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Tundra Swan (*Cygnus columbianus columbianus*) Habitat Selection during the Nonbreeding Period

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A thesis submitted in partial fulfillment of the requirements for the degree in Master of Science

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**TUNDRA SWAN (*CYGNUS COLUMBIANUS COLUMBIANUS*) HABITAT
SELECTION DURING THE NONBREEDING PERIOD**

(Thesis format: Monograph)

by

Katelyn H. A. Weaver

Graduate Program in Biology

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science

The School of Graduate and Postdoctoral Studies
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London, Ontario, Canada

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Abstract

Changes in availability and foraging profitability of agricultural and aquatic habitats have the potential to greatly influence population dynamics of waterfowl. Therefore, the purpose of my research was to understand habitat selection by Tundra Swans during the nonbreeding period and to explore the scale-dependency of these relationships. Habitat selection was influenced by seasonal changes in nutritional requirements and food availability; Tundra Swans selected open water and agriculture in winter, wetlands were weakly selected during migration when open water was strongly selected (especially during autumn), and there was a 2-fold increase in use of agriculture from autumn to spring. It appears that selection for agriculture and wetlands was influenced by continuous changes in habitat availability, whereas selection for open water changed discretely by region. Based upon my results, habitat management for large-bodied waterfowl should focus on protecting and improving aquatic habitats and ensuring availability of agriculture, especially during winter and spring.

Keywords

Migration, winter, habitat, telemetry, Tundra Swan

Co-Authorship Statement

I was responsible for all intellectual and analytical aspects of the development and completion of my thesis under the supervision of Dr. Scott Petrie and Dr. Hugh Henry. I received satellite telemetry data from Dr. Craig Ely (US Geological Survey Biologist at the Alaska Science Center), Dr. Scott Petrie (Executive Director of Long Point Waterfowl), and Dr. Khristi Wilkins (Chief of US Fish and Wildlife Service). With the assistance of Dr. Michael Schummer (Senior Scientist with Long Point Waterfowl), I developed modeling procedures that I executed in SAS. Monograph draft edits were received from Mr. Rodney Brooks, Dr. Irena Creed, Dr. Hugh Henry, Dr. Thomas Nudds, Dr. Scott Petrie, and Dr. Michael Schummer. All work within this thesis has been authored by Katelyn Weaver and will be published with Craig Ely, Scott Petrie and Michael Schummer.

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List of Abbreviations

AIC – Akaike Information Criterion

CI – Confidence Interval

DAR – Distance Angle Rate

DV – Departure Value

EP – Eastern Population

FDD – Freezing Degree Days

GME – Geospatial Modeling Environment

LC – Location Class

MRD – Maximum Redundant Distance

NARR – North American Regional Reanalysis

PTT – Platform Transmitter Terminal

SAV – Submerged Aquatic Vegetation

US – United States

w_i – Akaike Information Criterion Weight

WP – Western Population

Chapter One: Introduction

Statement of Direction

It is estimated that at least half of the developed world's wetlands were either drained, filled and converted to alternate uses, or highly degraded from pollution by the mid-1900s (OECD 1996). Loss of traditional foraging habitats and increased availability of agriculture resulted in many granivorous waterfowl species exploiting readily available agricultural grains. Consumption of agricultural grains led to substantial increases of several waterfowl populations due to increased energy intake and earlier arrival on breeding grounds (Ringelman 1990, Gauthier et al. 1992, van Eerden et al. 1996, Jefferies et al. 2004, Fox et al. 2005, van Eerden et al. 2005). Moreover, large-bodied waterfowl have altered their migration routes to closely coincide with agricultural availability (Bellrose 1980, Ringelman 1990, Fox et al. 2005). Despite the impacts of agricultural grain consumption, the relationship between use and availability of agricultural and aquatic habitats (i.e., habitat selection) by waterfowl is relatively unknown. The purpose of my thesis was to use Tundra Swan, *Cygnus columbianus columbianus* Ord, satellite telemetry data to investigate geographic and temporal selection of agricultural, open water, and wetland habitats by this large-bodied, Arctic nesting waterfowl species throughout the nonbreeding period.

Habitat Selection by Migratory Waterfowl

Seasonal migrants are vulnerable to changes in both current and future habitats as well as to factors that may interrupt migratory routes (Calvert et al. 2009). Moreover, decreased quantity and quality of migratory foraging and resting habitats have been linked to reductions and fluctuations in species abundance and reproductive output (Moore et al. 1995, Baker et al. 2004, Norris et al. 2004, Drent et al. 2006). Unfortunately, knowledge of migration ecology is often logistically constrained and limited to specific stopover sites (e.g., Barnacle Goose, *Branta leucopsis* Bechst., on outer Norwegian islands – Black et al 1991, Pink-footed Goose, *Anser brachyrhynchus* Baill., at Iceland staging area – Boyd and Fox 1992, Sedge Warbler, *Acrocephalus schoenobaenus* L., at Ramsar coastal estuary, Iberia – Arizaga et al. 2012). Limited understanding of migration and wintering

ecology has resulted in recent reviews identifying a need to address seasonal and regional changes in habitat selection during the nonbreeding period (Arzel et al. 2006, Calvert et al. 2009). Habitat selection is a hierarchical process, involving decision-making at a series of temporal and spatial scales (Johnson 1980, Zhang and Tankuo 2005).

Knowledge of selection of habitats at different seasonal and geographic scales will enable management of adequate resource availability throughout the annual cycle (Calvert et al. 2009). By understanding how known local habitat relationships compare to broad scale habitat selection, it may be possible to extrapolate on current research for resource and habitat management across the nonbreeding period (Zhang and Yankuo 2005).

Historical Use of Agricultural Habitats by Large-bodied Waterfowl

During the mid-to-late 1900s, conversion of wetlands and uplands to agriculture greatly decreased the availability of waterfowl habitats and foods. Following these land conversions, approximately 50% of North American waterfowl species began consuming agricultural foods, at least occasionally, where agricultural waste grains were seasonally available (Bellrose 1980). Shifting foraging strategies were accompanied by earlier arrival on spring stopover sites and on breeding grounds, where birds now arrived in better condition, and increased survival for many species of waterfowl (Gauthier et al. 1992, van Eerden et al. 1996). Furthermore, consumption of agricultural grains was largely responsible for range expansions and great population increases of many large-bodied waterfowl species (i.e., geese and swans; Ringelman 1990, Jefferies et al. 2004, Fox et al. 2005, van Eerden et al. 2005). However, the agricultural market is volatile, and future changes in crop selection and advancements in harvest efficiency may reduce the availability of waste grain below profitability thresholds that are necessary for foraging waterfowl (Fredrickson 1983, Krapu et al. 2004, Stafford et al. 2006, Foster et al. 2010). Therefore, it is important to understand how endogenous and exogenous factors influence selection of habitats by waterfowl.

Maximizing lifetime fitness through allocation of resources to reproduction is the focus of life-history theory (e.g., Roff 1992, Stearns 1992, Roff 2002). An important theoretical component is the storage and subsequent allocation of lipids and proteins for reproduction (Houston et al. 2006). Avian species, unlike mammals, have the ability to

catabolize lipid stores during times of energetic stress instead of burning carbohydrates (Ramenofsky 1990, Klaassen 1996). Large-bodied waterfowl that breed in the Arctic (e.g., Tundra Swans) migrate north during snow and ice melt, a time when food resources are at an annual low (Ebbinge et al. 1982, Hupp et al. 2001, Newton 2004). Moreover, a relatively short breeding period and limited food availability upon arrival to Arctic breeding grounds are associated with waterfowl building nutrient stores during winter, spring, or both, to enable immediate nesting upon arrival to breeding grounds (i.e., they use some endogenous stores for reproduction, classifying them as capital breeders; Drent and Daan 1980, Krapu and Reinecke 1992, Marra and Holberton 1998, Klaassen 2003, Clausen et al. 2003, Studds et al. 2008, Reudink et al. 2009). Following reproduction and moult, Arctic-nesters begin autumn migration when goslings and cygnets are continuing to grow and develop (Bellrose 1980, Sedinger 1992) and adults may be replenishing nutrient reserves catabolized during breeding and wing molt (Petrie et al. 2002, Badzinski et al. 2011). Because of the above nutritional demands, the availability of foods high in carbohydrates, proteins and other nutrients during the nonbreeding period is important to Tundra Swan productivity and survival (Klaassen 2003).

