the Netherlands (Beintema et al. 2010). In the Great Lakes region of North America, recent work has made use of long-term monitoring to identify species-habitat relationships for obligate marsh-nesting species in an effort to identify priority areas for conservation (Tozer et al. 2020). For example, the occupancy of American Bittern (*Botaurus lentiginosus*), Common Gallinule (*Gallinula galeata*), Least Bittern (*Ixobrychus exilis),* Marsh Wren (*Cistothorus palustris*), Pied-Billed Grebe (*Podilymbus podiceps*), and Sora (*Porzana carolina*) all increased with the presence of marsh habitat. In order to mitigate the threats faced by Black Terns in Saskatchewan it is critical to understand these habitat associations.

The Black Tern (*Chlidonias niger*) is an obligate marsh-breeding colonial waterbird. The North American Black Tern population has experienced population declines of up to 70% across its range over the past century (Shealer et al. 2006). Black Tern population density is highest in the PPR, an area that is often thought to be the “core” or “stronghold” for North American Black Terns as well as other waterbird species (Steen et al. 2016). Abundance also appears to be high where the PPR transitions to the BPE, an area known as the boreal transition zone (Fink et al. 2020). Based on data from the North American Breeding Bird Survey, Black Tern populations in the PPR and BPE have experienced long-term annual declines of -2.73%/year and -2.89%/year, respectively, from 1970-2019 (Smith et al. 2020), and research suggests that habitat loss and degradation are important factors contributing to these population declines (Naugle et al. 1999, Naugle et al. 2000). Although there is a lack of Canadian PPR data, Black Terns in the U.S. PPR have been predicted to lose up to 97% of suitable nesting sites by 2100 due to a decline in available wetlands caused by climate change (Steen and Powell 2012). Habitat association studies have been useful in uncovering habitat preferences as well as factors that negatively impact Black Tern occupancy in certain regions throughout the range, allowing researchers to identify the wetland traits most critical for Black Tern presence and create a framework for conservation targeted in those areas.

Black Tern habitat association studies have identified both large-scale factors such as wetland density, and local-scale factors such as vegetation type at wetlands, as important for Black Terns in the Great Lakes and the U.S. PPR (Naugle et al. 1999, Naugle et al. 2000, Steen and Powell 2012, Shealer and Alexander 2013, Wyman and Cuthbert 2016). These differences in the scale of important habitat features provide support for hierarchical habitat selection, whereby individuals first locate home range habitat based on large-scale geographic features, and then select specific local habitat features for needs such as nesting and foraging (Johnson 1980, Mayor et al. 2009, McGarigal et al. 2016). Despite these general findings, there appear to be some regional differences in specific habitat associations across the range. In the U.S. Great Lakes region, landscape suitability indices revealed that landscapes with higher availability of foraging wetland habitat within 2 km were more likely to host Black Terns colonies (Wyman and Cuthbert 2016). In Wisconsin, Black Tern presence was higher in wetlands characterized by a mix of open water and aquatic vegetation (Shealer and Alexander 2013). At a local scale, Black Tern presence was positively associated with the extent of emergent aquatic vegetation at individual wetlands in both the U.S. PPR and Great Lakes Region (Shealer and Alexander 2013, Steen and Powell 2012). One study using aerial imagery to assess wetland habitat for Black Tern presence in Wisconsin found suitable sites more likely to be associated with type 2 wetlands (a mix of open water and aquatic vegetation) and lower levels of human disturbance (Shealer and Alexander 2013). The same factors were also important in North and South Dakota, in addition to wetland size (Steen and Powell 2012).

Temporal trends in Black Tern abundance and site occupancy suggest that limited breeding habitat may be a contributing factor in population declines in some regions. For example, findings from both the Great Lakes Colonial Waterbird Survey and the Wisconsin Black Tern Survey showed a greater decline in the number of occupied Black Tern colony sites rather than total population size within each survey region, suggesting a concentration of birds in remaining suitable habitat, rather than a net loss of individuals (Cuthbert and Wires 2013, Matteson et al. 2012). In contrast, other studies have shown that large portions of seemingly suitable Black Tern breeding habitat remained unoccupied. In the U.S. Great Lakes region, a landscape suitability index created for Black Terns predicted that colony occupancy was less than 20% at sites that were deemed highly suitable (Wyman and Cuthbert 2016). A large study of 800 wetlands in South Dakota used remote sensing and GIS to predict wetland site suitability for Black Terns and found that only 22% of the wetlands classified as suitable were occupied (Naugle et al. 2000). Similarly, in Wisconsin, Black Terns were present at 47% of the sites considered suitable and 11% of the sites considered marginal or unsuitable (Shealer and Alexander 2013). Taken together, these findings highlight potential regional differences in important habitat characteristics and existing challenges in predicting Black Tern site occupancy.

One issue that could be driving the difficulty in predicting Black Tern site occupancy is the tendency towards low site fidelity and movement of individuals and colonies from year to year. Based on long-term banding data at a site in Wisconsin, only 77 of 728 (11%) adult Black

Terns banded and released between 1999 and 2006 were recaptured at least once (Shealer 2007). Furthermore, Black Tern chicks banded and later recaptured as adults were all found in different locations than those in which they were originally reared, suggesting that chicks are not bound to their natal sites (Shealer 2007). The same patterns have been found in other inland-breeding colonial waterbirds (e.g., Least Terns, Common Terns, American White Pelicans, Heron spp.; Renken and Smith 1995, Tims et al. 2004, Becker et al. 2008, Reudink et al. 2011, Mashiko and Toquenaga 2018).

In this study, I used wetland survey data and aerial imagery to examine the influence of various habitat, land use, and geographic covariates on Black Tern occupancy and abundance in the PPR and BPE regions of Saskatchewan, Canada. I predicted that wetland area and extent of emergent aquatic vegetation would positively influence, whereas the degree of human encroachment surrounding a wetland would negatively influence, the probability of Black Tern presence and abundance. Although habitat association studies have been conducted elsewhere in the Black Tern breeding range, similar studies are lacking in Saskatchewan – essentially the core of the breeding distribution (Fink et al. 2020). It is possible that large-scale features might create differences in the factors associated with occupancy and abundance across the range. For example, extreme wet-dry cycles dictate wetland abundance in the Canadian PPR, an influence that is not present in the Great Lakes region. Landscape level assessment of Black Tern habitat suitability is a critical first step towards developing management plans that prioritize Black Tern habitat.

2.2 Methods

2.2.1 Study Area

I selected study sites by using an existing database of wetlands compiled by McKellar et al. (2019) that identified the historic presence and abundance of breeding colonies of several waterbird species at wetlands across the Canadian prairies (Alberta, Saskatchewan, and Manitoba). In brief, the database was compiled from various sources, including scientific reports and data published by the Canadian Wildlife Service, Manitoba and Saskatchewan Conservation Data Centres, the Alberta Fisheries and Wildlife Management Information System, as well as citizen science resources such as eBird. Target species included Western Grebe (*Aechmophorus occidentalis*), Franklin's Gull (*Leucophaeus pipixcan*), Black Tern, Forster's Tern (*Sterna forsteri*), and Black-crowned Night-Heron (*Nycticorax nycticorax*). Data collected relevant to the current study included the presence or absence of a breeding colony of each species, the number of adults of each species at a colony, and the name and geographic coordinates of each colony location. For the current analysis, I restricted the wetland sites to those where Black Tern colonies did or did not occur during the period between 2007-2017. An additional six wetland sites discovered through ground-based surveys during the 2019 and 2020 field seasons were also included. For this study, I restricted the analysis to only those sites that fell within the province of Saskatchewan, for a total of 68 wetlands.

It should be noted that as a result of the wetland selection process, wetlands included in my study were not a random selection of used versus available wetlands on the landscape, and thus I did not attempt to create habitat selection or species distribution models. Rather, my goal was to examine the factors that influence the occupancy and abundance of Black Terns at the types of wetlands that are generally suitable for waterbird species in Saskatchewan.

2.2.2 Habitat Characteristic Assessment

Habitat characteristics of wetlands were assessed using aerial imagery from two sources: Google Earth and FlySask2, the Saskatchewan Geospatial Imagery Collaborative (Google, n.d., FlySask2.ca 2021). FlySask2 provides high resolution, up to date aerial photography for many rural or remote areas of Saskatchewan that are often missed by other imagery platforms (FlySask2.ca 2021). Although FlySask2 imagery provides high quality orthoimages for much of Saskatchewan, coverage is not consistent, and some locations are not included. As a result, Google Earth was used when FlySask2 was insufficient. Black Terns in Saskatchewan breed in late June to early July. Thus, if multiple images for a single site were available, images captured during the summer months (June-August) were given priority over those captured during other parts of the year in order to collect images that best represented Black Tern breeding habitat. Twenty-three of the 68 wetlands were analysed using FlySask2 with imagery dates ranging from 2008-2021 and fell within the June-August month range. Forty-five wetlands were analysed using Google Earth, with dates beginning on 18 June 2003; imagery for 20 wetlands fell within the June-August month range and 25 fell outside of the range. Despite the use of different imagery platforms, habitat characteristics did not differ substantially when I tested a subset of wetlands that had both sets of imagery available during the summer months.

Previous work by Shealer and Alexander (2013) used aerial imagery to assess habitat suitability and predict site occupancy of Black Terns in Wisconsin. The authors used habitat features assessed via aerial imagery to group wetlands into suitability rankings and then used ground-based surveys to determine occupancy at ranked wetlands. My study was similar in approach in the use of aerial imagery for assessment of habitat characteristics, and in the habitat covariates I selected to predict Black Tern occupancy as well as abundance. I measured four habitat covariates at each wetland site: the total area of the wetland, the extent of emergent vegetation present at each wetland, wetland classification, and the degree of anthropogenic encroachment surrounding each wetland. First, polygons were constructed around wetland perimeters to calculate total wetland area (km^2) using the measure tool in Google Earth. I considered the perimeter of a wetland as the point where open water or emergent aquatic vegetation stopped and dry land or terrestrial vegetation began. Next, I calculated the total extent of emergent aquatic vegetation for each wetland by estimating the percentage of the wetland area within the polygon populated by aquatic vegetation. These estimations were placed into one of five categories: 0 (no aquatic vegetation present), <25%, 26-50%, 51-75%, or >75%. Next, wetlands were inspected visually and identified as one of four wetland classes, based on the Stewart and Kantrud wetland classification system (Stewart and Kantrud 1971): class 2 (temporary ponds), class 3 (seasonal ponds/lakes), class 4 (semi-permanent ponds and lakes), or class 5 (permanent ponds and lakes). Finally, the degree of human encroachment surrounding each wetland (within 1 km) was inspected visually and classified into four categories: no disturbance (wetlands with no evidence of human use), minimal disturbance (wetlands with small or private accessibility), agricultural (wetlands bordering or in close proximity to farmland), or recreational/urban/agricultural (wetlands bordering or in close proximity to houses/buildings, with cottages and docks, or with evidence of high human activity; or any of the preceding in combination with farmland). In the final analysis, I combined no disturbance and minimal disturbance categories into a single category (minimal disturbance), as there were only two completely undisturbed wetlands in my database.

2.2.3 Data Analysis

My general approach involved first analyzing Black Tern occupancy using a Bernoulli generalized linear model, then analyzing Black Tern occupancy and abundance combined using a zero altered negative binomial model, also called a hurdle model. For both the Bernoulli and the hurdle analysis, I analyzed two separate types of models: those that involved spatial covariates, and those that involved habitat covariates. This allowed me to test whether the habitat covariates I collected were good predictors of Black Tern occupancy and abundance or if spatial patterns surpassed them, which might be reflective of landscape-scale factors not captured in the analysis or that colony occupancy/abundance is difficult to predict using habitat indicators.

In addition, due to my sample size of 68 wetlands, I was limited to including up to ~ 4 covariates in a single model (i.e., general rule-of-thumb is that 10-15 data points per regression parameter are recommended; Crawley 2012). Thus, by creating separate spatial and habitat models, I was able to directly test the predictive ability of one type of model versus the other, while avoiding over parametrizing my models given my sample size.

2.2.3a Bernoulli analysis of occupancy only

I used a Bernoulli generalized linear model (R package "plyr" [Wickham 2011]) to analyze Black Tern occupancy (1-0) in relation to spatial and habitat covariates. A Bernoulli generalized linear model is preferred over other generalized linear models as it is ideal for analyzing binary data, such as occupancy data, where the observed response is either one (occupied) or zero (not occupied). This type of GLM uses a Bernoulli distribution. The full spatial model included the effects of latitude, latitude^2, and longitude. Latitude^2 was included because a potentially strong non-linear effect of latitude was discovered during data exploration. The full habitat model included main effects of wetland area, the extent of emergent aquatic vegetation within a wetland, wetland classification, and the degree of anthropogenic encroachment surrounding a wetland. I used Akaike's Information Criterion (AIC) for model selection. The model selection process was done by manually removing covariates from the full models and comparing the AIC values of sub models. All possible covariate combinations were considered during this process, as well as a null model, and the final models (spatial and habitat) were considered as the ones with the lowest AIC value. I considered covariates to be important if in the final model, the confidence intervals of their parameter estimate did not overlap zero. I chose to base my conclusions on the final model with the lowest AIC score, although an alternative would be to assess parameter estimates from competitive models using model averaging. However, doing so does not change the final results substantially. A further benefit of focusing on a single best model is that this allowed me to directly compare the AIC of the final spatial and habitat models.

I verified model assumptions using the “binnedplot” function from the “arm” package (Gelman et al. 2020). This is a function that plots the averages of a y-value (residual values from the logistic regression) against the averages of an x-value (expected values from the logistic regression). The “binnedplot” function deals with the discrete nature of the logistic regression residual values by dividing the data into categories (bins) based on their fitted values and plotting the average residual versus the average fitted value for each bin (Gelman et al. 2020).

2.2.3b Hurdle model: combined analysis of occupancy and abundance

Next, I used a hurdle model (R package “pscl” [Zeileis et al. 2008]) to analyze Black Tern abundance in relation to both spatial and habitat covariates. A hurdle model is a two-step model which includes both a presence-absence “part” and a positive abundance “part”, in which data are restricted to occupied sites only (i.e., all zero values removed). A hurdle model is ideal when working with abundance data, which is often zero-inflated (an excess of zeroes in the data), something that a standard regression model is not, as it assumes the equal dispersion of all data within a dataset (Potts and Elith 2006). Another benefit of the hurdle model is the possibility to include and evaluate different covariates in both the presence-absence and the abundance response parts of the model, as occupancy and abundance may be driven by different factors. With a hurdle model, results show a combined AIC value and parameter estimates of both occupancy and abundance together. I used a Bernoulli distribution for the occupancy part of the model, and a negative binomial distribution for the abundance part of the model. As above, the full spatial model included main effects of latitude, latitude^2, and longitude for both the absence-presence and abundance parts of the hurdle model. The full habitat model included main effects of wetland area, the extent of emergent aquatic vegetation within a wetland, wetland classification, and the degree of anthropogenic encroachment surrounding a wetland for both the absence-presence and abundance parts of the hurdle model. I used the same procedure as above to determine the model with the lowest AIC for each type of model (spatial and habitat), except this time considering every combination of each covariate being either included or not included in the presence-absence or abundance parts of the model, as well as null models. As above, I considered covariates to be important if in the final model, the confidence intervals of their parameter estimate did not overlap zero; evaluating parameter estimates using model-averaging of competitive models did not alter the results substantially. Once a final spatial and habitat model were determined, they were also compared via AIC.