Agricultural grains represent a food source high in metabolizable energy, yet they are deficient in daily requirements of many inorganic elements, essential amino acids, and vitamins (Baldassarre et al. 1983, Delnicki and Reinecke 1986, Loesch and Kaminski 1989). Because waterfowl cannot obtain certain vital nutrients through agricultural foods, a monotypic diet of agricultural grains results in lower body mass and therefore cannot be maintained for long periods of time (Baldassarre et al. 1983, Jorde et al. 1983, Loesch and Kaminski 1989). When consuming a mixed agricultural and aquatic diet prior to spring migration, increasing the proportion of aquatic vegetation in their diets has been documented to improve body condition in Bewick's Swans (*Cygnus columbianus bewickii* Ord, measured by abdominal profile index; Hoye et al. 2012). Previous studies suggest that consideration of nutritional value of foods in combination with an individual's current and predictable future physiological requirements is important to understand habitat selection during the nonbreeding period (e.g., Hutto 1985, Prins and Ydenberg 1985, Brown 1988, McKay et al. 1994).

Optimal foraging theory states that animals strive to maximize fitness by increasing their long-term energy intake (Stephens and Krebs 1986). Following this theory, changes in habitat selection are often associated with the depletion of the quantity and quality of available foods (Sutherland 1996, Rowcliffe et al. 2001, Chisholm and Spray 2002). Waterfowl food depletion studies have determined that, although aquatic vegetation is abundantly available immediately following the summer growing period, its availability decreases between autumn and spring as a result of foraging and winter senescence (Alisauskas and Ankney 1992, Badzinski 2003, Badzinski et al. 2006). Moreover, accessibility of aquatic plants is often reduced by ice during winter and spring (Schummer et al. 2010). Agricultural grains, on the other hand, are a food source rich in carbohydrates, and are available throughout much of the nonbreeding range of Tundra Swans and other waterfowl (Ringelman 1990, Alisauskas and Ankney 1992, Petrie et al. 2002). Therefore, one would expect waterfowl to select agricultural resources during winter and spring when aquatic foods are less available, less accessible, or limited on both accounts.

Tundra Swan Life History

Tundra Swans are large-bodied (range in adult body mass = 3.4-9.6 kg), migratory waterfowl with a Holarctic distribution (Madge and Burn 1987). The species is commonly separated into two taxa, the Palearctic Bewick's Swan and the Nearctic Tundra Swan, formerly known as the Whistling Swan (hereon Tundra Swan; American Ornithologists' Union 1998). Tundra Swans are the most numerous and widely distributed swan in North America and are managed as Eastern and Western Populations (EP and WP, respectively) based upon different breeding and wintering ground affinities (Bellrose 1980). My research focused on EP Tundra Swans, which winter from North Carolina to the Great Lakes and breed in the tundra from Alaska's north slope to eastern Hudson Bay, including the Fox Islands and Baffin Island (Sladen 1973, Madge and Burn 1987). Overall, EP Tundra Swans spend 19% of the annual cycle on wintering grounds, 52% on autumn and spring staging areas, and 29% on breeding grounds (Petrie and Wilcox 2003). During migration, most of the population follows a relatively narrow corridor between the Atlantic Coast and northern Prairies, splitting into three distinct

corridors in the northern Boreal Forest before reaching their breeding grounds (Figure 1.1). During autumn migration, EP Tundra Swans spend approximately half of their time in the Boreal Forest and the other half in the Prairies and Great Lakes; during spring they spend the majority of their time in the Great Lakes and Prairies, passing quickly through the Boreal Forest (Petrie and Wilcox 2003).

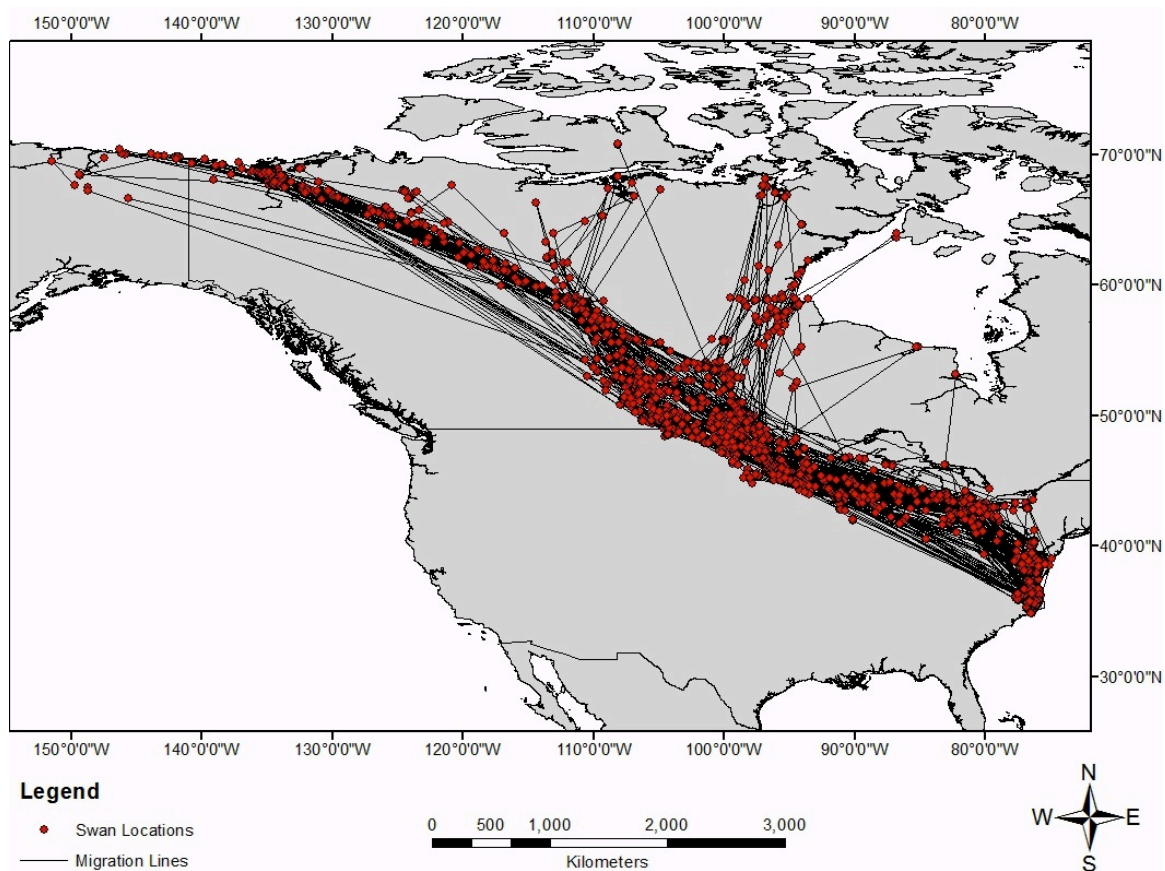


Figure 1.1 Map of Eastern Population Tundra Swan best of day locations (red dots) during the nonbreeding period as determined by satellite telemetry from 63 Tundra Swans (1998-2012); connected by migration lines (in black, delineates individual bird movements) to indicate migration corridors.

Habitat Switching by Tundra Swans

Tundra Swans began foraging in agricultural fields in the mid-1960s (Nagel 1965, Tate and Tate 1966). Following the consumption of agricultural grains, population numbers for Tundra Swans in North America nearly doubled between 1955-1989 (Serie and Bartonek 1991), with the EP now numbering just over 100,000 individuals (Serie et al.

2002). Because of the substantial changes to Tundra Swan populations brought on by the consumption of agricultural grains, it is paramount that we understand the selection of agricultural and aquatic habitats during the nonbreeding period to manage resource availability and maintain a stable population of Tundra Swans. Anecdotal evidence and a few location specific studies suggest that Bewick's and Tundra Swans rely primarily on aquatic vegetation during autumn migration, aquatic and agricultural foods through winter and primarily agricultural foods during spring (Munro 1981, Bortner 1985, Beekman et al. 1991, Earnst 1994, Nolet et al. 2002, Petrie et al. 2002). To my knowledge, no studies in North America have quantified changes in habitat selection by large-bodied waterfowl throughout the nonbreeding period. I explored the connection between previous location-specific knowledge and broad-scale geographic and temporal selection of agricultural, wetland and open water habitats by Tundra Swans. By increasing our understanding of the mechanisms (external factors driving selection) influencing nonbreeding habitat selection, it may be possible to more accurately predict the selection of habitats with changing habitat availability and environmental conditions.

Aquatic habitats can be classified into five systems: 1) marine – open ocean over the continental shelf, 2) estuarine – tidal habitats with access to open ocean, 3) riverine – all habitat within a channel, 4) lacustrine (lakes) – systems in a depression or dammed river channel with less than 30% plant coverage and an area exceeding 8ha, there is also generally considerable wave action, and 5) palustrine – non-tidal wetlands dominated by trees, shrubs, persistent emergents, emergent mosses or lichens. Palustrine also includes wetlands lacking vegetation that are less than 8ha in size and 2m deep with no wave-action and a salinity less than 0.5% (Cowardin et al. 1979). Throughout my thesis, open water habitats refer to rivers, lakes and estuarine and marine deep-water habitats; wetlands include all palustrine aquatic habitats (see Appendix A).

Satellite Telemetry and Habitat Selection

Satellite telemetry uses Platform Transmitter Terminals (PTTs) that are either attached externally or surgically implanted to remotely track animal movements (Hatch et al. 2000, Wilson et al. 2002). Signals from PTTs are sent to satellites orbiting Earth, which localize the signal and create a positional fix for the PTT, thereby identifying the latitudinal and

longitudinal location of each animal (Wilson et al. 2002). Telemetry technology, such as biotelemetry (remote monitoring of physiological, behavioural and energetic data), and mapping of migration routes, critical stopovers and anthropogenic barriers to migration has enabled scientists to study many aspects of migratory ecology in inaccessible environments (Perras and Nebel 2012). Because there is limited knowledge of seasonal and geographic habitat selection by waterfowl, I used satellite telemetry to investigate habitat selection by EP Tundra Swans, a large-bodied, Arctic nesting waterfowl species, during the nonbreeding period. Information from this study will contribute to scientific understanding of waterfowl migration and habitat selection and may help guide allocation of management resources for Arctic nesting waterfowl throughout the nonbreeding period (Martin et al. 2007).

Thesis Objectives and Competing Hypotheses

Consumption of agricultural foods and subsequent population level changes for many waterfowl species has created a potential bottleneck of resource availability to waterfowl during the winter and migratory periods. Changes in agricultural practices (resulting in lack of green weedy vegetation, reduced availability of waste grain, and altered crop types) and loss and degradation of aquatic systems have the potential to greatly impact the population dynamics of waterfowl. Moreover, because of the difference in nutritional profitability and the seasonal availability and accessibility of agricultural versus aquatic foods, it is important to understand selection of these habitats to ensure adequate resource availability to waterfowl during the nonbreeding period (Gates et al. 2001). Also, spring staging sites are underrepresented in the international network of protected wetlands (Arzel et al. 2006) and my research may help identify important wetland areas that should be protected. Therefore, I sought to increase knowledge of broad-scale selection of agricultural, open water, and wetland habitats by large-bodied waterfowl through use of satellite telemetry from 63 EP Tundra Swans. Results from my study will provide valuable insight into demographic patterns and conservation needs common to diverse migratory taxa (e.g., Martin et al. 2007, Bolger et al. 2008, Robinson et al. 2008, Sherrill-Mix et al. 2008).

The research questions I address within my thesis are: 1) do Tundra Swans differentially

select open water, wetlands and agriculture seasonally and geographically throughout the nonbreeding period; 2) do local seasonal habitat use patterns remain the same when explored on broad regional and temporal scales; and 3) what is the relative influence of habitat availability, nutritional requirements, and seasonal food availability on the temporal and geographic selection of agricultural and aquatic habitats. Because I was not able to measure directly the influence of habitat availability, nutritional requirements and seasonal food availability (i.e., the selection factors of interest), I included variables to represent their influence on habitat selection. I also included discrete and continuous measures of each variable to determine how habitat selection varied by location and time. When exploring selection of agricultural and aquatic habitats I chose regions (Atlantic Coast, Great Lakes, or Prairies) to represent discrete changes in habitat availability, and latitude and longitude to represent continuous changes in habitat availability. To address changes in nutritional requirements and seasonal food availability I chose season (autumn, winter, or spring; discrete changes) and study date (continuous changes) as representative variables. Because there are no agricultural habitats available in the Boreal Forest (Wiken 1986), I explored selection of aquatic habitats in the Boreal Forest separate from exploration of agricultural and aquatic habitats in the Atlantic Coast, Great Lakes and Prairies.

I hypothesized that habitat selection during the nonbreeding period could be most strongly influenced by: 1) geographic changes in habitat availability; 2) temporal variation in nutritional requirements and food availability; or 3) both geographic and temporal changes combined. I evaluated my competing hypotheses at different temporal and geographic scales through a set of candidate models to investigate selection intensity (i.e., the magnitude of difference between proportional use of a habitat and its availability on the landscape) of agriculture, open water, and wetlands by EP Tundra Swans during the nonbreeding period (see Statistical Analysis in Methods). Based upon previous literature on Tundra Swan habitat use and knowledge of food and habitat availability alongside nutritional requirements of Tundra Swans, I predicted that Tundra Swans would select aquatic habitats during autumn and a combination of agricultural and aquatic habitats during winter and spring. For the Boreal Forest, I predicted that both wetlands and open water would be selected during autumn and that open water would be

selected more strongly than wetlands during spring based upon the assumption that smaller wetlands would be ice-covered at that time.

Chapter Two: Methods and Experimental Design

Study Area

I classified geographic regions used by EP Tundra Swans during the nonbreeding period as: 1) Atlantic Coast; 2) Great Lakes; 3) northern Prairies; and 4) Boreal Forest (Figure 2.1). I explored yearly habitat selection of agricultural and aquatic habitats by EP Tundra Swans starting in the Prairies from late-September or early-October (dependent upon year), to the Great Lakes and Atlantic Coast through winter, back to the Great Lakes in spring, and finally leaving the Prairies in mid-to-late May for Boreal locales and Arctic breeding areas. Yearly habitat selection of open water and wetlands was explored separately in the Boreal Forest where Tundra Swans passed through during spring (mid-April to late-May or mid-June) and autumn (late-August or early-September to early-to-mid-November) migration.