I verified model assumptions by checking models for overdispersion and evaluating model fit by comparing residual values to fitted values and continuous covariates; I did not detect any violation of model assumptions. I conducted all statistical analysis using R v. 3.5.2. (R Development Core Team 2021).

2.3 Results

The database was comprised of 68 wetlands, of which 25 (37%) contained Black Tern colonies (Fig. 2.1). All wetlands were located within the province of Saskatchewan and ranged between 49° 5' 24" to 55° 35' 24"N and 110° 0' 0" to 101° 24' 36"W. Of the total 68 wetlands, 53 sites (78%) fell with the PPR, and 15 sites (22%) fell within the BPE. Wetland areas ranged from 19.15 – 86267 km^2 with a mean of 11051 km^2. When identifying the emergent wetland vegetation categories, 34 wetlands fell into category two (<25%), 18 fell into category three (26-50%), nine fell into category four (51-75%), and seven fell into category five (>75%). Only class 4 (n = 9) and 5 (n = 59) wetlands occurred in the database. For the degree of human encroachment categories, seven wetlands fell into the minimal disturbance category, 27 fell into the agricultural category, and 34 fell into the recreational/urban/agricultural category.

2.3.1 Associations between Wetland Characteristics and Colony Occupancy

Based on AIC model selection, the best spatial model included the effects of latitude, $latitude^2$, and longitude (Table 2.1). Confidence intervals for the effects of latitude and $latitude^2$ did not overlap zero and indicated that colony occurrence was positively associated with latitude and negatively associated with $latitude^2$. In other words, there was a strong non-linear effect of latitude, whereby colony occurrence was highest at mid-latitudes in Saskatchewan, but lower in the far north and south of the province (Table 2.2; Figs 2.1 and 2.2). The confidence interval for longitude did overlap zero, indicating that this covariate did not have an important influence colony occurrence. Based on AIC model selection, the best habitat model included only the effect of extent of emergent aquatic vegetation (Table 2.1). Confidence intervals for the effect of extent of emergent aquatic vegetation did not overlap zero and indicated that colony occurrence was positively influenced by the percentage of emergent vegetation coverage at a wetland (Table 2.2; Fig. 2.3). Other models within 4 AIC of the top model included effects of wetland area and wetland class. Comparing AICs of the final two models showed that Black Tern colony occurrence was better described by the spatial model (AIC = 75.75) than the habitat model (AIC = 86.09).

2.3.2 Associations between Wetland Characteristics and Colony Occurrence/Abundance Combined

Based on AIC model selection, all three spatial covariates were present in the best presence-absence (occupancy) part of the spatial hurdle model, but only the confidence intervals of latitude and latitude^2 did not overlap zero (Tables 2.3 and 2.4). For the abundance part of the hurdle model, the best spatial model also included the effects of latitude and latitude^2 (Table 2.3). Like the occurrence model, Black Tern colonies with higher abundance fell at mid-latitudes in Saskatchewan, but colonies with lower abundance more north and south (Table 2.4; Fig. 2.1). The best habitat model included extent of emergent aquatic vegetation in the presence-absence (occupancy) part of the hurdle model, and wetland area within the abundance part of the hurdle model (Table 2.3). Confidence intervals of wetland area did overlap zero indicating that this covariate did not have a strong influence on abundance; however, confidence intervals of aquatic vegetation did not overlap zero. In other words, extent emergent aquatic vegetation had a positive association with colony occupancy (Tables 2.3 and 2.4). Other models within 4 AIC of the top model included many combinations of habitat variable effects, however extent of emergent aquatic vegetation appeared as an effect in the occupancy or abundance parts of all but one of these models. Comparing AICs of the final spatial and habitat models revealed that Black Tern abundance was better described by the spatial hurdle model (AIC = 303.66) than the habitat hurdle model (AIC = 313.62).

2.4 Discussion

Black Tern populations are declining across their range, but here I demonstrate that colony occurrence and abundance in Saskatchewan can be predicted using both geographic and habitat models, which presents an important tool for identifying and protecting colony locations. I found that the latitude of a wetland was strongly associated with colony occurrence and abundance. This relationship was quadratic, indicating that there is a narrow latitudinal band within which individuals seem to be occupying wetlands, resulting in higher rates of occupancy and abundance at wetlands along mid latitudes, with lower rates at higher and lower latitudes. Additionally, the extent of emergent aquatic vegetation present at a wetland was associated with an increased likelihood of occupied Black Tern colonies. The importance of aquatic vegetation for Black Tern breeding habitat has been established in other parts of the range, but this is the first time this pattern has been identified in Saskatchewan.

2.4.1 Predicting Colony Occupancy and Abundance Using Spatial Covariates

My findings provide evidence that Black Terns are selecting breeding habitat at multiple scales, a pattern of site selection that has been noted in other animal species (Johnson 1980, Mayor et al. 2009, McGarigal et al. 2016). Results suggest that individuals may first be locating breeding sites based on large-scale landscape features driven by latitude, and then selecting specific wetland locations for breeding based on small-scale features such as emergent aquatic vegetation. Indeed, previous Black Tern habitat association studies have noted the importance of habitat features at multiple scales, both large and small (Naugle et al. 1999, Shealer and Alexander 2013, Wyman and Cuthbert 2016).

I uncovered a quadratic relationship between latitude of a wetland and the likelihood of Black Tern colony occurrence. Unlike the habitat variables, wetland latitude was similarly associated with Black Tern abundance at colonies; indeed, wetland latitude was a stronger predictor of Black Tern occurrence and abundance than any habitat covariate. It is possible that large-scale landscape variables could be driving this relationship. Although all wetlands were located within the species' range, the range extends north into boreal ecozones, and habitat suitability is likely limited by the boreal forest in the north. However, this pattern does not account for the reduction in abundance/occupancy in the most southern wetlands in my analysis. Rather, the high abundance and occupancy at mid-latitudes could in part be driven by variation in wetland density, which tends to increase when moving from the grasslands north into the parklands and boreal transition zone. It is because of the wetland density in central North America that the PPR has been considered the stronghold for waterbird species like the Black Tern (Steen et al. 2016), and in the Great Lakes Region, occupancy increases with wetland density and connectivity to larger wetland systems (Shealer and Alexander 2013, Wyman and Cuthbert 2016). As wetland density increases, so does the presence and abundance of insect species, many of which may used as food sources for Black Terns (Sánchez-Bayo and Wyckhuys 2019). It is possible that the increased presence and abundance of Black Terns in landscapes with high wetland density is also related to the increase in food availability within these landscapes. Similar to my findings, occupancy and abundancy of several other marshbird species were found to be highest in the northern portion of the Canadian PPR and boreal transition zone (Prairie Habitat Joint Venture 2014).

The distribution of Black Terns in Saskatchewan may also be related to cyclical prairie droughts. These fluctuations in water levels drastically affect the landscape through the drying of wetlands and waterbodies. Waterbodies can fluctuate from open water lakes to dry marshes, and cycle durations can last anywhere from 5-35 years but more commonly occur every 10-20 years

(Weller and Spatcher 1965, Kantrud et al. 1989). These extreme multi-annual changes not only affect water availability, but also the vegetation in a landscape (van der Valk 2005), which would have a direct impact on the preferred breeding habitat for Black Terns. In dry years, individuals may be forced to range further north towards wetter areas of the breeding range in the northern prairies (Sirois and Fournier 1993). Thus, it is possible that due to unpredictability in the location and suitability of wetlands across years, Black Terns in this region tend to select sites in the mid-latitude areas where wetland density is greatest even during drought years.

Large-scale geographic patterns could also be explained by species range dynamics. Species are often most abundant at the core of their geographical range and become less abundant towards the periphery ('abundant-center hypothesis'; Lawton 1993, Sagarin et al. 2006). Such a pattern may occur if populations at the core of the species range act as a source for the population where the highest quality habitat exists, and habitat quality declines while dispersal distances increase towards the peripheries of the range (Guo et al. 2005, Hargrove and Rotenberry 2011).

2.4.2 Predicting Colony Occupancy and Abundance Using Habitat Covariates

At a smaller scale, previous studies have noted the importance of aquatic vegetation for Black Tern occupancy and abundance, similar to my findings (Naugle et al. 2000, Steen and Powell 2012, Shealer and Alexander 2013). Black Terns prefer wetlands in hemi-marsh conditions, with an equal mix of open water and aquatic vegetation for nesting (Bergman et al. 1970, Brown and Dinsmore 1986, Hickey and Malecki 1997). Habitat association studies from Wisconsin and North and South Dakota have found presence or extent of emergent aquatic vegetation at a wetland to be important in predicting Black Tern occurrence (Naugle et al. 2000, Steen and Powell 2012, Shealer and Alexander 2013). In Wisconsin, Black Tern occurrence was associated with wetlands that had hemi-marsh conditions, that were part of a larger wetland system, and that had minimal human encroachment. In North and South Dakota, Black Tern occupancy was associated with wetlands defined by a mix of aquatic vegetation and open water (Steen and Powell 2012), and in in South Dakota, Black Tern occupancy was associated with wetlands that had hemi-marsh conditions (Naugle et al. 2000). In contrast, I did not find any association with Black Tern abundance or occupancy and wetland area or human disturbance. The lack of association between Black Tern occupancy and abundance and wetland area has been noted previously in Wisconsin (Shealer and Alexander 2013). Although some authors have found this to be an important association (Wyman and Cuthbert 2016), contrasting studies have noted the importance of wetland density within a landscape, rather than specific wetland size (Shealer and Alexander 2013). The lack of a relationship in my study between Black Tern occurrence or abundance and the degree of human encroachment surrounding a wetland could have been due to the sample sizes of disturbed and undisturbed wetland sites in my database; of the 68 wetlands included in my analysis, only seven were considered minimally disturbed. Much of the landscape in southern Saskatchewan, particularly in the PPR, is dominated by agriculture, resulting in most wetlands being disturbed by human activity at least to some degree (Doherty et al. 2018). Our results suggest that Black Terns are able to tolerate the range of human disturbance present at wetland sites in my analysis. Since my analysis relied on wetlands that had been occupied by at least one of five focal waterbird species based on the McKellar et al. (2019) database, it is likely that extremely disturbed wetlands would not have been included at all, and these may be sites that Black Terns would avoid. I also did not find any association between wetland class and Black Tern occupancy or abundance. Similar to the above, my analysis was restricted to class 4 and 5 wetlands, because these were the only sites that had been occupied by at least one of the focal species in the McKellar et al. (2019) database. Thus, my analysis did not include potentially unsuitable wetlands and was restricted to those with certain characteristics already established as preferred by Black Terns (Shealer and Alexander 2013). An additional caveat is that imagery acquisition was dependent on what was available from Google Earth or FlySask2, and thus would not likely have corresponded to the exact year of colony occupancy during the period 2007-2017. Given that wetland characteristics can change over time due to annual water level fluctuations, it is possible that the habitat covariates I measured did not correspond exactly to what the birds experienced during the year of colony occupancy. However, this variation would have been more prominent at lower wetland classes compared to the class 4 and 5 wetlands included in my study. Future studies using a larger sample of randomly selected wetlands, including both suitable and less suitable sites, may be able to tease apart relationships between human disturbance and wetland type on Black Tern occupancy and abundance in Saskatchewan.

Although habitat association studies similar to ours have been conducted previously in other parts of the Black Tern breeding range, my study demonstrates the benefit of using existing survey data alongside aerial imagery to identify important habitat characteristics for the species. Using aerial imagery appears particularly useful for species like Black Terns where the most important habitat features for predicting occupancy can be easily discerned with remotely sensed imagery (Shealer and Alexander 2013). Work is currently underway to create a Canada-wide wetland inventory based on remotely sensed data, similar to what is available in the U.S. through the National Wetland Inventory (Ducks Unlimited Canada, https://www.ducks.ca/initiatives/canadian-wetland-inventory/). Such an inventory, perhaps in combination with large-scale bird survey data such as from the North American Breeding Bird Survey, eBird, or provincial Breeding Bird Atlases, could then be used to allow for a much more rapid assessment of Black Tern and other waterbird habitats at larger spatial scales. Ultimately, these analyses could be used to predict abundance and occupancy across the landscape and prioritize areas for conservation of waterbirds in the Canadian prairies. These results continue to demonstrate the capabilities of aerial imagery in characterizing and identifying the biologically relevant habitat features outlined previously in Wisconsin (Shealer and Alexander 2013). Using online tools could allow researchers to easily assess large areas of the landscape and gather a better understanding of important wetland locations for Black Terns, allowing targeted field visits to sites predicted to be most suitable. This is especially true for areas of the Black Tern breeding range like the PPR and BPE where wetland density is high, making traditional wetland assessment methods at a large scale unfeasible. Our work highlights the benefit of using aerial imagery platforms such as FlySask2 for assessing landscapes, particularly in areas of Canada where landscapes have not been inventoried. Unfortunately, products similar to FlySask2 are not available across all provinces, resulting in many areas of remote and rural Canada lacking in high quality aerial imagery coverage.

2.4.3 Occurrence and Abundance in the Panmixia Paradigm

In addition to the difficulty of predicting colony occupancy and abundance, individual Black Terns appear to exhibit low site fidelity and high breeding dispersal from year to year (Shealer 2003, Heath et al. 2020). While aerial imagery can allow us to gain a better understanding of what constitutes suitable breeding sites, factors that lead to breeding dispersal and why Black Terns exhibit low philopatry have yet to be studied. Studies of other waterbird species have noted similar unpredictability in the location of occupied breeding sites from year to year. For example, genetic analyses have shown that American White Pelicans (*Pelecanus erythrorhynchos*) display complete panmixia across the continent (Oomen et al. 2011, Reudink et al. 2011). High rates of colony abandonment, high stable isotope variation among individuals at breeding colonies (Reudink et al. 2016) and the propensity of American White Pelicans to move long distances for foraging (Knopf and Evans 2020) indicated that genetic panmixia appears to be driven by high rates of long-distance dispersal (Oomen et al. 2011, Reudink et al. 2011, Reudink et al. 2016). The unpredictability of Black Tern occurrence and lack of occupancy at seemingly suitable breeding sites (Naugle et al. 2000, Shealer and Alexander 2013), a tendency towards low site fidelity (Shealer 2003, Heath et al. 2020), and shared winter sites among individuals from across the range (see Chapter 3) suggest the likelihood of genetic panmixia in North American Black Tern populations. Indeed, results of preliminary genetic analyses suggest a lack of genetic structure across the range (P. Szczys, pers. comm.). It is possible that Black Terns in Saskatchewan return to the same general latitude to breed, then select breeding colonies based on annual habitat cues within that latitudinal band. This unpredictable movement makes management of a species like the Black Tern particularly difficult. However, high breeding dispersal is likely an evolved trait which is beneficial on an individual level as it allows individuals to easily relocate to more suitable breeding habitats from year to year. In order to fully understand the causes and consequences of breeding dispersal, multi-year tracking of Black Terns on the breeding grounds is necessary. This research, along with genetic analyses, would provide greater insight into site fidelity, habitat associations, and meta-population structure, ultimately leading to information that could inform conservation actions (Harms et al. 2017).

Table 2.1. AIC model selection of Bernoulli generalized linear models for spatial and habitat models, ranging from the full model (all covariates included) to the best model (the model with the lowest AIC score). Only those models within 4 AIC of the top model are shown, in addition to the full model. (Lat = latitude, Lat^2 = $latitude^2$, Lon = longitude, Aq.Veg. = extent of emergent aquatic vegetation, Area = wetland area, Class = wetland classification, Deg.Encr. = degree of human encroachment).

Model	K	AIC	Delta AIC	AIC Weight	Cumulative Weight	Log-likelihood
Spatial Models						
Lat + Lat^2 + Lon (Full)	4	75.75	0	0.59	0.59	-33.56
Lat + Lat^2	3	76.50	0.75	0.41	1	-35.06
Habitat Models						
Aq.Veg.	2	86.09	0	0.52	0.52	-40.95
Aq.Veg. + Area	3	86.92	0.83	0.34	0.87	-40.27
Aq.Veg. + Area + Class	4	89.03	2.95	0.12	0.99	-40.20
Ag.Veg. + Area + Class + Deg.Encr. (Full)	6	93.32	7.23	0.01	1	-39.97

Table 2.2. Parameter estimates and 95% confidence intervals for covariates included in the best spatial and habitat Bernoulli occupancy models, based on AIC model selection.

	Estimates (CIs)
Best Spatial Model	
Latitude	68.874 (30.918, 121.392)
Latitude^2	-0.655 (-1.155, -0.293)
Longitude	-0.283 (-0.637, 0.0356)
Best Habitat Model	
Extent of Aquatic Vegetation	0.7 (0.196, 1.259)

Table 2.3. AIC model selection of hurdle models for spatial and habitat models, ranging from the full model (all covariates included) to the best model (the model with the lowest AIC score). Covariates placed before the vertical line are for the presence-absence (occupancy) part of the hurdle model, covariates placed after the vertical line are for the abundance part of the hurdle model. Only those models within 4 AIC of the top model are shown, in addition to the full model (Lat = latitude, Lat^2 = $latitude^2$, Lon = longitude, Aq.Veg. = extent of emergent aquatic vegetation, Area = wetland area, Class = wetland classification, Deg.Encr. = the degree of human encroachment).

Model	K	AIC	Delta AIC	AIC Weight	Cumulative Weight	Log-likelihood
Spatial Models						
Lat + Lat^2 | Lat + Lat^2	7	303.66	0.00	0.73	0.73	-143.90
Lat + Lat^2 + Lon | Lat + Lat^2 + Lon (Full)	9	305.64	1.98	0.27	1.00	-142.27
Habitat Models						
Area|Aq.Veg.	5	313.62	0	0.09	0.09	-151.32
Aq.Veg.|Aq.Veg.	5	314.36	0.74	0.06	0.16	-151.69
Class|Aq.Veg.	5	314.50	0.89	0.06	0.21	-151.77
Area|Aq.Veg. + Area	6	314.67	1.05	0.05	0.27	-150.65
Aq.Veg.|Aq.Veg. + Area	6	315.41	1.79	0.04	0.31	-151.02
Class|Aq.Veg. + Area	6	315.56	1.94	0.03	0.34	-151.09
Aq.Veg. + Area|Aq.Veg.	6	315.59	1.97	0.03	0.38	-151.11
Area + Class|Aq.Veg.	6	315.72	2.11	0.03	0.41	-151.17
Area|Aq.Veg + Class	6	315.87	2.25	0.03	0.44	-151.24
Deg.Encr.|Aq.Veg.	6	316.42	2.80	0.02	0.46	-151.52
Aq.Veg.|Aq.Veg. + Class	6	316.61	2.99	0.02	0.48	-151.61
Aq.Veg. + Area|Aq.Veg. + Area	7	316.72	3.11	0.02	0.50	-150.43
Class|Aq.Veg. + Class	6	316.75	3.14	0.02	0.52	-151.69
Aq.Veg. + Class|Aq.Veg.	6	316.76	3.14	0.02	0.54	-151.69
Area + Class|Aq.Veg. + Area	7	316.86	3.24	0.02	0.56	-150.49
Area|Aq.Veg. + Area + Class	7	317.01	3.40	0.02	0.57	-150.57
Aq.Veg. +Area + Class|Aq.Veg.	7	317.04	3.42	0.02	0.59	-150.59
Area|Area	5	317.21	3.59	0.02	0.61	-153.12
Null	3	317.46	3.84	0.01	0.61	-155.54
Deg.Encr.|Aq.Veg. + Area	7	317.55	3.49	0.01	0.62	-150.84
Area + Aq.Veg. + Class + Deg.Encr.|Area + Aq.Veg. + Class + Deg.Encr. (Full)	13	324.28	17.40	0.00	1.00	-149.14

Table 2.4. Parameter estimates and 95% confidence intervals for covariates included in the best spatial and habitat hurdle models, based on AIC model selection. Covariates beginning with "Occupancy" are for the presence-absence part of the hurdle model, covariates beginning with "Count" are for the abundance part of the hurdle model.

	Estimates (CIs)
Best Spatial Model	
Occupancy: Latitude	8.915 (1.0722, 16.757)
Occupancy: Latitude^2	-14.918 (-25.289, -4.546)
Count: Latitude	4.328 (-3.494, 12.15)
Count: Latitude^2	-11.489 (-20.575, -2.403)
Best Habitat Model	
Occupancy: Extent of Aquatic Vegetation	0.7 (1.754, 1.224)
Count: Wetland Area	2.215 (-1.917, 6.348)

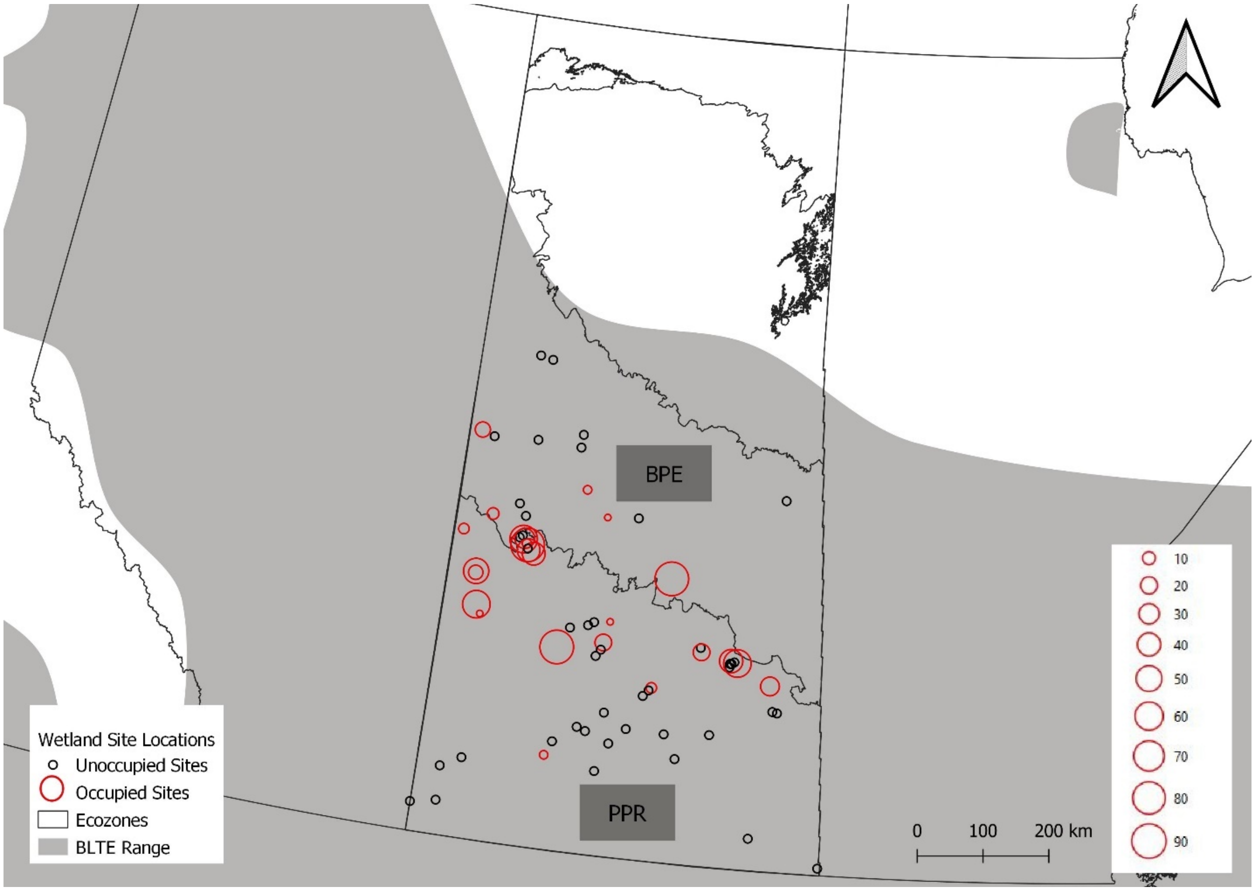

Figure 2.1. Location of wetland sites within Saskatchewan that were assessed for Black Tern colony presence, size, and habitat covariates. Black circles represent surveyed sites where Black Tern colonies were absent, red circles represent sites where colonies were present. The size of the red circle represents the total number of individuals present at the colony. The known breeding range is shaded, and the Prairie Pothole Region (PPR) and Boreal Plains Ecozone (BPE) are indicated.

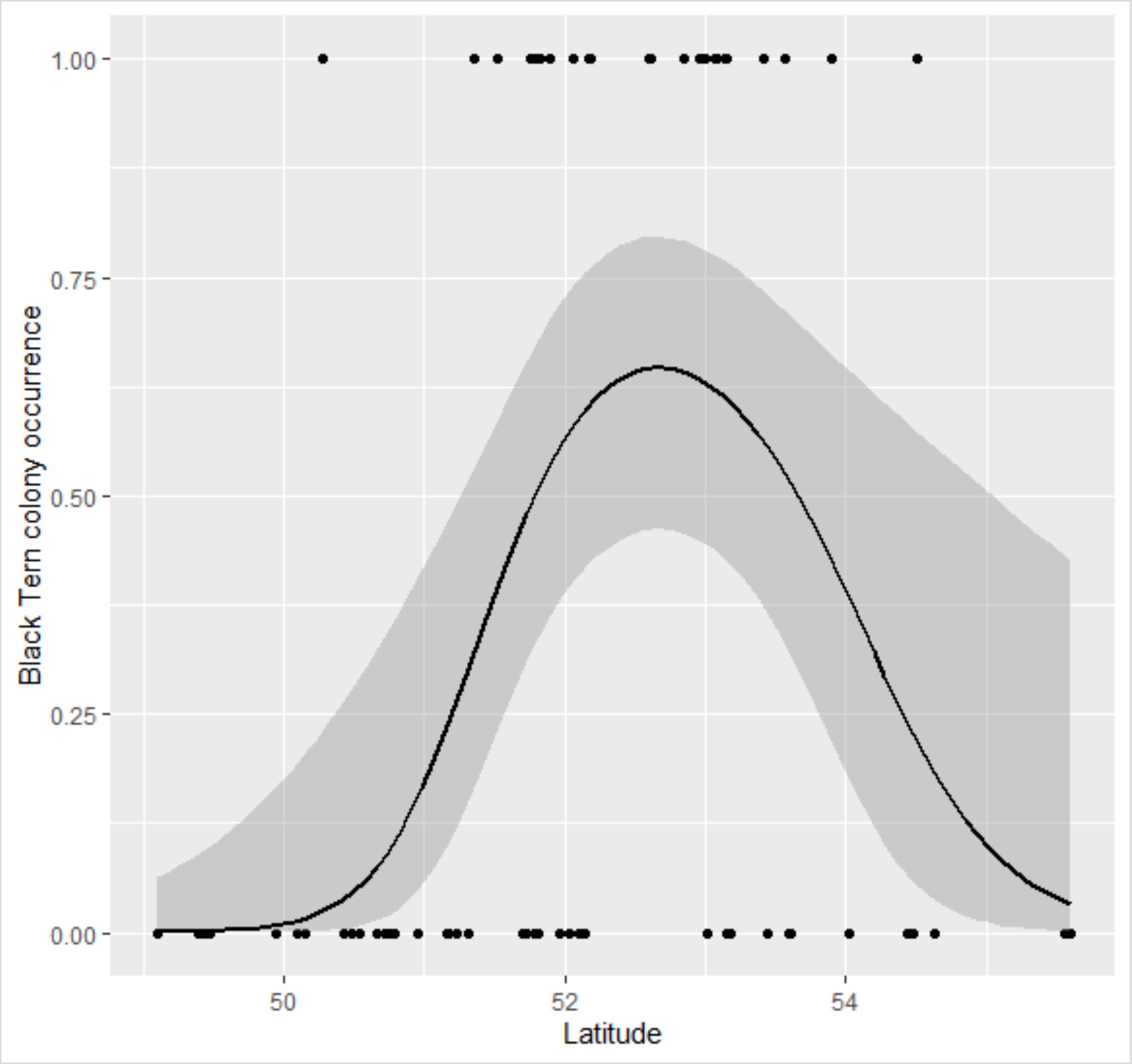

Figure 2.2. Relationship between Black Tern colony occurrence and latitude, based on a Bernoulli generalized linear model. The shaded area represents the 95% confidence interval of predicted values. The non-linear relationship was visualized using the "geom_smooth" function in R and a polynomial smoothing function.

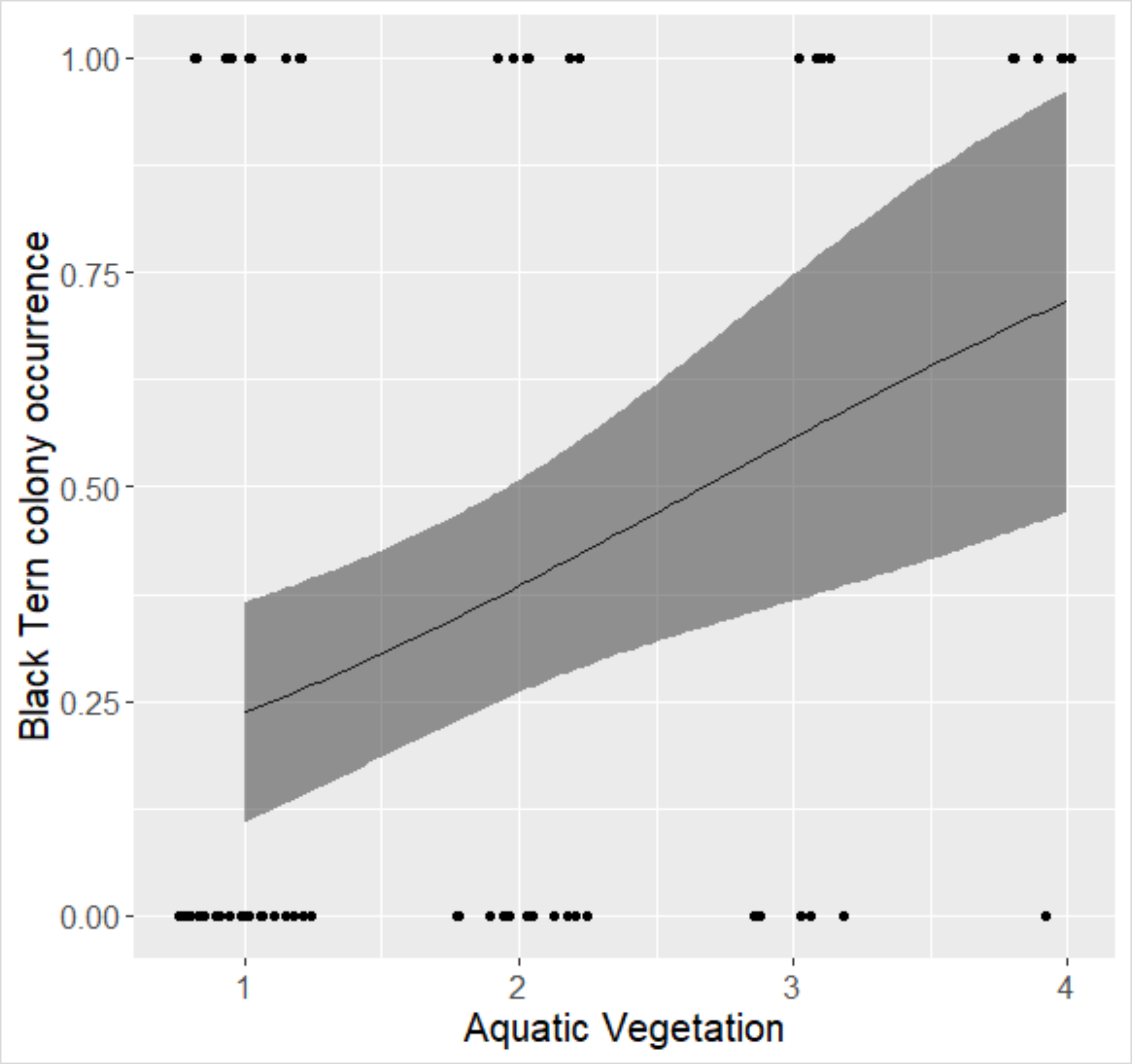

Figure 2.3. Relationship between Black Tern colony occurrence and extent of emergent aquatic vegetation at wetlands, based on a Bernoulli generalized linear model. The shaded area represents the 95% confidence interval of predicted values. Values along the x axis are offset for ease of visualization.