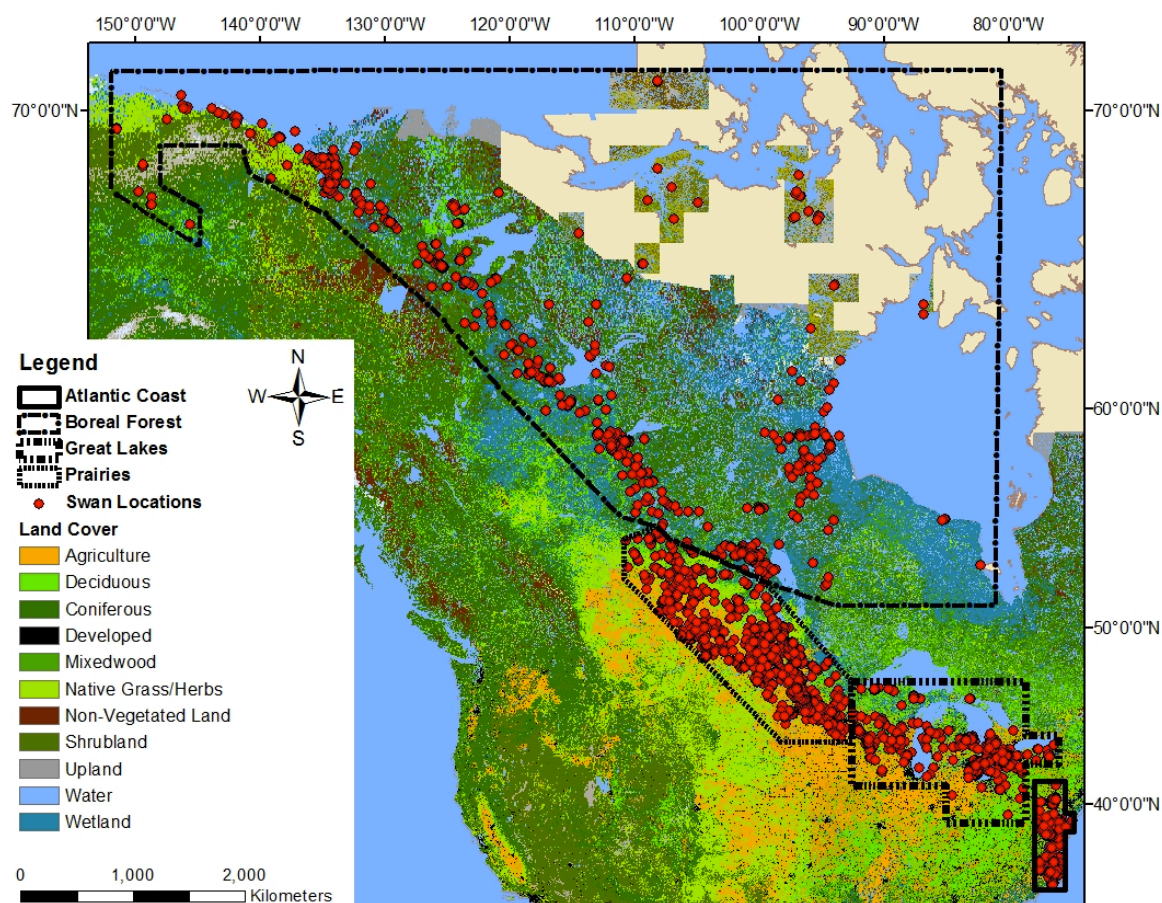


Figure 2.1 Eastern Population Tundra Swan nonbreeding habitat range (based upon best of day locations from satellite telemetry data from 63 Tundra Swans, shown in red) with assigned geographic regions (Atlantic Coast, Boreal Forest, Great Lakes and Prairies) determined by designated ecoregions, land cover and Tundra Swan location data. Colours on map indicate habitat type (see map legend).

Capture and Marking of Tundra Swans

Sixty-three adult EP Tundra Swans were marked with satellite telemetry units between 1998 and 2008; 12 at Long Point, Ontario (42.579 N, 80.430 E) in the Great Lakes during spring and autumn migration (Petrie and Wilcox 2003), 41 in the Atlantic Coast overwinter (Wilkins et al. 2010), and 10 in the Arctic Coastal Plains in Alaska during the breeding period (Ramey et al. 2012). Of the transmitters attached at Long Point, seven Tundra Swans were marked in spring and autumn of 1998 (95 g backpack harnesses) and five in spring of 1999 (30 g neck collar transmitters). Transmitters attached in 1998 were programmed to transmit data for 24 h a day for the first 30 days and for 8 h every 3 days

afterwards, lasting for approximately 100 days after December 1998. Transmitters attached in 1999 were programmed to transmit for 8 h every 5 days and lasted until September 2000 (Petrie and Wilcox 2003). Of the 41 Tundra Swans marked on mid-Atlantic wintering grounds, six were in Maryland, 18 in North Carolina, 10 in Pennsylvania, and seven in Virginia from November 2000-March 2002 (39 g neck collar transmitters; Wilkins 2007, Wilkins et al. 2010). Transmitters for Tundra Swans marked on wintering grounds provided location information for 8 h every 4 days during September – May and 8 h every 8 days during June – August, 2001–2003. The 10 Alaskan transmitters were attached in August and transmitted data for 5 h every 18 h, from mid-September – December 2008 and mid-March – mid-May 2009, for 5 h every 72 h from December 2008 – mid-March 2009, and for 5 h every 80 h mid-May 2009 – December 2011 (Craig R. Ely, USGS Research Wildlife Biologist, personal communication, Ramey et al. 2012).

Data Processing and Analysis

The Argos Data Collection and Location System is used worldwide to provide satellite telemetry information by emailing raw location data to researchers on a daily basis (Service Argos 2008). Argos has five polar-orbiting satellite receivers and calculates geographical positions as a satellite passes over the transmitter using the Doppler shift (Miller et al. 2005, Krapu 2011). Further information about the Argos system can be found in Fancy et al. (1988) and Harris et al. (1990). Accuracy of Argos satellite location data is classified according to seven Location Classes (LCs) based on satellite-to-transmitter geometry, the number of transmissions received and the stability of the transmission frequency. The seven accuracy ratings are grouped as Standard, LC-3 = <250 m radius, LC-2 = 250-500 m radius, LC-1 = 500-1500 m radius; and Auxiliary, LC-0 = >1500 m radius, and LC-A, -B and -Z = no accuracy assessment (Service Argos 2008). Because there must be a certain level of error assumed with each locational fix (Minton et al. 2003), I created a circle around each fix, known as Used Polygons, with a radius matching the assigned LC to account for satellite inaccuracies (e.g., Used Polygon with LC-1 had a 1500 m radius).

I used the following criteria to filter location data and to classify these data by time of day and period:

- 1) **Filtering for Accuracy:** I used the Douglas Argos-Filter Algorithm (Douglas-Filter) in Movebank to filter satellite location data (Douglas 2006, Douglas et al. 2012). The Douglas-Filter has three different filtering methods. Each filter acts upon raw tracking data of each individual animal, evaluating three consecutive locations at a time. The first filter method, Maximum Redundant Distance (MRD), addresses spatiotemporal redundancy under the assumption that significant location errors are unlikely to occur consecutively in the same geographic area. For MRD, the user sets a maximum distance from each location beyond which all other locations are rejected within a set time frame. The second filter method, Distance Angle Rate (DAR), removes Argos locations that exceed travel rate and bearing between three consecutive locations and the location under evaluation by evaluating velocity, internal angle of intersection and length of adjoining locations. The third filter method, Hybrid, merges the previous MRD and DAR and is used for birds that intermittently migrate long distances or remain in relatively localized nesting, molting, staging or wintering areas (Douglas et al. 2012). I used the Hybrid filter based upon default parameters; 10 km redundancy value, 50 km/h maximum rate of travel, and $>150^\circ$ angle of divergence.
- 2) **Diurnal or Nocturnal:** I classified each Tundra Swan location as a daytime or nighttime fix using available macro equations for Microsoft Excel (Minton 2003, Sunrise/Sunset - <http://www.ecy.wa.gov/programs/eap/models.html>). I considered locations occurring between civil sunrise and sunset (when the sun is 6° below the horizon) as diurnal, and locations between civil sunset and sunrise the next day as nocturnal.
- 3) **Best of Day:** I manually filtered the Douglas-Filtered location data by choosing the most accurate LC available for each diurnal and nocturnal period. Due to the scale of my research, I used Standard locations only to ensure use of the most accurate locations (Miller et al. 2005). In the event of a tie with equally accurate LCs, the location with the greatest IQX prevailed, and if another tie occurred, the location with the highest number of messages was chosen. If there was still a tie, the

location with the highest IQY was chosen. If all three of these values were a tie, I randomly chose one location to remain (*sensu* Service Argos 2008). IQX and IQY give information on the PTTs in terms of 2 digits, the X is the first digit and indicates residual error on the frequency calculation and Y is the second digit and indicates the drift in transmitter oscillator frequency between two satellite passes (Service Argos 2008).

- 4) **Period:** I categorized each Tundra Swan location as autumn, winter, or spring (*sensu* Wilkins 2007) to compare seasonal habitat selection. I categorized PERIOD on movements of individual Tundra Swans because timing of migration and wintering have greater biological relevance than calendar dates used to define seasons. I considered autumn migration to be initiated on the day a Tundra Swan traveled >150 km from the breeding grounds, and to be ended upon arrival at a terminal southern location (with Maryland to North Carolina representing one location; Wilkins 2007). Subsequent sites were considered winter locations until a northerly movement >150 km was detected, which I interpreted as the onset of spring migration for that Tundra Swan. From the spring onset date forward, sites were considered spring migration until arrival on the breeding grounds, defined as satellite locations that did not vary by >150 km during late spring and early summer. Because this was a nonbreeding period study, I removed all breeding locations and any further erroneous location data (e.g. dead birds or dropped transmitters).

I used conditional habitat analyses to control for changes in habitat availability by location by pairing Used and Available Polygons at each Tundra Swan location (Figure 2.2; Duchesne et al. 2010). I created Used Polygons by exporting filtered location data from Movebank as ESRI Shapefiles, importing these data in ArcGIS, creating unique layers for LC-1, -2, and -3 and buffering by the radius of the estimated error. I merged all three layers to create one file for all Used Polygons. The radii of Available Polygons were based on the 90% upper confidence interval of average daily foraging distance. I determined average daily foraging distance by tracking Tundra Swans from roost, to daily foraging sites and back to roost using the following criteria:

- 1) The Tundra Swan demonstrated at least one before-sunrise, one diurnal, and one after-sunset location within a given day (selected from Argos-Filtered dataset before manual filtering). Before-sunrise, diurnal and after-sunset locations were manually filtered to include only one best location for each time period within the 24-hour set (n = 81 sets).
- 2) The 24-hour set demonstrated a “back and forth” pattern unless consecutive locations were within 2 km of each other (these were considered the same location and were included in analysis as a single location). I defined “back and forth” patterns by first drawing a straight line between the before-sunrise and diurnal locations, next I created a perpendicular line and after-sunset locations that stayed on the same side of 180° boundary as the before-sunrise locations were considered to demonstrate a “back and forth” movement (Figure 2.3).
- 3) All breeding locations were excluded from analysis, leaving 44 24-hour sets (17 during autumn, 15 during winter and 12 during spring; total of 88 roost to forage or forage to roost flights) for analysis.