CHAPTER 3:

MIGRATION ROUTES AND WINTERING LOCATIONS OF NORTH AMERICAN BLACK TERNS FROM ACROSS THEIR BREEDING RANGE, REVEALED THROUGH LIGHT-LEVEL GEOLOCATION

3.1 Introduction

Understanding full annual cycle movement and the strength of migratory connectivity is crucial for effective protection and conservation of migratory bird species (Harrison et al. 2011, Small-Lorenz et al. 2013, Marra et al. 2015). Recent advances in both tracking technology and analytical techniques are allowing researchers to understand patterns and processes throughout the annual cycle and effectively measure the spatial connectedness among populations of a species (i.e., migratory connectivity; Ambrosini et al. 2009). A population has strong migratory connectivity when individuals in a population breed, migrate, and overwinter in the same areas, resulting in low mixing among populations. On the other hand, weak migratory connectivity exists when individuals of a population from one breeding area migrate and overwinter over a large area, resulting in high individual mixing with other populations (Webster et al. 2002). Knowledge of migratory connectivity is particularly important for migratory species in decline, as it allows us to better predict the probability of local extinction and develop strategies to address the causes of population declines (Cohen et al. 2014, Bracey et al. 2018).

Recent research on the Kirtland's Warbler (*Setophaga kirtlandii*) has revealed how understanding migratory connectivity is critical to the conservation of a threatened species (Cooper et al. 2017, 2018). Kirtland's Warblers have a restricted breeding range in Michigan and winter almost exclusively in the Bahamas (strong migratory connectivity), making the entire population of Kirtland's Warblers potentially susceptible to a single damaging ecological event. Understanding this pattern of connectivity allowed researchers to enact conservation measures on the wintering grounds, eventually leading to population recovery and de-listing (USFWS 2012). Studies on migratory connectivity have increased rapidly over the past decade; however, for many species of conservation concern we still have only a rudimentary understanding of migratory connectivity and full annual cycle dynamics. Among these species is the North American Black Tern (*Chlidonias niger surinamensis*), a declining waterbird that breeds in inland wetlands across the northern United States and southern Canadian provinces (Heath et al. 2020). The successful identification of patterns of migratory connectivity would benefit Black Tern populations through the ability to identify key sites (both stop-over and over-wintering) that could be targeted for conservation efforts.

Despite years of study and previous conservation efforts aimed at protecting breeding populations, especially in the eastern portion of the range, Black Terns are in decline across their breeding range in North America (Shealer et al. 2006). These declining trends are consistent with many other waterbird species worldwide (Wetlands International, 2010). Populations of waterbirds are particularly sensitive to increasing global anthropogenic threats such as the disturbance and destruction of aquatic environments, changing weather regimes and drought, the prolific spread of invasive species, and increasing anthropogenic encroachment (Baldock 1984, Rashford et al. 2011, Matteson et al. 2012). As a result, many waterbirds are a priority for conservation efforts (Kirby et al. 2008).

Based on North American Breeding Bird Survey data, Black Terns have declined by -2.96%/year (CI: -1.32 – -4.49, 1970-2019; Smith et al. 2020) across the breeding range. Current estimates state that the North American Black Tern population is approximately one-third the size of what it was in the 1960s (Stephens et al. 2015). The severity of population declines appears to vary across the breeding range, with peripheral sites experiencing steeper declines than those located in the core of the breeding range – generally considered to be the Prairie Pothole Region (Heath et al. 2020). For example, populations of Black Terns around the Great Lakes region in Manitoba, Ontario, Michigan, Minnesota, and Wisconsin have declined drastically based on the Breeding Bird Survey (Bird Conservation Region (BCR) 12 – Boreal Hardwood Transition: -7.43%/year, BCR 13 – Lower Great Lakes/St. Lawrence Plain: -6.21%/year, BCR 23 – Prairie Hardwood Transition: -8.54%/year, from 1970-2019). On the very western and eastern edges of the species range in Oregon and Maine, site-specific surveys have also revealed drastic declines (Stephens et al. 2015; Maine Dept. of Inland Fisheries and Wildlife 2016). In comparison, in the Prairie Pothole Region (BCR 11), declines have been less severe (-2.68%/year from 1970-2019). As a result of widespread population declines, the Black Tern has become a target for conservation efforts across the range. In the prairies, a population objective of an increase by 100% was set (ECCC 2013a). In Ontario, the Black Tern is listed as "Special Concern" under Ontario's *Endangered Species Act, 2007.* In Wisconsin, extensive surveying has revealed a population decrease of 60% resulting in the Black Tern being listed as a Species of Special Concern (WDNR 1999, Matteson and Mossman 2000). The cause of population declines remains unclear, with some studies attributing population declines to the loss of nesting and foraging habitat due to the destruction of wetland environments (Burke 2012), and others suggesting that mortality may be occurring primarily during the non-breeding season (Heath et al. 2020).

Research remains conflicted on whether loss of suitable breeding habitat is the main driver of population declines. Wyman and Cuthbert (2016) found that suitable breeding sites in the Great Lakes Region had less than 20% occupancy of Black Terns during the breeding season, suggesting that breeding habitat may not be the limiting factor for populations. Similarly, in Wisconsin, Black Terns were found at less than half of the sites considered suitable and at only 11% of the sites considered marginal or unsuitable (Shealer and Alexander 2013). On the other hand, in recent years, colony site occupancy in the Great Lakes Region has declined more than population size, possibly indicating a limited availability of suitable breeding habitat (Matteson et al. 2012, Cuthbert and Wires 2013). Additional research from Servello (2000) used a population model to analyze the sensitivity of Black Tern population growth rates to different demographic parameters, and suggested that adult survival may be the key limiting factor. These contrasting results suggest that populations may be limited by events occurring during migration or on the wintering grounds, but that breeding habitat or other factors on the breeding grounds may also play a role. In addition, it is possible that different populations across the breeding range could be limited by different factors. In order to fully understand how and where Black Tern populations are being limited, it is necessary to track their range-wide full annual cycle movement.

The collection of band re-sighting data has traditionally been used to track the movement of individual birds. Despite intense banding efforts, little band re-sighting data exist for the Black Tern (See Supplementary Fig. 3.5). As a result, it is not known whether Black Terns, both within and among populations, and across the breeding range, overlap in non-breeding site use (and potentially experience similar threats) or whether they use different sites with different threats. Little information exists on migration timing, routes, stop-over sites, or the range and conditions of over-wintering locations. The use of individual tracking technologies, such as satellite and radio transmitters, geolocators, or stable isotope analysis, is one way to fill these gaps and understand how Black Terns move throughout their annual cycle (Marra et al. 2015). In this study, I make use of light-level geolocators to track multi-year migratory movements and examine migratory connectivity in North American Black Terns.

Thus far, the only study that has tracked Black Terns was conducted on the European subspecies (*Chlidonias niger niger*) in the Netherlands (van der Winden et al. 2014). Six individuals were tracked using light-level geolocators, revealing important post-breeding staging areas and new sites along the Mediterranean coast that may be important migratory stopover locations, as well as ultimate wintering destinations in West Africa. Furthermore, the pattern of individual migration was idiosyncratic, with large variation in migration routes, staging sites, and timing among individuals. Reasons for individual variation are still uncertain but may suggest that the marine resources that Black Terns rely on during migration are unpredictable and vary within and among years. The unpredictability of non-breeding site use by Black Terns could pose issues from a conservation perspective, although whether the patterns observed in European populations are consistent in North American populations remains unknown.

The objectives of my study were to examine full annual cycle movements and potential differences in migratory stop-over and over-wintering locations from Black Terns breeding at colonies in the core (Saskatchewan, Canada) and periphery (Ontario, Canada and Michigan, USA) of the species range. I attempted to measure the strength of migratory connectivity between breeding colonies during the non-breeding season, and used multi-year tracks when possible to examine individual variation in migratory patterns and breeding dispersal. This is the first examination of full annual cycle tracking data for the North American subspecies of Black Tern, and my hope is that my results will be a first step in elucidating potential causes of long-term population declines by revealing important areas of use during breeding and non-breeding seasons, and inform conservation and stewardship efforts for the species.

3.2 Methods

3.2.1 Study Sites

Black Tern breeding colonies were identified in central and eastern North America. Five colonies were located in Saskatchewan and Ontario, Canada, and Michigan, USA. From west to east, study sites included: a ~750 marsh-fringed shoreline at Jackfish Lake, a large recreational lake located in south-western Saskatchewan (53.132, -108.426), Bricksaw Marsh, an ~15 ha semi-permanent wetland located on private land near Foam Lake in south-eastern Saskatchewan (51.780, -103.585), an ~4 ha section of hemi-marsh in Good Spirit Lake, a large recreational lake located in south-eastern Saskatchewan (51.552, -102.629), St Clair Flats, the world's largest freshwater delta consisting of ~25000 ha located in eastern Michigan (42.586 -82.640), and Tiny Marsh an ~600 ha managed wetland within a Provincial Wildlife Area located in southern Ontario (44.607 , -79.935) (Fig. 3.1).

3.2.2 Field Methods

I deployed 88 archival light-level geolocators on Black Terns across the five colonies during the breeding seasons of 2016-2019 (Table 3.1). I conducted fieldwork in early spring (late May/early June) to locate nests and determine egg-laying dates. Black Tern adults were trapped on the nest during the late-incubation period from mid-late June through mid-late July, depending on the colony (Heath et al. 2020). Fieldwork only occurred during favorable weather conditions (i.e., no extreme temperatures or precipitation) to minimize adverse effects on adults, chicks, and eggs. I followed protocols of Shealer and Haverland (2000) for the trapping and banding of Black Terns, as they have been found to not have detrimental effects on reproductive success. Adults were trapped on the nest when they returned to incubate using wire mesh remote-controlled treadle traps, remote-controlled bow traps, manual treadle traps, drop-in traps, or noose traps, all of which were placed over the eggs. Handling time for each individual was approximatley 15 minutes, during which timeIattached an aluminum Canadian Wildlife Service (CWS) or United States Fish and Wildlife Service (USFWS) band on one leg, a geolocator on the other leg, took a blood sample for genetic sex analysis (one drop taken from metatarsal vein), and weighed and measured (weight and tarsus, bill, head-bill, tail, and wing length) individuals.

Individuals were fit with Intigeo geolocators (model W65A9; Migrate Technology, Cambridge, UK) using a darvic band, similar to the methods of Nisbet et al. (2011). At certain colonies, I tagged a subset of birds with a field-readable colour band (Bricksaw Marsh n = 4, Jackfish Lake n = 3, St. Claire Flats n = 13, Tiny Marsh n = 27) but without a geolocator. The combined weight of all attachments for birds receiving a geolocator was 0.9g, less than 2% of an adult Black Tern's body weight (~50-60g); for birds receiving a colour band, the combined weight was substantially less. A total of 19% of birds were recaptured at breeding colonies during the breeding seasons of 2017-2021 (Table 3.1). Procedures for the recapture of geolocator-tagged birds were the same as initial capture, except that I removed the geolocator, and did not take a blood sample.

3.2.3 Data Analysis

Intigeo geolocators use a light sensor to record the entire light range that occurs between the dawn and dusk each day. Light readings were recorded every minute, and a maximum light level was recorded every 5 min. I used the R package "GeoLight" to import data and define twilight times (when sunrise and sunset occurs) with a light-level threshold of 0.5 (Lisovski and Hahn 2012). This allows twilight times to be automatically identified as the periods of increasing or decreasing light prior to or after sunsrise and sunset. Geolocators were callibrated to estimate the error in calculation of lattitudes and longitudes using the "on-bird" method, where recordings post-deployment but prior to migration are used to callibrate the device using light-level readings that more closely resemble the birds' environment (Rakhimberdiev and Saveliev 2016). For birds with geolocators that were still logging data upon recapture, I used two callibration periods: a period of two weeks post deployment and pre migration, and a period of two weeks pre retrieval and post migration. For individuals with geolocators that were no longer logging data upon retrieval, a second callibration period comprised of stationary dates collected during the annual cycle were used if necessary. An additional callibration period consisting of one week of pre-deployment data at a fixed location was collected on each geolocator deployed in Saskatchewan, which was used to callibrate location data from individuals recaptured in Saskatchewan in 2021.

Data collected from geolocators were analyzed using the R package "FlightR," which provided estimates of geographic positions, movement timing, and stationary periods (Rakhimberdiev et al. 2015, Rakhimberdiev and Saveliev 2016, Rakhimberdiev et al. 2017). This package uses a template fit to estimate locations using the shape and timing of light transitions between twighlight periods recorded by the geolocator. A Hidden Markov Model refines these estimates using a particle filter algorithm. The particles are simulated locations and each particle represents a potential location; the algorithm then uses the current and preceding twilights in the movement model to enhance position models. By weighing the likelihood of generated particles, the model is able to determine the location of an individual on a given day, and calculate the amount of uncertainy associated with that location. Because Black Terns use inland, coastal, and plegaic habitats, no spatial or behavioural constraints were added to further refine positions. To identify stationary periods used by individuals,Iused the FLightR function "stationary.migration.summary" to differentiate these locations from regular movement.Iconsidered locations as stationary periods when individuals remained within a 250 km radius for a minimum of three days (Bracey et al 2018). Stationary periods identified during migration were considered stopover locations. Breeding sites were buffered by a 250 km radius, andIconsidered movement occuring within this radius as local movement during the breeding period.Iused median dates to estimate arrivals and departures from breeding sites based on the porportion of particles arriving with the 250 km radius around each breeding site. I defined wintering locations as locations in Central and South America from the latitude 30ºN, corresponding roughly to the Mexican border, to the southern border of Peru, where individuals remained within a 250 km radius for a minimum of three days. All stationary periods after individuals travelled south of the latitude 30ºN during the fall migration, as well as those before individuals travelled north of 30ºN during the spring migration were classified as wintering locations. I chose the latitude 30ºN as the threshold for defining wintering periods due to the high individual variation in migratory timing and stopover locations used by Black Terns. As is seen in other waterbirds (Haig et al. 1998, Bracey et al. 2018), there was no clear or consistent transition from the migratory period of the annual cycle to the wintering period, and individuals moved throughout the winter period. I calculated the total distance of migration for each individual by adding the daily distances travelled by each bird between stationary periods.

I attempted to use geolocator data to determine the strength of migratory connectivity between 1) breeding locations and the first major stopover, and 2) breeding locations and wintering locations (Hallworth et al. 2021). I focused on migratory connectivity in relation to the breeding grounds because my objective was to inform potential causes of variation in population declines across the Black Tern breeding range. Because I had no a priori knowledge of spatial connectedness among breeding regions,Iran the analysis considering either two (Saskatchewan and combined eastern sites) or three (Saskatchewan, Ontario, Michigan) different breeding locations. I defined the first stopover location as the first stationary periods after departing breeding sites where individuals remained within a 250 km radius for a minimum of three days. As above, I defined wintering locations as locations in Central and South America from the latitude 30°N, to the southern border of Peru, where individuals remained within a 250 km radius for a minimum of three days. Although any latitudinal threshold I chose would be somewhat arbitrary, results of the migratory connectivity analysis do not differ considerably if a slightly higher (35 °N) or lower (25 °N) latitude was used. For individuals (n = 3) with over one year of tracking data, only the first full annual cycle was included in the migratory connectivity estimate.Iestimated migratory connectivity using the "estMC" function in the R package "MigConnectivity" (Cohen et al. 2018). Migratory connectivity values are defined as either weaker or stronger: negative values indicate weaker migratory connectivity, while positive values indicate stronger migratory connectivity. Values of migratory connectivity become stronger as they approach one (Tonra et al. 2019).

3.3 Results

I retrieved 17 of the 88 (19%) geolocators deployed on birds between 2016 and 2019 (Table 3.1). Geolocator recaptures varied between colonies. Three of 23 (13%) were retrieved from Jackfish Lake, Saskatchewan. All three individuals (one in 2020, two in 2021) were found to be breeding at a different colony site on Jackfish Lake, about 2.5 km from their original 2019 breeding colony, where they were recaptured. Three of nine (30%) geolocators were retrieved from St. Claire Flats, Michigan, and 11 of 31 (35%) were retrieved from Tiny Marsh, Ontario. There were no recaptures elsewhere in Saskatchewan due to the abandonment of the two colonies at Bricksaw Marsh and Good Spirit Lake in the years following deployment in 2018 and 2019. This was likely due to extreme drought in spring 2019 and 2020, leading to drying of the marshes and apparently unsuitable breeding habitat (pers. obs.). One geolocator deployed at Tiny Marsh in 2016 and recaptured in 2017 failed after 48 days and no migration data were collected. One geolocator deployed at Jackfish Lake in 2019 and recaptured in 2021 collected one year of data but has not been included in the main analysis due to high levels of uncertainty and seemingly unrealistic tracking data (See Supplementary Material Fig. 3.6). Of the remaining geolocators, 12 recorded data for a full year, two recorded data for 2 years, and one recorded data for over 2 years (three fall migrations, two spring migrations). Of the 15 retrieved geolocators that were included in the analysis, eight were from females (Jackfish Lake n = 1, St. Claire Flats n = 2, Tiny Marsh n = 5), six were from males (Jackfish Lake n = 1, St. Claire Flats n = 1, Tiny Marsh n = 4), and one was from and individual of unknown sex (Tiny Marsh).

3.3.1 Fall Southward Migration/Staging

Generally, birds from the eastern breeding colonies (Ontario and Michigan) showed a southward migration along the Atlantic coast (Fig. 3.2). Florida and the Carolinas stood out as the key stopover sites for individuals from the eastern breeding colonies, with all birds funnelling through these locations. Two individuals from the central breeding colony (Saskatchewan) migrated through the central flyway during the fall migration, with one individual taking a westerly route with stopover locations along the western coast of Mexico and the second travelling east with stopover locations on the Gulf of Mexico near Corpus Christi, Texas (Fig. 3.3). Inland locations in both North and South Dakota stood out as important stopover locations for both individuals during fall migration. Departure and arrival dates varied substantially among individuals. Fall departure dates ranged from July 14 to August 23. Ultimate arrival dates at wintering locations also varied among individuals, ranging from September 6 to November 22.

3.3.2 Non-breeding Locations

The mean duration of stay at non-breeding locations for individuals departing from all breeding sites was ~80 days (Table 3.2). On average, individuals used ~3.1 distinct wintering locations. During the defined wintering period, all individuals spent time in Central America and northern South America, from the Venezuela/Colombia border to southern Peru and into Chile. Of the wintering locations identified, 14 out of the 15 individuals spent the vast majority of the wintering period on the seas surrounding Panama. The remaining individual, originally captured in Ontario, wintered off the coast of Venezuela. The mean distance travelled by individuals throughout the entire annual cycle was ~13,706 km (range 14,150 – 18,030 km) for Ontario, ~12,776 km (range 11,274 – 13,959 km) for Michigan, and ~ 13,126 km (range 12,952 – 13,301 km) for Saskatchewan breeders.

3.3.3 Spring Northward Migration/Staging

Generally, individuals from the eastern colonies showed a northward migration through the Gulf of Mexico and Mississippi Flyway (Fig. 3.2). During spring migration, the Gulf of Mexico from Corpus Christi to Florida, as well locations near New Orleans stood out as important stopover locations with 11 of the 14 individuals from the eastern breeding colonies staging in these areas. One individual returned to the breeding grounds using the Atlantic Flyway. Both individuals from the central breeding colony migrated through the Central Flyway during the spring migration (Fig. 3.3). For one individual, spring migration staging occurred on the western coast of Mexico, followed by an apparent stopover in the Galapagos Islands, then northward migration through the Central Flyway. The second individual staged along the Gulf of Mexico near Corpus Christi before continuing northward through the Central Flyway. Spring arrival dates to the breeding grounds ranged from May 11-26 for Ontario, May 14-22 for Michigan, and May 27-30 for Saskatchewan.

3.3.4 Breeding Ground Mixing Across Deployment Sites

There was evidence of low breeding site fidelity for individuals. For example, an individual tagged in Ontario in 2016 was recaptured with multiple years of migration data (two spring migrations, three fall migrations) in 2019 (Fig. 3.4). Geolocator data indicated that during the 2017 spring migration, staging occurred in the Gulf of Mexico for 23 days, then the individual returned to Ontario for 13 days. Rather than breed in Ontario, this individual continued directly to a disparate breeding location in Manitoba approximately 1400 km west. The 2017 fall migration shows a direct flight path from the Manitoba breeding site to staging grounds north of Florida where the individual continued the typical southward migration along the Atlantic flyway. The 2018 spring migration track is consistent with others collected from the east, with staging at the Gulf of Mexico and breeding at Tiny Marsh. However, the individual was not recaptured in 2018. The individual then flew south to Central America near the Caribbean Sea, before the geolocator stopped working in the winter of 2018. This individual was subsequently recaptured at Tiny Marsh during the 2019 breeding season. Thus, despite the switch in breeding grounds in 2017, the individual's major staging locations and routes generally followed those of other eastern breeding birds.

Migratory connectivity was stronger between breeding sites and the first migratory stopover location (MC = 0.27) than it was between breeding sites and wintering locations (MC = -0.18) when breeding sites were treated as two separate locations (Saskatchewan and the eastern sites). Migratory connectivity remained stronger between breeding sites and the fist migratory stopover location (MC = 0.22) than between breeding sites and wintering locations (MC = -0.17) when breeding sites were treated as three separate locations (Saskatchewan, Ontario, and Michigan). These results indicate that individuals from different breeding colonies generally remained more closely linked to other individuals from their same breeding colony during the early part of fall migration, but that subsequent mixing of the populations occurred among individuals from multiple breeding locations on the wintering grounds.

3.4 Discussion

I provide the first detailed migratory routes for the North American Black Tern, uncovered from geolocators deployed in Saskatchewan, Michigan, and Ontario, which is an important first step towards understanding the non-breeding biology, patterns of movement, and use of staging and wintering sites of the species. I found that individuals from central and eastern colonies used different migratory routes and stopover sites, yet ultimate wintering destinations showed substantial overlap among individuals and between regions. Individuals from the breeding colony in Saskatchewan used the Central Flyway, while individuals from colonies in Ontario and Michigan used the Atlantic and Mississippi flyways. During the winter, all individuals spent some or all of their time near Panama, indicating this as a key location for population mixing. Additionally, one individual tracked over multiple years bred in both central and eastern regions, providing the first evidence of long-distance breeding dispersal and population mixing on the breeding grounds. Results of my migratory connectivity analysis were consistent with the above, with strong connectivity between breeding locations and first fall stopover, but weak connectivity between breeding locations and wintering grounds.

3.4.1 Migratory Routes and Stopover Locations

Migratory routes collected from eastern breeding locations showed that individuals varied in their specific migratory timing, duration, and routes taken, but some general patterns emerged. Individuals generally used the Atlantic Flyway during fall migration and the Mississippi Flyway during spring migration, an elliptical migration pattern that is typical of some waterbirds (Myers et al. 1990, Gratto-Trevor and Dickson 1994). For eastern individuals during fall migration, Florida stood out as a major stopover location or migratory funnel; 13 out of 14 tagged birds passed through or stopped over in Florida during fall migration. During spring migration, the Gulf Coast of the USA stood out as a major stopover location. All tagged individuals stopped over or passed through the Gulf Coast between Corpus Christi, Texas, to Florida. These general patterns of movement are similar to those found in the European Black Tern subspecies. Individual migrations were idiosyncratic, with variations in migration routes, staging sites and timing among individuals. However, like the tracks collected here from Ontario and Michigan, routes used by European birds revealed patterns of shared use of some post-breeding staging and wintering areas (van der Winden et al. 2014).

In contrast, Black Terns from Saskatchewan used the Central Flyway during spring and fall migration. Although I was only able to obtain accurate tracks for two individuals, a third individual's irregular tracking data suggested the possibility of a similar migration route taken (Supplementary Fig. 3.6). Staging sites used by the two individuals included the Gulf of California on the western coast of Mexico and Corpus Christi in the Gulf of Mexico. Inland locations such as North and South Dakota stood out as important stopover locations for both individuals during fall migration.

The use of different migratory flyways by different regions of a species range is not uncommon, and has been used as a way to understand and delineate subpopulations (Davidson et al. 1999, Madsen et al. 2014). Although Black Tern band recoveries are limited, this data also supports the hypothesis that eastern and western individuals generally use different migratory flyways (Supplementary Fig. 3.5). Recent genetic work on the European Black Tern subspecies revealed population genetic structure among breeding colonies in the Netherlands, Latvia, southern Ukraine, and eastern Siberian Russia, which was associated with use of distinct staging sites among populations (Szczys et al. 2017b). In contrast, genetic structure is generally weaker in waterbird species that show overlap among breeding populations during the non-breeding season (Friesen 2015), as I have shown in the North American Black Tern during the winter period. Indeed, preliminary genetic evidence suggests a lack of genetic structure across the North American Black Tern range (P. Szczys pers. comm.). Thus, despite differences in migratory routes, there is currently little evidence to suggest that breeding populations in North America should be considered as distinct subpopulation units.

3.4.2 Important Wintering Locations

Movement of tracked Black Terns throughout the nonbreeding or “wintering” period of the migratory cycle varied among individuals, with the length of stationary periods at a single location ranging from weeks to months. Wintering locations were distributed throughout Central and South America, from the southern border of Mexico to the western coast of Peru. However, all tagged individuals spent some or most of the wintering period at or off the coast of Panama. Five birds spent entire wintering period in Panama or on the surrounding seas, while six others returned to Panama after spending time at different Central or South American locations. This concentration of individuals around Panama, as well as the frequency of visits and duration of stay by individuals highlights the importance of this location during the wintering period. These results suggest Panama is a key location of population mixing on the wintering grounds. The fact that all tagged individuals spent time, with many spending most of their time, in Panama during winter suggests that a large portion of the Black Tern population could be vulnerable to a catastrophic event in this area. Indeed, studies have noted that populations displaying low connectivity can be susceptible to localized catastrophic events on wintering grounds, with effects impacting multiple breeding populations (Webster and Marra 2005). Panama has previously been recognized as a particularly important wintering area for migratory waterbirds, described as a continental crossroads where large numbers of North America's migrants converge (Watts 1998). The coastal regions of Panama have been noted as important locations for many species of waterbirds, seabirds, and shorebirds (Butler et al. 1997, Kushlan et al. 2017). Migratory birds may face a number of threats while wintering in Panama, such as pollution, contamination from agricultural and urban areas, urbanization, and tourist and agricultural development (Angehr and Kushlan 2007).

Individual Black Terns used similar habitats during the wintering period, with the majority of tagged individuals occupying marine environments. Based on a visual analysis of the non-breeding stationary sites used by tagged birds, many birds used marine environments for multiple days/weeks. Of the tagged birds, 13 out of 14 utilized marine habitats during the wintering period. Five individuals used coastal habitats, and nine individuals used a mix of coastal and marine habitats, where individuals spent >50 days off the coast. On the breeding grounds, Black Terns use inland wetlands and waterbodies (Naugle et al. 2000, Shealer and Alexander 2013). Our results suggest that Black Tern habitat preferences switch depending on the phase of the annual cycle, with individuals occupying inland marsh habitat while breeding, and mostly marine habitats in the wintering period. Furthermore, based on a qualitative examination of eBird checklist data (pers. obs.), it appears that the two highest concentrations of Black Terns during the non-breeding phase occurred over the marine shelf off the Pacific coast of Panama (Fink et al. 2020). This assessment is concurrent with findings that show the densities of seabirds in the Panama Bight, an area of the Pacific Ocean that extends westwards from the coasts of Panama, Columbia, and Ecuador, were highest over the continental shelf (Spear and Ainley 1999). Results from tagged European Black Terns have also noted the use of mainly marine environments during the winter, with most individuals spending their time off the coast of Africa (van der Winden et al. 2014). It is hypothesized that wintering distributions are related to Black Tern marine food sources during the non-breeding phase (Haney 1986, Van der Winden 2002, Larson and Leyva 2007). As such, populations of Black Terns may be affected by the quality and abundance of these food resources off the coast of Central America.

Because of this switch in habitat use that occurs at different phases of the annual cycle, Black Terns likely face a multitude of different stressors while occupying a variety of habitats. Negative effects of climate change may be compounded due to this reliance on a network of spatially dispersed sites (Maclean et al. 2007). Availability of food resources, variations in water levels, and changing habitat conditions may pose the greatest challenges to the Black Tern during the wintering period, when marine habitats are mainly used. On the other hand, the high mobility of Black Terns during winter may indicate that they are able to move to track resources, which could buffer them against negative effects of habitat change in particular areas, at least to some extent. The effects of threats on the breeding grounds including land conversion for agriculture use, wetland drainage, and agrochemical runoff (Rashford et al. 2011, Matteson et al. 2012), in combination with potential carry-over effects between seasons (Marra et al. 2015) warrant further study in order to determine when in the annual cycle populations of Black Terns are most limited (Harrison et al. 2011).