Legend

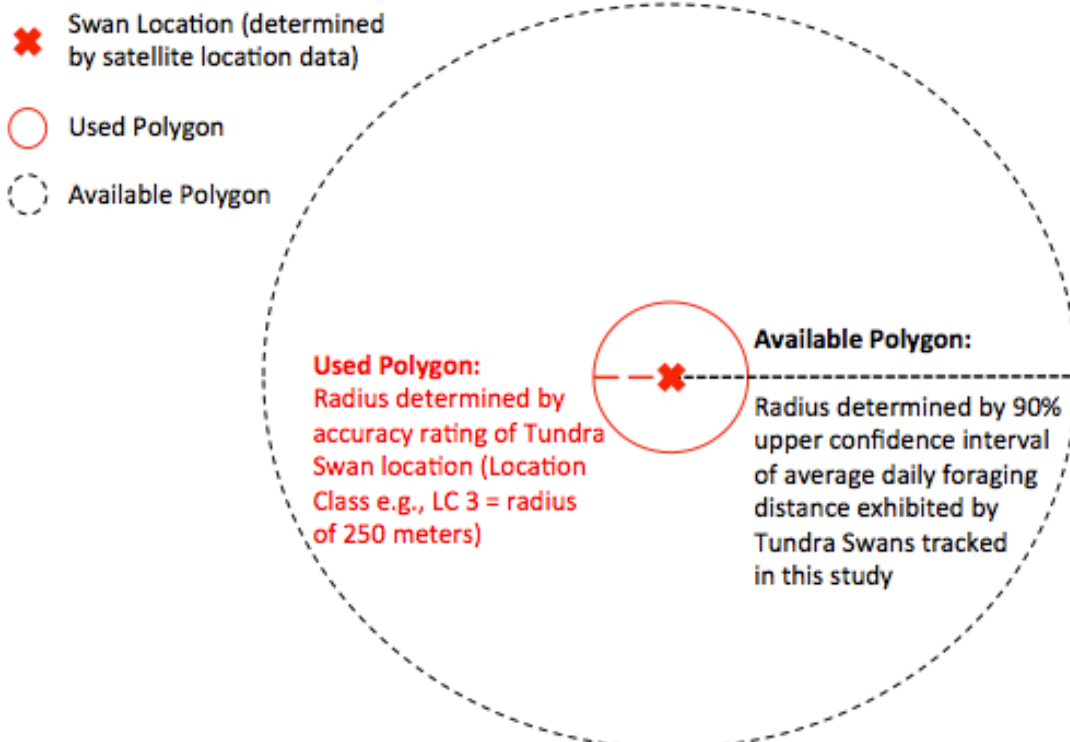


Figure 2.2 Visual representation of the methodology used to create Used Polygons and Available Polygons in ArcGIS 10.

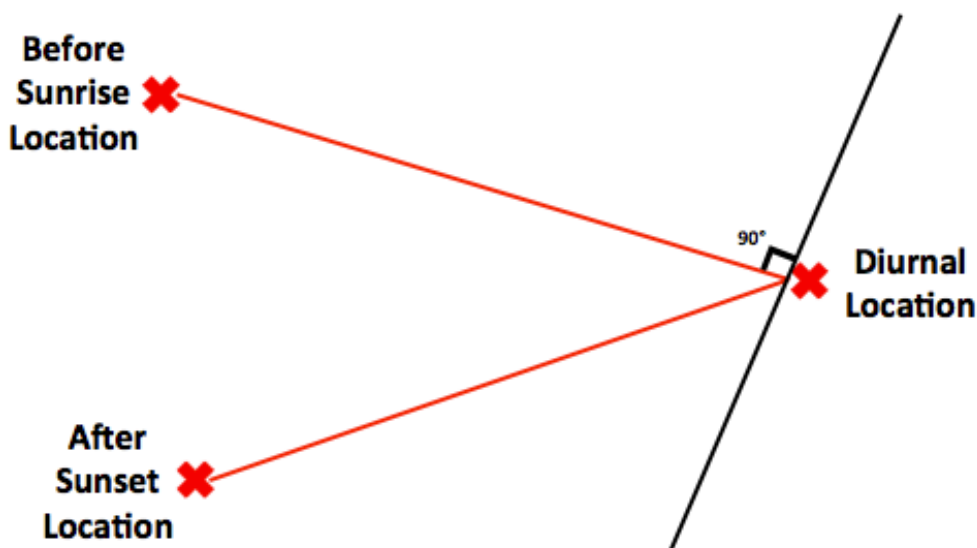


Figure 2.3 Back-and-forth criteria used to determine average daily foraging distance. As long as the After Sunset Location remained on the same side of the 180° line as the Before Sunrise Location, the set was considered as Daily Movements.

Habitat Analysis

I mapped habitats along migration routes and on wintering areas by projecting land cover and aquatic habitat data in ArcGIS (Minton et al. 2003). For Canada, I used the Ducks Unlimited Hybrid Wetland Layer and supplemented with Natural Resources Canada's Circa 2000 for northern Canada obtained from GeoBase. For the United States (US), I used the National Land Cover Database 2001 from the US Geological Survey database (Homer et al. 2007). Because habitat data were obtained from different sources, I created a new classification system called the Habitat Analysis Classification System using a cross-walk method to ensure continuity between Canada and US land cover designations (see Appendix A); the habitat types which I chose to explore were open water, wetlands and agriculture. To determine proportions of each habitat type present in Used and Available Polygons, I used the *Intersect Polygons with Raster* and *Intersect Polygons with Polygons* functions in Geospatial Modeling Environment (GME; Hawthorne 2001-2012). The GME functions produced output values between 0 and 1 for each habitat type, representing the proportion of the polygon that habitat type occupied. I then calculated

selection intensity of each habitat type by subtracting the proportion of each habitat type present in Available Polygons from those present in their paired Used Polygon (e.g., polygon pair: proportion of agriculture in Available Polygon = 0.3, proportion of agriculture in Used Polygon = 0.8, selection intensity = 0.5). I also obtained mean raw habitat use and availability information by region and season to aid in interpretation of results.

Habitat accessibility plays a major role in habitat selection and is influenced by many social, inter-specific and environmental factors, such as human disturbance, predation, and weather (Garshelis 2000, Matthiopoulos 2003, Aarts et al. 2008). Generally, habitat accessibility cannot be quantified, but because weather data are readily available at great spatial scales, and given the potential for changing climates (Crick 2004, Inkley et al. 2004), I included indices of snow and ice as covariates in my analysis to determine if selection intensities were influenced by these weather variables (Schummer et al. 2010). I calculated a snow index from snow depth data obtained through Movebank from the National Centers for Environmental Prediction's North American Regional Reanalysis (NARR) Snow Depth databank. I considered snow depth >1 cm as the presence of snow. I indexed ice using Freezing Degree Days (FDD) because this metric is correlated with percent ice cover and thickness in lakes and wetlands in North America (Boyd 1975, Assel 1990). To calculate FDD I completed the following based on Boyd (1975):

- 1) I obtained mean daily temperature values from NARR for all Tundra Swan locations from the date the location was recorded, backdated to 1 October of that nonbreeding period (e.g., if a Tundra Swan was located at location X on 20 January 2002, I calculated the mean daily temperature for location X from 1 October 2001 – 20 January 2002)
- 2) I calculated the amount each mean daily temperature departed from freezing (0 °C; termed departure value, DV).
- 3) I calculated Freezing Degree Days as $FDD = \sum (- DV)$, whether DV was positive or negative. Including positive DVs controlled for days >0 °C when there would be a tendency for ice to melt or ground to thaw. Including a negative sign before DV ensured that the FDDs calculated would be a positive value for the period.