3.4.3 Migratory Connectivity

Although only two reliable migratory tracks were collected from the core of the Black Tern breeding range, migratory connectivity results were consistent with the general patterns described above. Specifically, Black Terns showed stronger connectivity in fall migratory routes which were dictated by breeding site location, whether I considered two (Saskatchewan and eastern sites) or three (Saskatchewan, Michigan, Ontario) separate breeding locations. Individuals from Saskatchewan travelled through the centre of the continent, and individuals from eastern breeding locations travelled along the Atlantic coast. However, migratory connectivity broke down during the wintering stage of the annual cycle, with weak connectivity and individuals from both the central and eastern regions overlapping in Central and South America. Similar patterns of migratory connectivity have been noted in North American Common Terns, with populations displaying weak connectivity on the wintering grounds with high individual mixing at stationary locations in Peru (Bracey et al. 2018). Additionally, these patterns have been observed in other migratory bird species such as Connecticut Warblers (*Oporornis agilis*; Hallworth et al. 2021), Prothonotary Warblers (*Protonotaria citrea*; Tonra et al. 2019), and Purple Martins (*Progne subis*; Fraser et al. 2013), where subpopulations migrate along distinct routes but overwinter in shared locations.

3.4.4 Breeding Dispersal

One tagged individual Black tern showed the first evidence of breeding ground mixing between central and eastern breeding locations. This individual was originally captured and banded in Tiny Marsh, near Georgian Bay in southwestern Ontario during the 2016 breeding season, and was recaptured at the same site during the 2019 breeding season. During the 2017 breeding season, rather than breed in Ontario, this individual apparently stopped at or somewhere near the Ontario site, then flew directly to a different breeding location in Manitoba. Although only from a single bird, this behaviour shows evidence of long-distance breeding dispersal: information that is rarely obtained from studies that use archival tags such as geolocators, which must be retrieved from individuals, usually at the site of deployment. Further evidence for extensive inter-annual breeding movement in this species comes from the complete abandonment of two colonies in Saskatchewan, and generally low return rates of birds at all sites, but especially in Saskatchewan. In addition, the three tagged individuals that were recaptured in Saskatchewan were actually found nesting at a separate marsh on Jackfish Lake upon recapture, about 2.5 km from their original breeding colony, indicating short distance relocation between years. Thus, in addition to individuals from different breeding populations mixing at common locations during the wintering period, I have evidence of mixing during the breeding period. As noted above, these patterns of movement are consistent with preliminary genetic analyses which suggest panmixia in North American Black Terns (P. Szczys, pers. comm.).

Study on annual survival and breeding recruitment of Black Terns in Wisconsin showed that vital rates at this location were far below those required to maintain a stable population. Adult apparent survival was lower than 70% and pre-breeding survival was approximately 2%, yet breeding populations increased between 1999 and 2003 (Shealer 2003). These results suggest emigration was necessary to maintain the population. One possibility is that eastern populations may be ecological traps acting as population sinks – an idea that is supported by stronger population declines in eastern populations versus in the core of the range. In this sense, the prairie core may represent a population source, while the edges act as population sinks (Pulliam 1988). Demographic studies at sites across the range would be needed to test this hypothesis. In light of these new insights uncovered by geolocator track data, I suggest some important next steps for understanding North American Black Tern population dynamics. Many areas of the North American Black Tern breeding range remain understudied with little information on population demographics and movement patterns. Thus far, migratory tracks have only been collected from a small area of the North American breeding range, and collecting tracks from individuals belonging to understudied regions of the continent, such as the eastern and western coasts, would provide more information about range-wide connectivity. Understanding the connectivity and metapopulation dynamics of Black Tern populations across the entirety of the breeding range is imperative for the conservation of this species. Doing so would allow for a better understanding of what factors may be influencing population declines, as well as aid in the ability to predict local population extinction (Cohen et al. 2014).

Table 3.1. Light-level geolocators deployed, retrieved, and resighted (seen but not able to be recaptured) on Black Tern adults each year at breeding colonies in Saskatchewan, Michigan, and Ontario. Date ranges refer to the times when geolocaotrs were deployed at colonies, or when recaptures occurred. Numbers in parentheses refer to the number of individuals of each sex (F = Female, M = Male, U= Unknown).

			Geolocators		
Breeding Colony	Year	Deployment/Retrieval Dates	Deployed	Retrieved	Resighted
Bricksaw Marsh, SK, CA	2018	June 26-30	23	-	-
	2019		-	-	-
	2020		-	-	-
Jackfish Lake, SK, CA	2019	June 22-July23	23	-	-
	2020	June 21	-	1 (1F)	-
	2021	June 19	-	2 (1F, 1M)	-
Good Spirit Lake, SK, CA	2019	June 17	2	-	-
	2020		-	-	-
St. Claire Flats, MI USA	2017	June 21-23	9	-	-
	2018	June 19-22	-	3 (2F, 1M)	-
Tiny Marsh, ON, CA	2016	June 28-July14	31	-	-
	2017	June 13-July	-	5 (2F,3M)	6
	2018	25	-	4 (4F)	-
	2019	June 7-July 25	-	1 (M)	-
	2020	June 7-July 10	-	1 (U)	-
		June 26-July 8			

Table 3.2. Mean (range) number of days of all stationary periods, including breeding sites, wintering locations, and stopover locations. The number of individuals tracked and duration of stay in days are based on light-level geolocators deployed on Black Terns at breeding colonies in Saskatchewan, Michigan, and Ontario.

	Jackfish Lake, SK		St. Claire Flats, MI		Tiny Marsh, ON	
	n	Mean (range)	*n*	Mean (range)	*n*	Mean (range)
Fall Stopover Sites						
FL Panhandle	-	-	2	18 (14-22)	3	22 (13-27)
The Carolinas	-	-	1	26	10	29 (20-60)
Georgian Coast	-	-	1	14	-	
The Bahamas	-	-	-	-	1	20
The Dakotas	2	18 (8-20)	-		-	
Gulf of California	1	35	-		-	
Corpus Christi	1	37	-	-	-	-
Wintering Sites						
HOND Coast	-		1	34 (46-22)*	1	37
HAT Coast	-	-	-	-	1	63
COL Coast	-	-	1	42	2	128 (89-167)
PA Coast	2	89 (50-129)	3	103 (47-182)	10	61 (33-131)
PE Coast	1	39	-	-	2	111 (92-131)
Rio Abiseo, PE	-	-	-	-	1	46
Yucatan Eastern Coast	-	-	2	35 (28-43)	-	-
ECUA Coast	-	-	-	-	2	82 (72-93)
Caribbean Sea	-	-	-	-	1	104
Maracaibo Bay, VE	-	-	-	-	2	164 (84-244)
The Galapagos Islands	1	30	-	-	-	-
Spring Stopover Sites						
Gulf Coast (Corpus Christi, TX to Florida)	-	-	3	4 (3-6)	7	19 (6-35)
The Carolinas	-	-	-	-	1	21
Oklahoma	1	10	-	-	-	-

Nebraska	1	8	-	-	-	-
Additional Breeding Sites						
Manitoba	-	-	-	-	1	61

* One individual spent two stationary periods during the non-breeding season at this location.

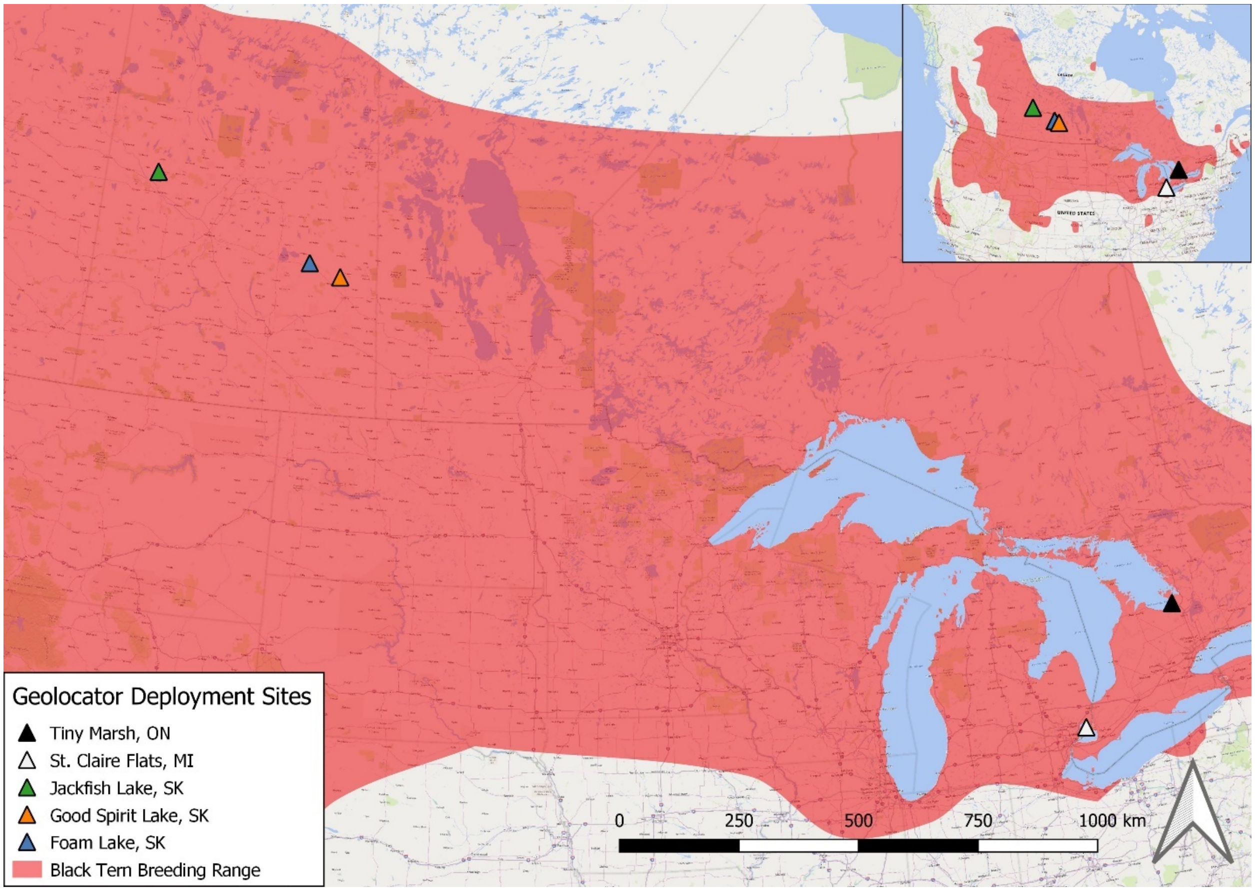

Figure 3.1. Locations of five breeding colonies where light-level geolocators were deployed on Black Terns. The red area represents the Black Tern breeding range.

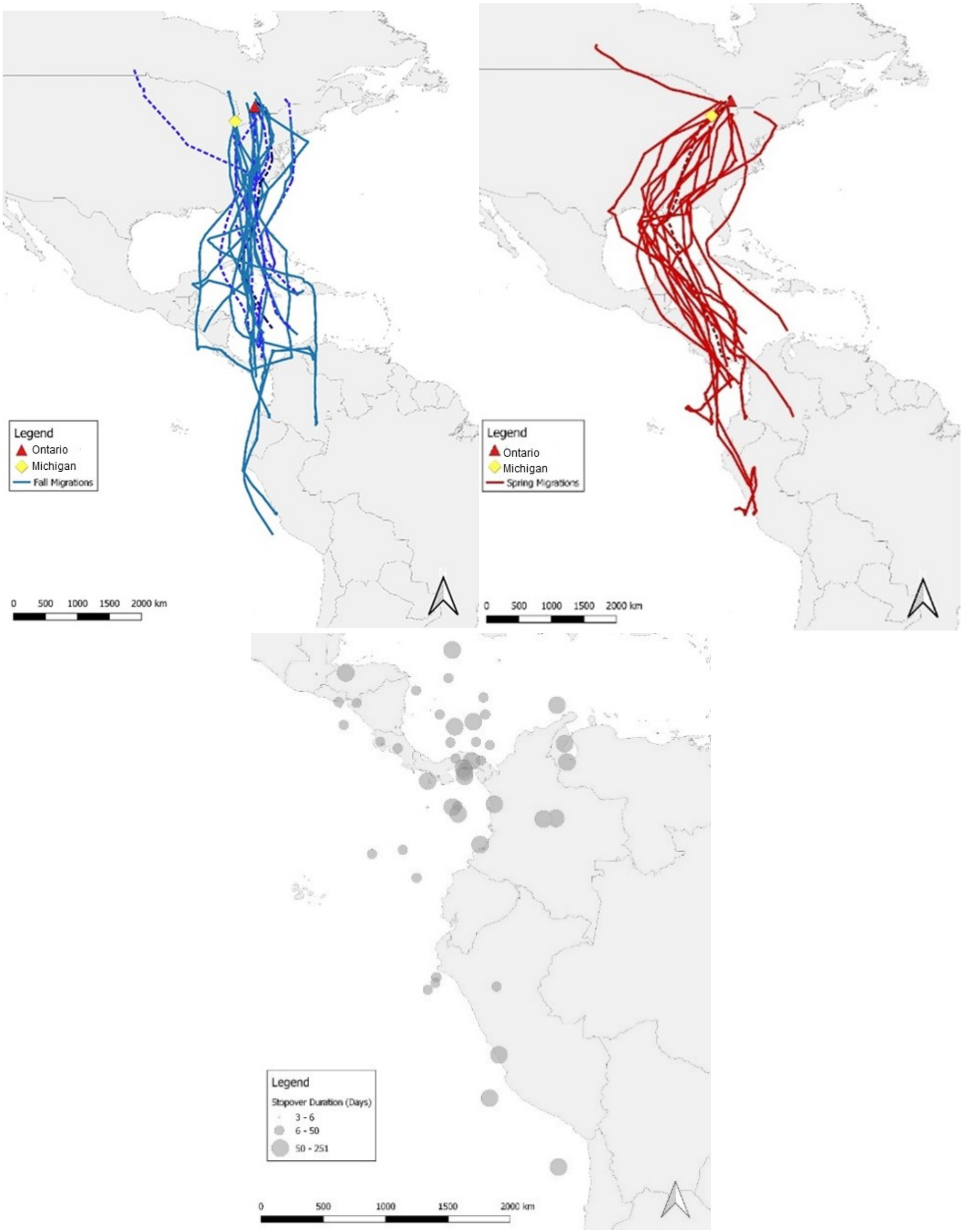

Figure 3.2. Fall migration (blue), spring migration (red), and wintering locations (grey dots) of Black Terns recaptured from eastern breeding locations, n = 13 (Ontario and Michigan). Solid lines represent first year tracks, dashed lines represent second year migratory tracks.

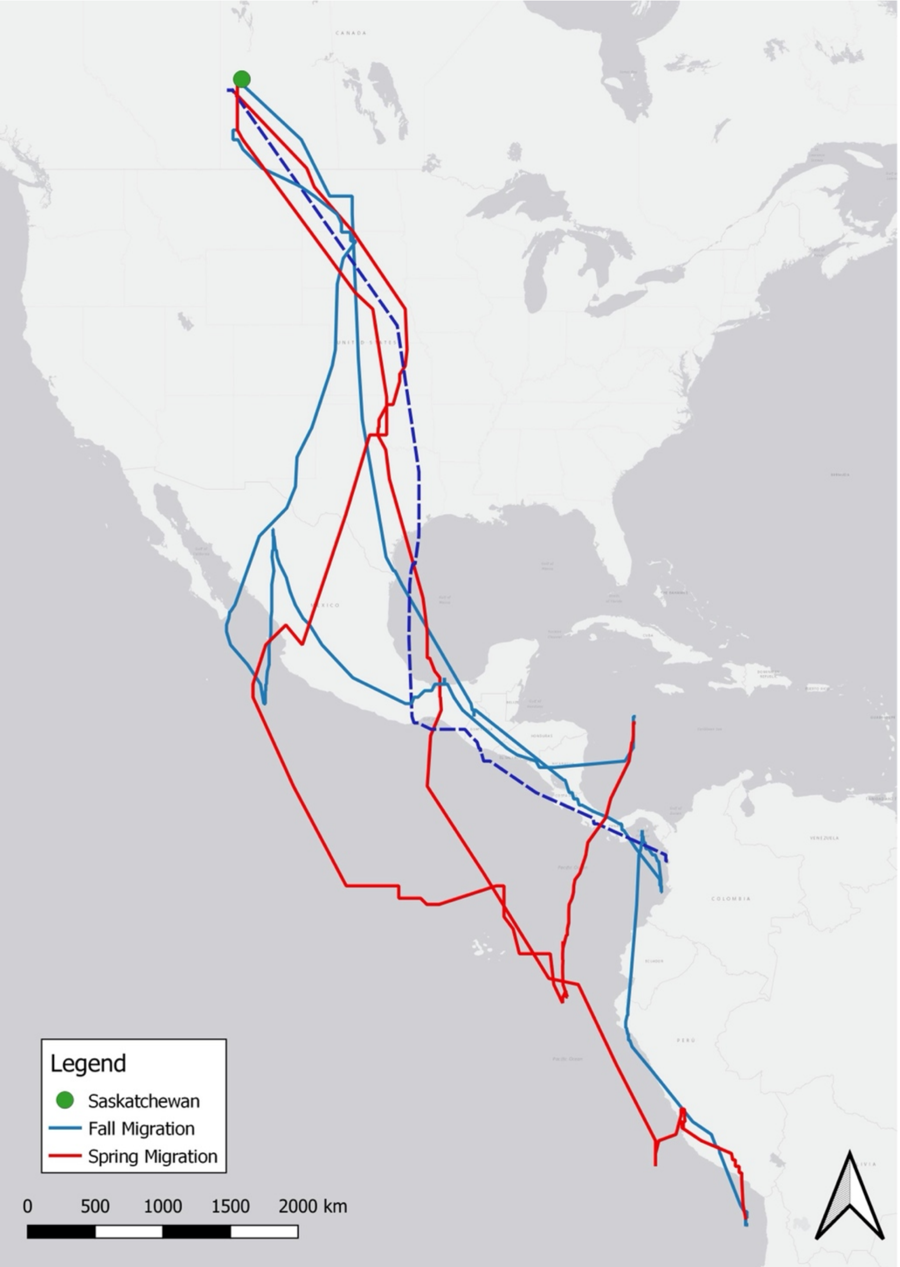

Figure 3.3. Fall southward migrations (blue) and spring northward migrations (red) of Black Terns recaptured from a central breeding location, n = 2 (Saskatchewan). Solid lines represent first year migratory tracks, dashed lines represent second year migratory tracks.

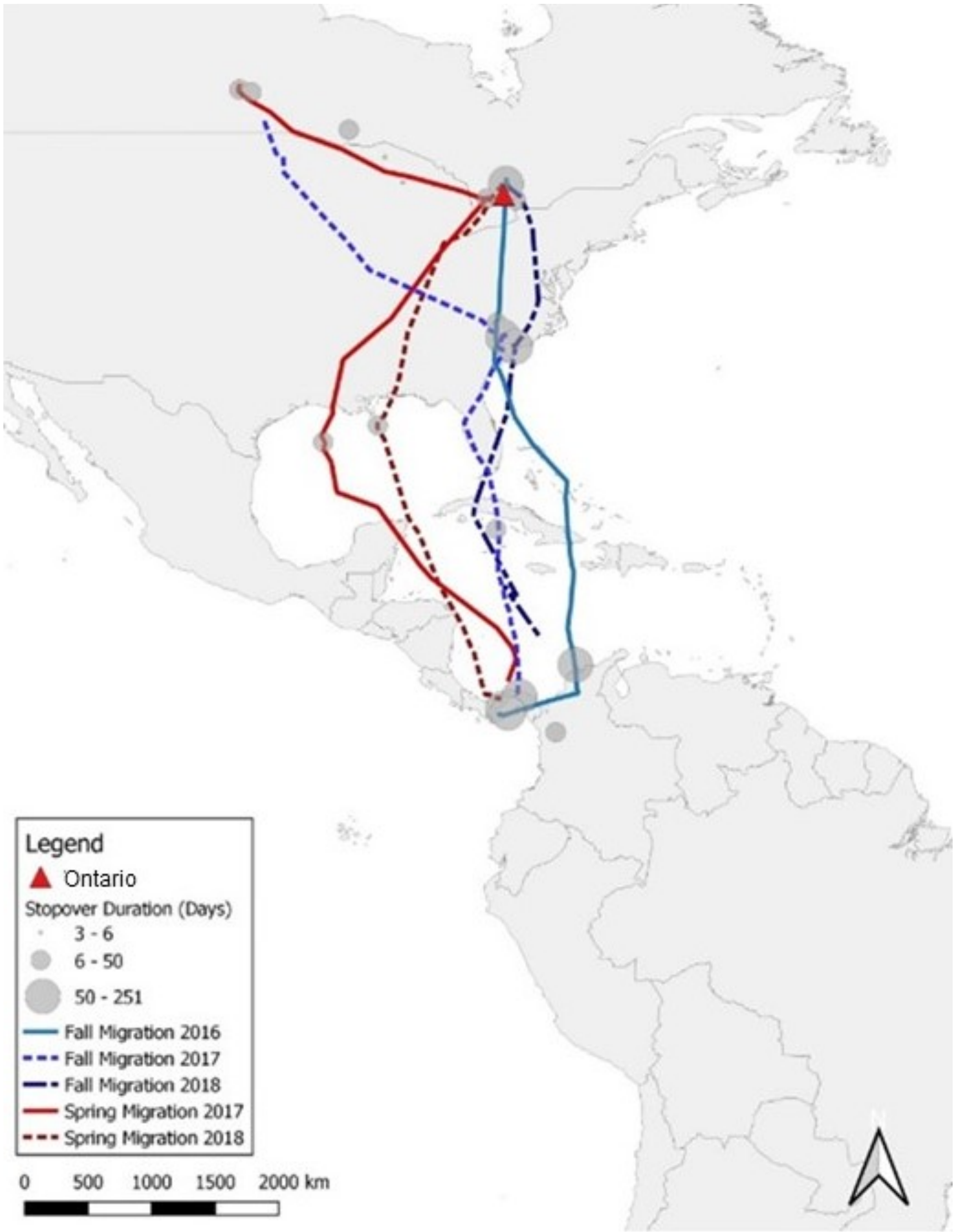

Figure 3.4. Fall migrations (blue), spring migrations (red), and stationary locations (grey dots) of a Black Tern originally tagged at Tiny Marsh, Ontario, in 2016, which subsequently bred in Manitoba in 2017, and was recaptured at Tiny Marsh in 2019.

Supplementary Material:

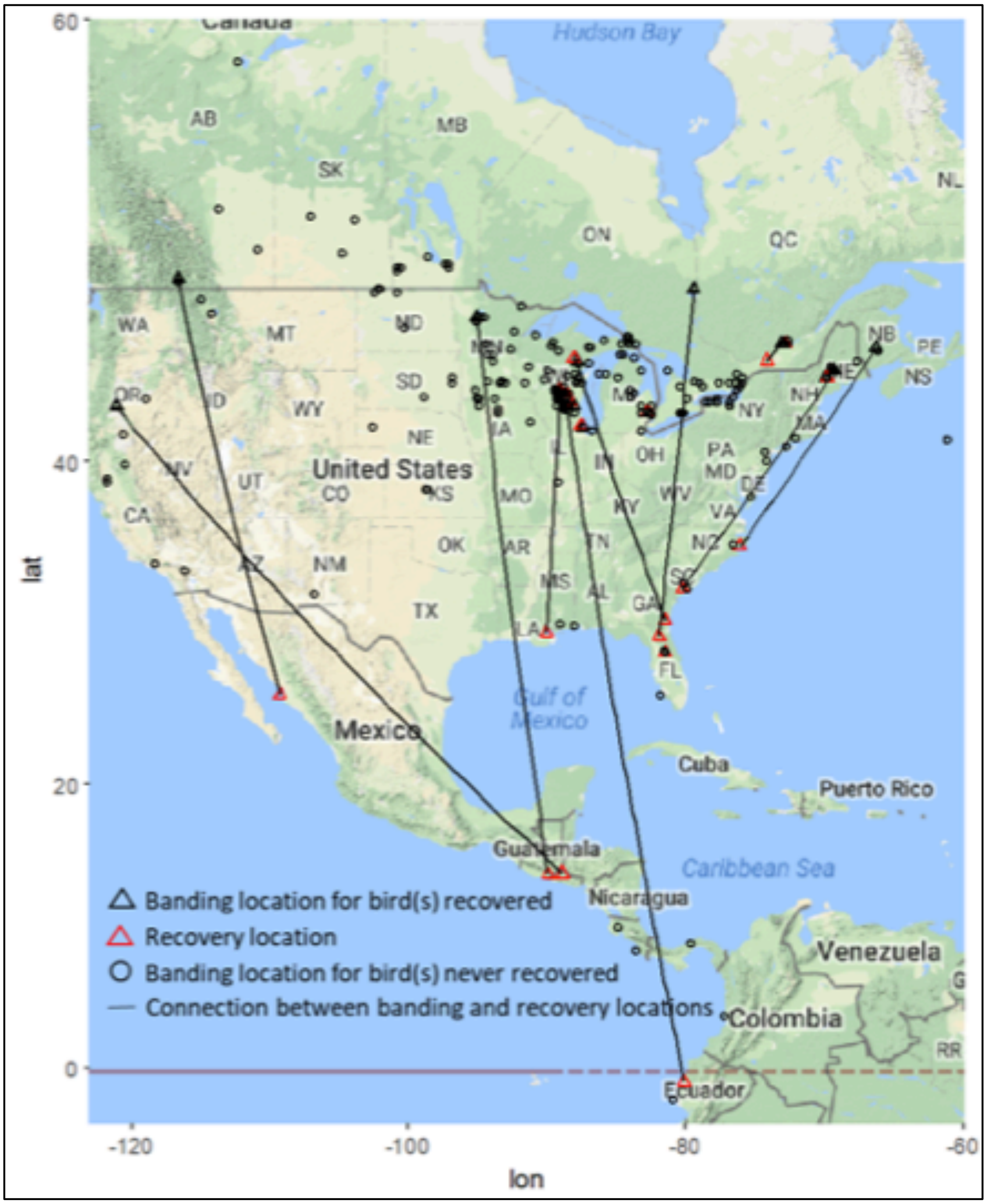

Figure 3.5. Locations of band recoveries from Black Terns across the North American range, based on data accessed from the Canadian Bird Banding Office in January, 2018.

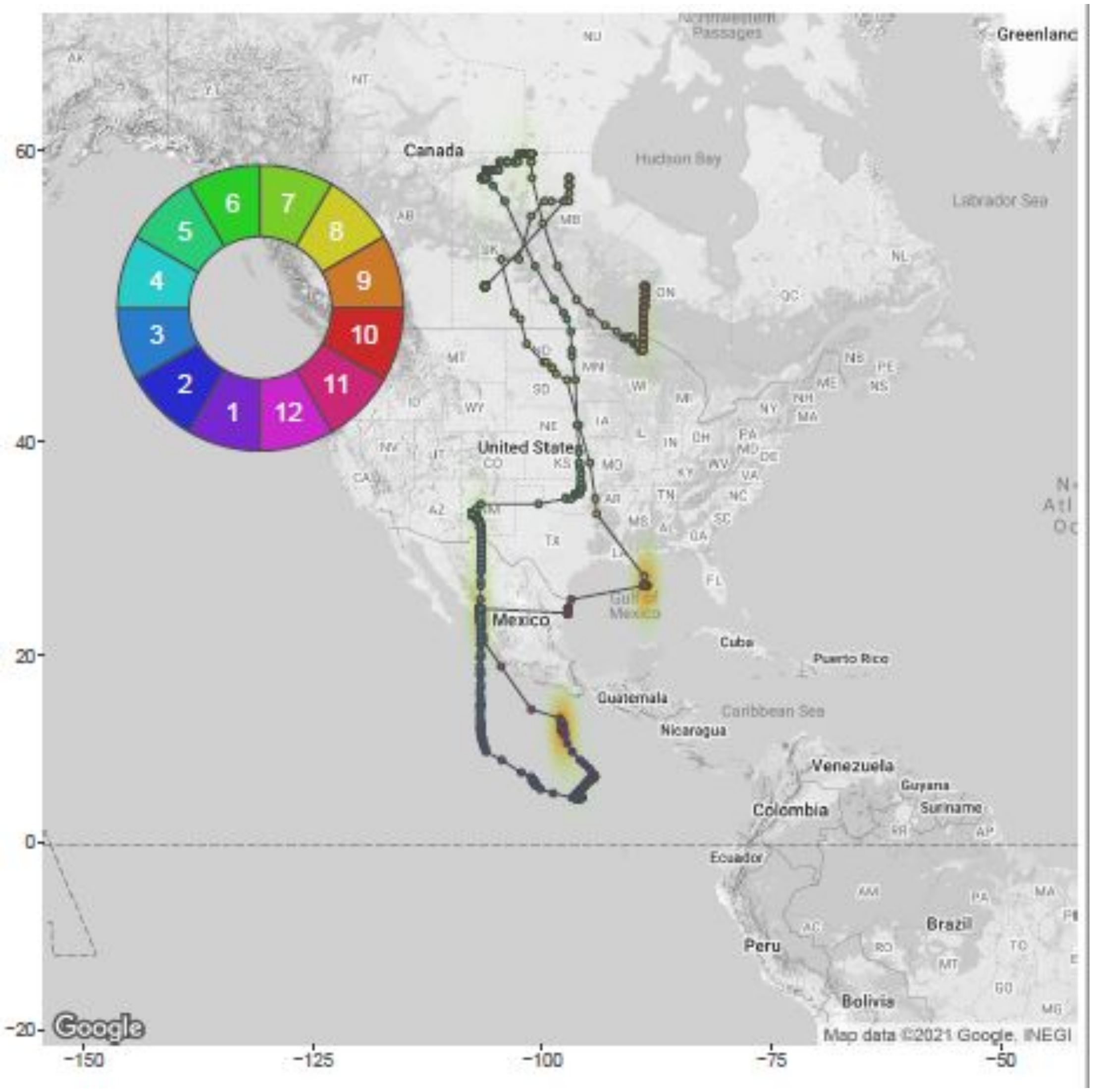

Figure 3.6. Potential migration track of an individual (BR986) originally tagged at Jackfish Lake, SK in 2019, and recaptured in 2021. The tag recorded data from spring 2019 to fall 2020. The colour wheel represents the month of the year, and corresponds with the track colour. This track was not included in the main analysis due to uncertainty surrounding the migratory locations, especially those around Mexico, Ontario, and northern Saskatchewan. Locations in these areas are unlikely to be representative of true movements, but rather an error in the recording of twilight times by the geolocator. Although there is uncertainty in the track, it is possible that this individual travelled south through the centre of the continent during fall migration before possibly staging in the Gulf of Mexico near Texas/Louisiana. Wintering may have occurred off the western coast of Mexico and off the Pacific coast of Central America. Spring staging may have occurred near the Gulf of California before travelling north through central North America and returning to Saskatchewan.