Statistical Analyses

I investigated factors influencing selection intensity for open water, wetland, and agricultural habitats using Generalized Linear Mixed Models in SAS (Zurr et al. 2009); a mixed model approach was necessary because I included both fixed and random effects. Using an information-theoretic approach for science based, a priori model selection (i.e., presenting plausible mechanisms for habitat selection and choosing appropriate variables to represent these mechanisms; Burnham and Anderson 2002, Richards 2005), I developed a candidate set of 10 models. The candidate model set was used to assess the amount of variation in selection intensity for OPEN WATER, WETLANDS, or AGRICULTURE explained by REGION (Atlantic Coast, Great Lakes and Prairies), LATITUDE and LONGITUDE, PERIOD (autumn, winter, spring), STUDY DATE, and biologically plausible combinations (explored concurrent contribution of these independent variables on selection intensity; Table 2.1; PROC Mixed, SAS Institute 2009). REGION, LATITUDE and LONGITUDE address changes in location, and support for either variable would suggest changes in selection are driven by habitat differences rather than seasonal availability of food and physiological requirements, as would be suggested by PERIOD and STUDY DATE. Support for REGION would suggest that discrete regional differences influence habitat selection in Tundra Swans, whereas LATITUDE and LONGITUDE would suggest a gradient of change by location. Support for PERIOD would suggest that changing food availability and physiological needs of Tundra Swans drive changes in habitat selection and these shifts occur at discrete times such as initiation of migration. STUDY DATE would also suggest habitat selection was influenced by food availability and timing of physiological requirements, but that these influential variables scale to continuously changing time rather than seasonal endpoints. To investigate selection intensity of OPEN WATER and WETLANDS for the Boreal Forest, I removed all candidate models containing REGION and was left with six models (Table 2.1).

I included LC and DAYNIGHT (diurnal or nocturnal location classification) as categorical fixed covariates to control for variation attributable to differences in size of error circles and diurnal and nocturnal selection, respectively. Because weather variables

may influence habitat accessibility, I included SNOW as a fixed categorical covariate and ICE as a fixed continuous covariate. I included STUDY DATE nested in YEAR as a repeated measure to account for sampling of the same individual through time (Zurr et al. 2009). Including Tundra Swan ID as a random repeated variable was necessary to account for the nested nature of the data (i.e., repeated measures from individual birds) because individual birds are more likely to exhibit similar habitat selection repeatedly. Including YEAR and ID as a random variable rather than a fixed variable also allowed me to make statistical inferences about the entire EP, instead of limiting the application of my results to the 63 Tundra Swans in my study (Zurr et al. 2009). I used Studentized Residuals of model outputs to confirm that all data within models approximated a normal distribution and used Compound Symmetry covariance structure for my analysis because it produced the least Akaike Information Criterion (AIC) value from a suite of tested covariance structures (Littell et al. 2007).

I used AIC to determine which model(s) best explained variation in selection intensity for each habitat type by comparing ΔAIC and AIC weights (w_i ; Akaike 1973, Burnham and Anderson 2002). Delta AIC provides a measure of each model relative to the best model (model with the lowest AIC value) by comparing AIC values from the best model and the model in question; $\Delta AIC \leq 2$ suggests substantial evidence for the model, ΔAIC between 3–7 indicate considerably less support, and $\Delta AIC \geq 10$ indicate the model is very unlikely. Another measure of strength of evidence for the model is w_i , which indicate the probability that the model is the best among those considered in the candidate model set (Burnham and Anderson 2002). When interpreting selection results, I only considered models ≤ 2.0 ΔAIC units from top models and, when multiple models were ≤ 2.0 ΔAIC , I used model averaging to estimate parameters, 95% confidence intervals (CI), and model-adjusted predicted values of OPEN WATER, WETLANDS or AGRICULTURE (Burnham and Anderson 2002). Model averaging provides a weighted estimate of parameter values for each variable included in the top models and is done by averaging the estimates according to how likely each model is. By averaging estimates of each variable across top models you include model selection uncertainty in the estimate of precision of the parameter and produce unconditional estimates of variances and standard errors (Wasseman 2000).

Table 2.1. Candidate model sets conducted in SAS as General Linear Mixed Models and compared using AIC weights to determine relative influence on selection intensity of OPEN WATER, WETLANDS, or AGRICULTURE.

Competing Hypothesis	Influence Explored	Models
Habitat Availability	Discrete influence of location	REGION
Habitat Availability	Continuous influence of location	LATITUDE AND LONGITUDE ^a
Food Availability and Nutritional Requirements	Discrete influence of time	PERIOD ^a
Food Availability and Nutritional Requirements	Continuous influence of time	STUDY DATE ^a
Food Availability and Nutritional Requirements	Continuous influence of time within discrete periods	PERIOD + STUDY DATE ^a
Habitat Availability, Food Availability and Nutritional Requirements	Discrete influence of location with discrete influence of time	REGION + PERIOD
Habitat Availability, Food Availability and Nutritional Requirements	Discrete influence of location with continuous influence of time	REGION + STUDY DATE
Habitat Availability, Food Availability and Nutritional Requirements	Continuous influence of location with discrete influence of time	LATITUDE AND LONGITUDE + PERIOD ^a
Habitat Availability, Food Availability and Nutritional Requirements	Continuous influence of location with continuous influence of time	LATITUDE AND LONGITUDE + STUDY DATE ^a
Habitat Availability, Food Availability and Nutritional Requirements	Discrete influence of location with continuous influence of time within discrete periods	REGION + PERIOD + STUDY DATE

^aModels incorporated parameters of satellite telemetry error ratings (LC), diurnal and nocturnal selection differences, snow, and ice as fixed effects. Individual Tundra Swans were identified and included, along with year, as random repeated effects.

^bModels included for analysis of aquatic habitats in the Boreal Forest.

Chapter Three: Results

Raw location data from Argos resulted in 65,608 observations; after filtering, 5,042 observations remained [by period: autumn (n = 1,674), winter (n = 1,363) and spring (n = 2,005); by region: Atlantic Coast (n = 1,344), Great Lakes (n = 1,107), Prairies (n = 1,422) and Boreal (n = 1,169)]. The average daily foraging distance traveled by Tundra Swans was 6.5 ± 8.2 km, with a median distance of 3.5 km and range from 210.5 m – 48.7 km. The 90% upper CI was 8.0 km; thus, I created 8 km buffers around filtered Tundra Swan locations to represent available habitat.

I included raw use and availability information to establish a baseline understanding of the average availability of each habitat type by period and region to aid in interpretation of selection intensity results. Availability of each habitat type does not reflect overall habitat availability in the region, but was a function of the scale of my study and was based upon habitats available within each Tundra Swan's daily foraging zone. In general, agriculture was highly available to Tundra Swans, ranging from 30% of available habitat in the Atlantic Coast to 80% in the Prairies, whereas availability of aquatic habitats was more limited, representing approximately 50% of habitats in the Atlantic Coast, 35% in the Great Lakes and only 10% in the Prairies. Agricultural availability was greatest during spring and least during winter, open water was least available during spring and most available during winter, and wetlands were least available during autumn and spring (Tables 3.1 and 3.2). In the Boreal Forest, availability of open water was more than 2× greater than wetlands during autumn and 1.5× greater than availability of wetlands during spring (Table 3.3). Because my analysis included diurnal and nocturnal locations, I conducted a paired t-test and determined that diurnal habitat use was not statistically different from overall habitat use ($t_{17} = 0.154$, $p = 0.88$). Use and availability are raw data and therefore have the potential to be statistically biased because mean values are not controlled for pseudoreplication of individual Tundra Swans (i.e., individual birds may bias the results) or for spatial and temporal autocorrelation.

Table 3.1 Mean use and availability of open water, wetlands and agriculture by region in the Atlantic Coast (n = 1344), Great Lakes (n = 1107) and Prairies (n = 1422). Mean proportion values (0.0 to 1.0) are obtained from raw data and are therefore not controlled for repeated measurement of individual Tundra Swan habitat use through time.

Region	Habitat Type	Diurnal				Total			
		Used	SE	Available	SE	Used	SE	Available	SE
Atlantic Coast	Open Water	0.347	0.017	0.253	0.011	0.296	0.010	0.232	0.007
	Wetlands	0.215	0.011	0.255	0.008	0.191	0.007	0.256	0.005
	Agriculture	0.304	0.015	0.299	0.009	0.383	0.010	0.316	0.006
Great Lakes	Open Water	0.423	0.020	0.245	0.012	0.425	0.013	0.226	0.007
	Wetlands	0.109	0.009	0.094	0.005	0.103	0.005	0.091	0.003
	Agriculture	0.323	0.015	0.448	0.013	0.334	0.012	0.453	0.009
Prairies	Open Water	0.175	0.011	0.054	0.003	0.193	0.008	0.055	0.002
	Wetlands	0.063	0.005	0.053	0.003	0.059	0.004	0.051	0.002
	Agriculture	0.696	0.012	0.808	0.007	0.685	0.009	0.813	0.005

Table 3.2 Mean use and availability of open water, wetlands and agriculture by season (data in the Atlantic Coast, Great Lakes and Prairies are all pooled); autumn (n = 1045), winter (n = 1363) and spring (n = 1465). Mean proportion values (0.0 to 1.0) are obtained from raw data and are therefore not controlled for repeated measurement of individual Tundra Swan habitat use through time.