CHAPTER 4:

CONCLUSIONS AND RECOMMENDATIONS

My thesis provides colony occurrence data and habitat associations of Black Terns breeding in Saskatchewan as well as the first detailed tracks for Black Terns breeding in North America. My thesis objectives were to 1) use wetland survey data and aerial imagery to examine the influence of various habitat, land use, and geographic covariates on Black Tern occupancy and abundance in Saskatchewan; and 2) examine full annual cycle movements and potential differences in migratory stop-over and over-wintering locations from Black Terns breeding across their range using light-level geolocators. Habitat association results show that colony occurrence can be predicted using both geographic and habitat covariates and that the latitude of a wetland was associated with the likelihood of Black Tern colony occurrence and abundance. This relationship was quadratic, indicating that there is a narrow latitudinal band within which individuals seem to be occupying wetlands, resulting in higher rates of occupancy and abundance at wetlands along mid latitudes, corresponding to the northern edge of the PPR, and southern edge of the BPE. Additionally, similar to findings from other parts of the breeding range, the extent of emergent aquatic vegetation present at a wetland was associated with an increased likelihood of occupied Black Tern colonies. Tracking results show that migratory routes varied among individuals and colonies; Black Terns from different central and eastern regions used different migratory routes, with birds from the eastern periphery of the range using the Atlantic and Mississippi flyways and birds from the central region using the Central Flyway. All tagged individuals spent some or most of the wintering period at or off the coast of Panama, highlighting the importance of this location during the wintering period. These results suggest Panama might be a key location of population mixing on the wintering grounds. This high degree of intermixing suggests high population spread and weak connectivity between eastern and central regions.

My results are a first step towards filling some of the gaps in knowledge that exist for the North American Black Tern. My research begins to provide insight into how Black Terns are selecting breeding habitats in the core of their range in Saskatchewan. Similar to my findings, previous research in other areas of the breeding range have identified both large-scale and local-scale factors as important for Black Terns in the Great Lakes and the U.S. PPR (Naugle et al. 1999, Naugle et al. 2000, Steen and Powell 2012, Shealer and Alexander 2013, Wyman and Cuthbert 2016). These results imply that the conservation of both individual wetlands as well as larger landscapes is important for the protection of Black Tern populations. Revealing habitat associations for Black Terns in the PPR/BPE is a first step towards understanding how best to protect breeding populations in this important area that has been subjected to long term wetland loss and degradation (Doherty et al. 2015, Niemuth et al. 2017). The timing and use of migratory routes, stop-over sites, and wintering locations by Black Terns were largely unknown, and the migratory tracks collected in this study are the first for the North American subspecies, and as such provide the first preliminary understanding of the Black Tern annual cycle. Revealing migratory route and site use is an important first step towards understanding the non-breeding biology of Black Terns, a process that would allow future research to prioritize important locations used by Black Terns, and identify major threats faced outside of the breeding range. These tracks also allow for an initial estimate of the strength of connectivity across the breeding range, and between breeding and non-breeding locations, an insight that allows for the greater understanding of site use by populations and how local events or threats might impact different portions of the breeding range. Specifically, migratory connectivity was stronger (MC = 0.27 or

0.22, depending on whether two or three breeding locations were considered) between breeding colonies and their first fall stopover, but weaker (MC = -0.18 or -0.17) between breeding colonies and wintering grounds, indicating mixing among individuals from different breeding colonies on the winter grounds. Panama stands out as a focal region during the non-breeding season for individuals in both central (Saskatchewan) and eastern (Ontario, Michigan) breeding areas, with all individuals but one spending some or all of their time at this location during the winter.

4.1 Implications for Waterbirds and Wetland Conservation

The PPR, and to a lesser extent the southern BPE to the north, is a breeding stronghold for a suite of waterbird species (Steen et al. 2016) and supports the vast majority of many breeding waterbird populations including species of gulls, grebes, and terns (Niemuth and Solberg 2003). However, wetland loss in this region, largely as a result of agricultural practices, has altered the landscape and destroyed large proportions of the habitat that breeding waterbirds depend on (Dahl 1990, Watmough and Schmoll 2007). Furthermore, in the face of climate change, the region is projected to experience even greater rates of wetland loss, resulting in the decrease of available breeding habitat for waterbirds, reduction of waterbird breeding ranges, and loss of foraging and nesting opportunities (Drilling 2007, Steen and Powell 2012, Steen et al. 2016).

My habitat association results showed that the presence of Black Terns breeding in the Saskatchewan PPR and BPE is directly associated with the extent of emergent aquatic vegetation present at a wetland. These results build upon the Black Tern habitat association studies previously conducted in the U.S. Great Lakes and PPR (Shealer and Alexander 2013, Wyman and Cuthbert 2016), which highlight the critical importance of wetland ecosystems for Black Tern occurrence. These findings further add to the suite of literature which describe the relationship that exists between waterbirds and wetlands in the PPR (Niemuth and Solberg 2003, Steen et al. 2016, Prairie Pothole Joint Venture 2017). Conserving wetland habitat for wetland dependent species not only benefits species like the Black Tern, but also benefits wetland conservation (Smith and Chow-Fraser 2010, Tozer 2016, Wyman and Cuthbert 2017). Managing and conserving wetland composition and structure, a practice that the results of this study show could directly increase Black Tern presence in Saskatchewan, can help restore wetland ecosystems.

Habitat retention and restoration programs such as Ducks Unlimited Inc. and the Prairie Joint Habitat Venture have already successfully conserved wetlands across North America for waterfowl based on habitat association data (Vanausdall and Dinsmore 2019). Much of the wetland conservation work in the PPR thus far has focused on waterfowl, as waterbirds are comparatively understudied and do not appear to have shown the same degree of benefit as waterfowl from current programs (Prairie Pothole Joint Venture 2017). New habitat models for waterbirds, not just waterfowl, in the PPR could provide greater insights into how wetlands should best be protected for a greater suite of species. As a result, conservation dollars could be prioritized in the future to protect wetlands that host a suite of wetland dependent species including both waterfowl and waterbirds. Perhaps the highest priority action for restoration and the prevention of future wetland habitat destruction is the reduction of wetland drainage and conversion for agriculture, a practice that remains the most pervasive cause of wetland loss and degradation in the region (Doherty et al. 2018). Wetland dependant waterbird species like the Black Tern would benefit from provincial policies that prevent the drainage of wetlands, especially in the PPR, an area where conflicts over wetland drainage are likely to increase in the face of climate change (Breen et al. 2018). In Saskatchewan, the 2016 amendment of the Water Security Agency Act has given the provincial government the authority to remove drainage work, and has made it so that all drainage, existing or future, must be approved by the provincial Water Security Agency (Breen et al. 2018). Despite improvements, these policy changes further highlight the provincial perspective of wetlands as a resource for agriculture, that although now more strictly managed, will continue to be used. Rather, policy changes should begin to incorporate perspectives outside of the agricultural sector including those that prioritize wetland conservation for wildlife and ecosystem services.

4.1.1 Habitat Prioritization Models

Prioritizing habitat for conservation requires specific knowledge about a species distribution and density, information that is often derived from studying patterns of occurrence and abundance (Johnston et al. 2015). However, prioritizing waterbird habitat for conservation can be challenging due to the destruction and degradation of wetland habitat that has already occurred on the breeding grounds (Stralberg et al. 2011). Results from my study revealed that Black Tern colony occurrence can be predicted using both geographic and habitat models and that the latitude of a wetland was associated with the likelihood of colony occurrence and abundance, and that the extent of emergent aquatic vegetation present at a wetland was associated with an increased likelihood of occupied colonies. These results provide a first step for habitat assessment that can inform future habitat models and eventual spatial prioritization of habitats for Black Terns across the Canadian PPR and BPE. The wealth of data available from the citizen science project eBird or other large-scale inventories could be a useful tool in creating more comprehensive Black Tern habitat models in the future (eBird 2020). eBird documents the distribution, abundance, habitat use, and trends of birds worldwide through bird identification entries submitted by participants across the globe and can be used to gain a large-scale picture of species distribution over time. Similar habitat prioritization models have already been created for waterfowl, grassland birds, and shorebirds in the U.S. PPR using open access data including eBird (Doherty et al. 2015, Niemuth et al. 2017). These models can be used to inform areas of grassland and wetland habitat where protection would most benefit non-waterfowl species, in order to complement the significant work that has already gone into protecting waterfowl habitat.

4.2 Future Research Needs for Black Terns

4.2.1 Range-wide Tracking and Migratory Connectivity

Although my results are the first detailed migratory tracks of Black Terns breeding in North America, and have provided some initial insights into migratory routes, stopover site use, migratory duration, and migratory connectivity, these tracks have only been collected from a small portion of the North American breeding range. The migratory routes of individuals from the far eastern and western borders, as well as many areas throughout the central and southern reaches of the breeding range, have yet to be described.

Further migration tracking of Black Terns from unstudied regions of the North American breeding range, particularly those at the furthest eastern and western borders, would present a more complete, range-wide description of Black Tern migratory patterns, and may reveal reasons for the different population trajectories found throughout the range. Furthermore, a greater sample from the core of the range would help to confirm patterns of non-breeding site and flyway use revealed through the three Saskatchewan birds tracked in this study. In addition to providing a more thorough description of Black Tern migratory routes, range-wide tracking will also offer a more complete picture of the strength of migratory connectivity across the breeding range. Understanding the strength of migratory connectivity is crucial for effective protection and conservation of migratory bird species (Harrison et al. 2011, Small-Lorenz et al. 2013, Marra et al. 2015), and is particularly important for migratory species in decline, as it allows us to better predict the probability of local extinction and develop strategies to address the causes of population declines (Bracey et al. 2018, Cohen et al. 2014). For example, is Panama a winter hotspot for individuals across the entirety of the breeding range? Again, studies using eBird data could begin to address this, and combining eBird and tracking data could help to further identify critical time periods for migration, important habitats or areas used by individuals or groups, and may begin to describe associations between Black Terns and existing protected areas used outside of the breeding season. Together, this information will begin to reveal what threats Black Terns face throughout the migratory cycle and could inform the prioritization of staging and winter sites that should be protected for Black Tern use. This will allow for more informed conservation decisions that will maximize benefits for Black Terns.

4.2.2 Understanding Breeding Dispersal and Population Genetic Structure

My study raised further questions and research needs regarding Black Tern breeding dispersal and population genetic structure. These questions were primarily raised due to low recapture rates of geolocators deployed in Saskatchewan. Of the 48 geolocators deployed on Black Terns breeding in Saskatchewan, only 3 were recaptured, resulting in a low return rate of 6%. This in part was due to the disappearance of two colony sites, Bricksaw Marsh and Good

Spirit Lake, in the years following deployment in 2018 and 2019, which likely occurred due to drought. Specifically, spring 2019 was one of the driest on record, and the marsh at Bricksaw was much shallower that year, and completely dry by 2021 (pers. obs.). Additionally, the Black Tern colony at Jackfish Lake, where 23 geolocators were deployed in 2019, was much smaller during the 2020 field season (~24 pairs in 2019 vs 4 pairs in 2020) despite a lack of obvious human disturbance or changes to water levels at this site. The population appeared to rebound in 2021 (~15 pairs), but all three geolocator recaptures from the Jackfish site (one in 2020 and two in 2021) occurred at a different nesting colony located approximately 2.5 km away. It is possible that low geolocator return rates at banding locations and unpredictable breeding site occupancy are a result of high inter-annual breeding dispersal among Black Terns breeding in Saskatchewan. Previous band recapture rates from Wisconsin were also low (11%), indicating that high inter-annual breeding dispersal may also be characteristic at some sites outside of Saskatchewan as well (Shealer 2007). In contrast, geolocator return rates were reasonably high in Ontario and Michigan (Ontario = 35%, Michigan = 30%).

Many bird species show adaptations to seasonal changes through short distance movement, and understanding these movements may reveal insights into a species' genetic structure (Hornell-Willebrand et al. 2014). Dispersal between breeding sites is often a critical demographic process that is important for predicting the population structure and dynamics of a species (Yaber and Rabenold 2002). This process can affect population genetics by promoting gene flow within a population, therefore reducing inbreeding, and potentially increasing productivity (Daniels and Walters 2000). However, reasons for individual dispersal can vary drastically, with dispersal on the breeding grounds occurring to avoid inbreeding, to locate a more desirable mate, to find more suitable breeding area, or to avoid intra-specific competition

(Daniels and Walters 2000). Although North American Black Tern breeding dispersal and population genetics have yet to be studied specifically, previous research and a lack of band re-sighting data suggest that breeding dispersal among populations of Black Terns is high and site fidelity is low (Shealer 2003, Heath et al. 2020). This suggests Black Terns may show high levels of gene flow and correspondingly low genetic structure. Our tracking work also supports this idea, given that different breeding populations showed overlap on the wintering grounds, which is often seen as a mechanism to explain a lack of genetic structure in waterbirds (Friesen 2015). Research in the Ukraine has recently found that breeding site fidelity was high among some local Black Tern populations and low at others, as terns easily re-nested in new nearby locations when faced with unfavourable conditions (Atamas and Tomchenko 2020). In contrast, genetic work on the Eurasian subspecies on a range-wide scale has demonstrated strong genetic structure, perhaps promoted by limited contact at staging sites among breeding populations using different flyways (Szczys et al. 2017b). Only through understanding the genetic structure of the Black Tern can we understand why differences in gene flow might exist between the North American and Eurasian subspecies. Range-wide genetic work on the North American subspecies is thus a research priority; knowledge of the degree of genetic structure would reveal whether different breeding subpopulations exist which should be managed separately, and whether gene flow is asymmetric among breeding populations, perhaps explaining to some degree the differences in population trajectories across the range.

My results suggest that geolocators may not be the most appropriate method for tracking Black Terns in Saskatchewan. Previous studies have noted negative effects of tagging on the behaviour and survival of birds (Bodey et al. 2018). Although there is no evidence suggesting a negative impact of tagging on individuals in this study (Pers. Obs., Shealer and Haverland 2000), low return rates in the prairies indicate that alternative tracking methods may be more suitable. In order to better understand patterns of breeding dispersal and their causes and consequences at an individual level, future research should make use of tracking devices such as radio-transmitting nanotags and satellite transmitting tags, both of which do not require individuals to be recaptured, although the former requires individuals to be within range of a receiver. These are technologies proven to be successful at tracking the movements of small birds (Taylor et al. 2017). The use of nanotags and satellite tags will allow tracking and receiving data from tagged birds over short distances, at a much finer scale than is possible with geolocators or genetics. Inter-annual breeding dispersal could be examined over a small scale via manual tracking of nano-tagged birds, and over larger scales via satellite tags. From a habitat management perspective, understanding the small-scale year to year movements of a species is important for the proper conservation and protection of habitat. For species like the Black Tern which may exhibit a high degree of inter-annual breeding dispersal, it is important to protect and maintain a matrix of habitat types, even if some areas are not occupied in a given year. Satellite tracking could further allow for an identification of important foraging habitats during the breeding season, which could also be targeted for protection.

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