Season	Habitat Type	Diurnal					Total				
		Used	SE	Available	SE	Used	SE	Available	SE		
Autumn	Open Water	0.479	0.019	0.177	0.010	0.505	0.012	0.177	0.006		
	Wetlands	0.090	0.008	0.071	0.004	0.094	0.005	0.073	0.002		
	Agriculture	0.348	0.017	0.589	0.015	0.324	0.011	0.574	0.010		
Winter	Open Water	0.357	0.017	0.260	0.011	0.306	0.010	0.237	0.007		
	Wetlands	0.216	0.011	0.259	0.008	0.192	0.007	0.260	0.005		
	Agriculture	0.308	0.015	0.304	0.009	0.385	0.010	0.320	0.006		
Spring	Open Water	0.147	0.011	0.100	0.007	0.136	0.008	0.090	0.005		
	Wetlands	0.074	0.006	0.064	0.004	0.065	0.004	0.059	0.002		
	Agriculture	0.658	0.014	0.702	0.010	0.679	0.009	0.715	0.007		

Table 3.3 Mean use and availability of open water, wetlands and agriculture by season in the Boreal Forest, autumn (n = 629) and spring (n = 540). Mean proportion values (0.0 to 1.0) are obtained from raw data and are therefore not controlled for repeated measurement of individual Tundra Swan habitat use through time.

Season	Habitat Type	Diurnal				Total			
		Used	SE	Available	SE	Used	SE	Available	SE
Autumn	Open Water	0.666	0.020	0.441	0.015	0.652	0.014	0.440	0.010
	Wetlands	0.138	0.012	0.189	0.010	0.146	0.008	0.186	0.007
Spring	Open Water	0.470	0.020	0.299	0.014	0.472	0.016	0.300	0.011
	Wetlands	0.174	0.013	0.205	0.011	0.191	0.010	0.208	0.008

Agriculture and Aquatic Habitats

Agriculture. The model explaining the most variation in selection intensity for AGRICULTURE included PERIOD and LATITUDE and LONGITUDE and was strongly supported ($w_i = 1.0$; Table 3.4). Model-predicted selection intensity for AGRICULTURE was greater during winter (6.91 ± 0.12 %) than spring (-4.12 ± 0.16 %), and suggested avoidance during autumn (-23.83 ± 0.19 %; Table 3.5, Figure 3.1). AGRICULTURE selection intensity increased by 1.67% for each degree decrease in LATITUDE and increased by 0.80% for each degree decrease in LONGITUDE (Table 3.5 Figure 3.2). These results suggest that after including influence of PERIOD, selection intensity increased as Tundra Swans moved south and east.

Open Water. The model explaining the most variation in selection intensity for OPEN WATER included REGION and PERIOD and was strongly supported ($w_i = 1.0$; Table 3.4). Model-predicted selection intensity for OPEN WATER was greater during autumn (32.16 ± 0.23 %) than winter and spring (6.60 ± 0.18 and 4.78 ± 0.18 %, respectively; Table 3.5, Figure 3.3) and greater in the Great Lakes (20.03 ± 0.44 %) and Prairies (13.26 ± 0.40 %) than Atlantic Coast (6.34 ± 0.17 %; Table 3.5, Figure 3.4).

Wetlands. Models retained within 2.0 AIC units included LATITUDE, LONGITUDE and PERIOD as fixed variables (Table 3.4). Model-averaged selection intensity for WETLANDS was greatest during autumn and spring (0.44 ± 0.10 % and 0.73 ± 0.09 %, respectively), and slightly negative during winter (-6.7 ± 0.11 %; Table 3.5, Figure 3.5). After correction for season, selection intensity for WETLANDS increased by 0.64% for each degree increase in LATITUDE and increased by 0.22% for each degree increase in LONGITUDE (Table 3.5, Figure 3.6).

Table 3.4 Mixed-effects models of selection intensity^a for terrestrial and aquatic habitats in the Atlantic Coast, Great Lakes and Prairies based upon nonbreeding movements by 63 EP Tundra Swans, 1998 – 2004 (n = 1636) and 2008 – 2011 (n = 2236).

Habitat Type	Models ^b	K	ΔAIC^c	w_i
AGRICULTURE	PERIOD, LATITUDE and LONGITUDE	7	0.0	1.00
	PERIOD, STUDY DATE	6	16.3	0.00
	Null ^d	4	633.8	0.00
OPEN WATER	REGION, PERIOD	6	0.0	1.00
	REGION, PERIOD, DATE	7	15.1	0.00
	Null ^d	4	400.7	0.00
WETLANDS	LATITUDE and LONGITUDE	6	0.0	0.69
	PERIOD, LATITUDE and LONGITUDE	7	1.6	0.31
	Null ^d	4	131.1	0.00

^aSelection intensity = difference between proportion of habitat used and available (0.0 – 1.0).

^bModels incorporated parameters of satellite telemetry error ratings (LC), diurnal and nocturnal selection differences, snow, and ice as fixed covariate effects. Individual Tundra Swans were identified and included, along with year, as random repeated effects.

^cModels are sorted by Akaike Information Criterion (AIC), the top two models (models with the lowest AIC values) and null models are shown. The AIC values for top models were 584.8, 741.5, and -2337.3 for AGRICULTURE, OPEN WATER and WETLANDS, respectively.

^dNull model includes all covariates and the intercept.

K – number of parameters

ΔAIC – difference between AIC of the top model and AIC of model of interest

w_i – model weight, indicates probability that model is best among the candidate models

Table 3.5 Parameter estimates (θ), standard errors, and 95% confidence intervals derived from candidate models ($\Delta AIC \leq 2$) of selection intensity^a for agricultural and aquatic habitats in the Atlantic Coast, Great Lakes and Prairies based upon nonbreeding movements by 63 EP Tundra Swans, 1998 – 2004 (n = 1636) and 2008 – 2011 (n = 2236).

Habitat Type ^b	Parameter	θ	SE	95% CI
AGRICULTURE	Intercept	0.386	0.064	0.245 to 0.528
	Autumn	-0.201	0.021	-0.242 to -0.160
	Winter	0.000	.	.
	Spring	-0.101	0.022	-0.144 to -0.058
	Latitude	-0.008	0.004	-0.015 to -0.001
	Longitude	0.001	0.002	-0.002 to 0.004
	OPEN WATER	Intercept	0.024	0.038
Autumn		0.267	0.032	0.205 to 0.329
Winter		0.000	.	.
Spring		0.028	0.031	-0.032 to 0.088
Atlantic Coast		0.073	0.033	0.008 to 0.137
Great Lakes		0.096	0.014	0.069 to 0.123
Prairies		0.000	.	.
WETLANDS	Intercept	-0.221	0.034	-0.295 to -0.147
	Autumn	0.014	0.004	0.005 to 0.023
	Winter	0.000	.	.
	Spring	0.008	0.005	-0.001 to 0.017
	Latitude	0.019	0.002	0.015 to 0.023
	Longitude	0.007	0.001	0.005 to 0.009

^aSelection intensity = difference between proportion of habitat used and available (0.0 – 1.0).

^bModel-averaged parameter estimates are reported for WETLANDS, whereas statistics for AGRICULTURE and OPEN WATER are based on the model with the lowest AIC score.

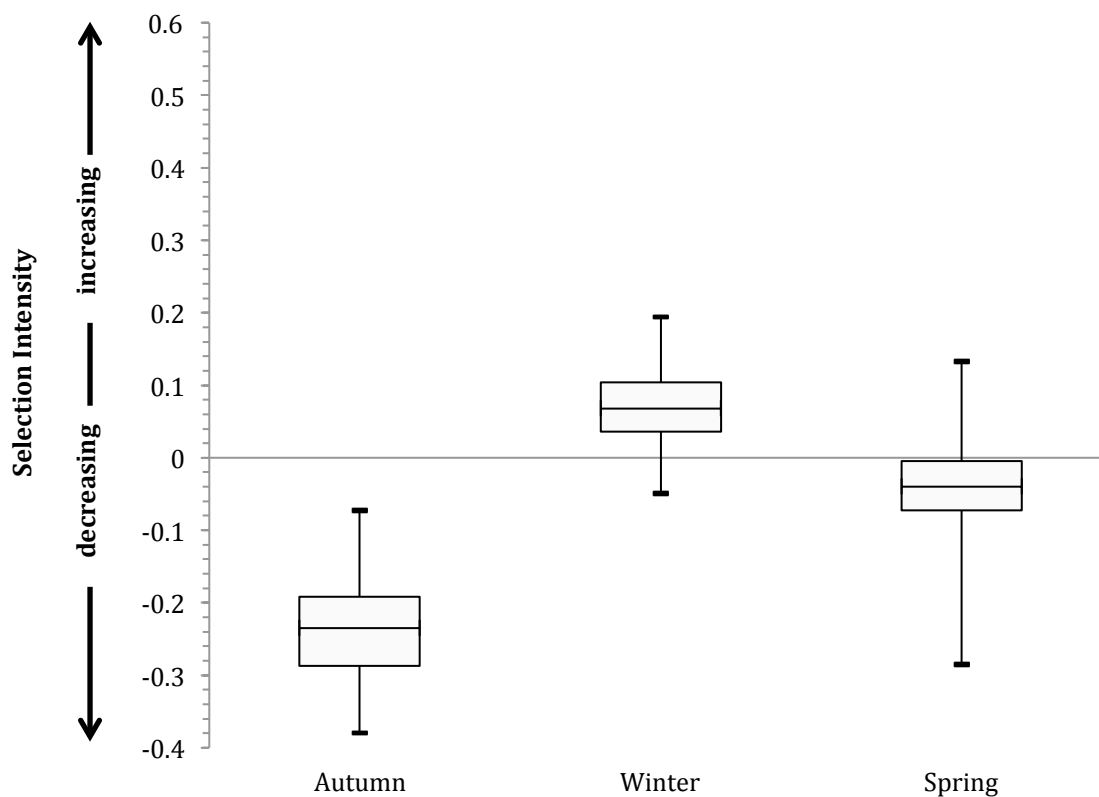


Figure 3.1. Boxplot of model predicted selection intensity for agriculture by season in the Atlantic Coast, Great Lakes and Prairies, autumn (n = 1045), winter (n = 1363) and spring (n = 1465).

The upper and lower limits of each box outline the areas where 25% of the data is greater than or lower than the median. The whiskers represent the maximum and minimum values observed (excluding outliers), and the line in the middle of the boxes is the median value observed.

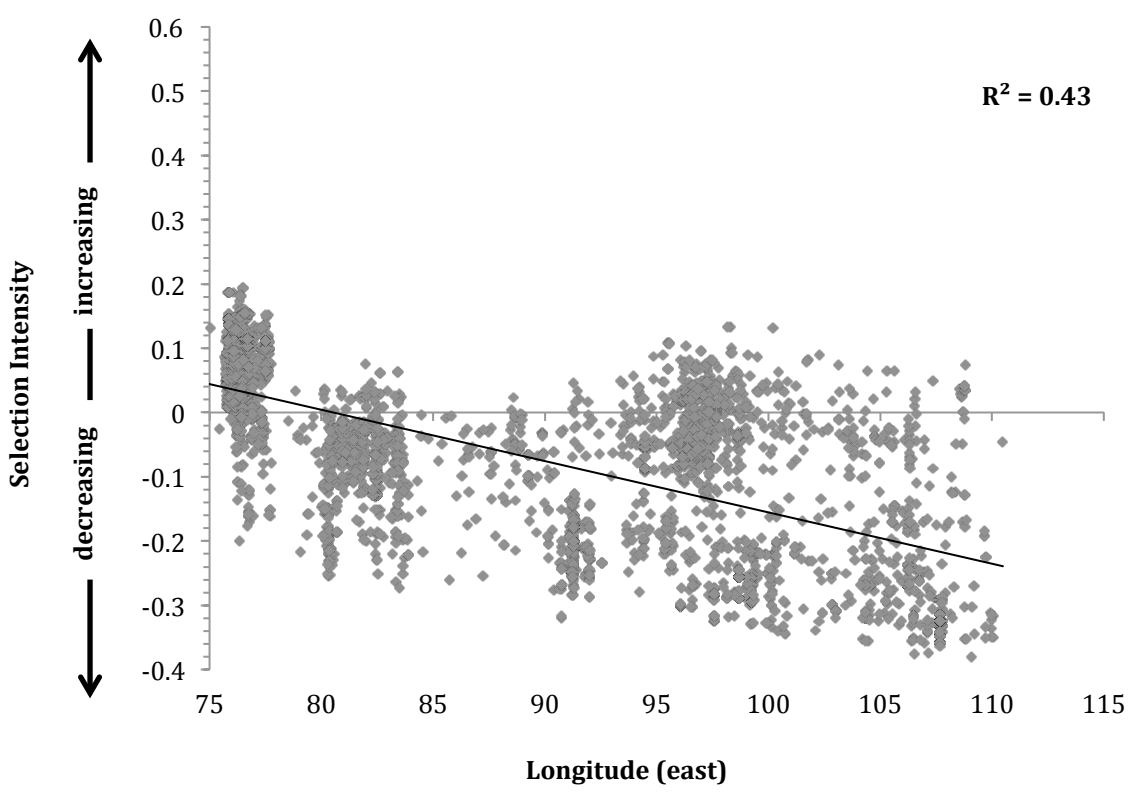
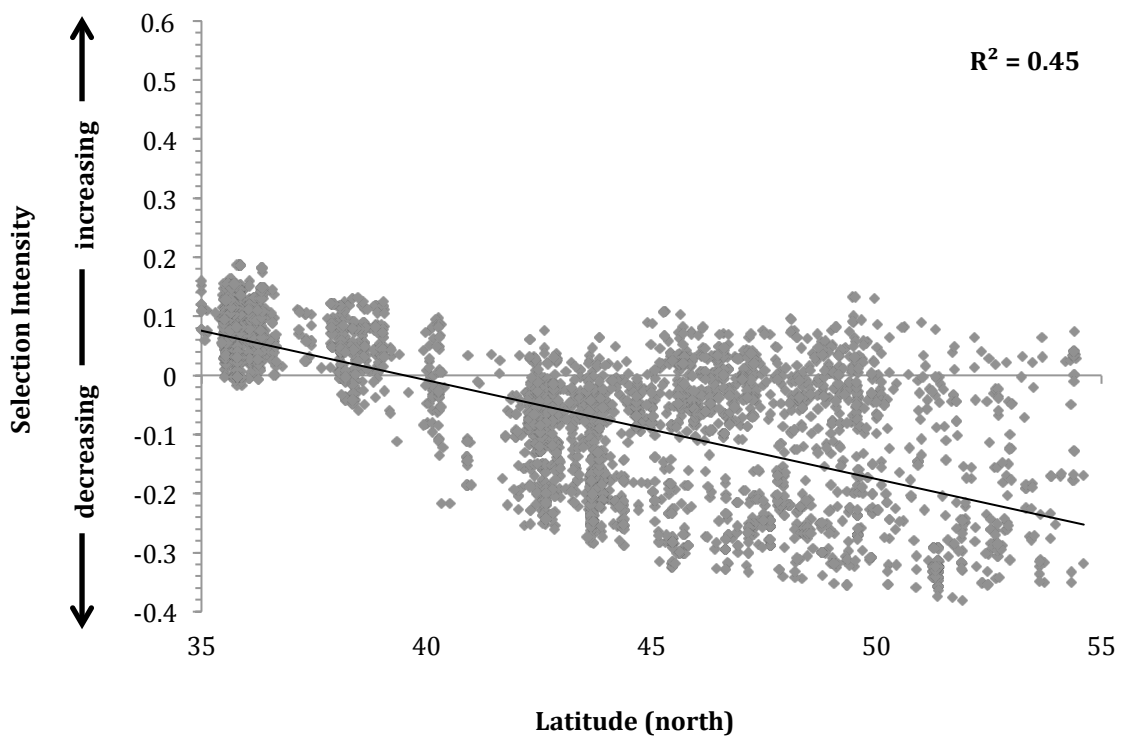


Figure 3.2 Scatterplot of model predicted selection intensity for agriculture by latitude and longitude (n = 3873) in the Atlantic Coast, Great Lakes and Prairies.

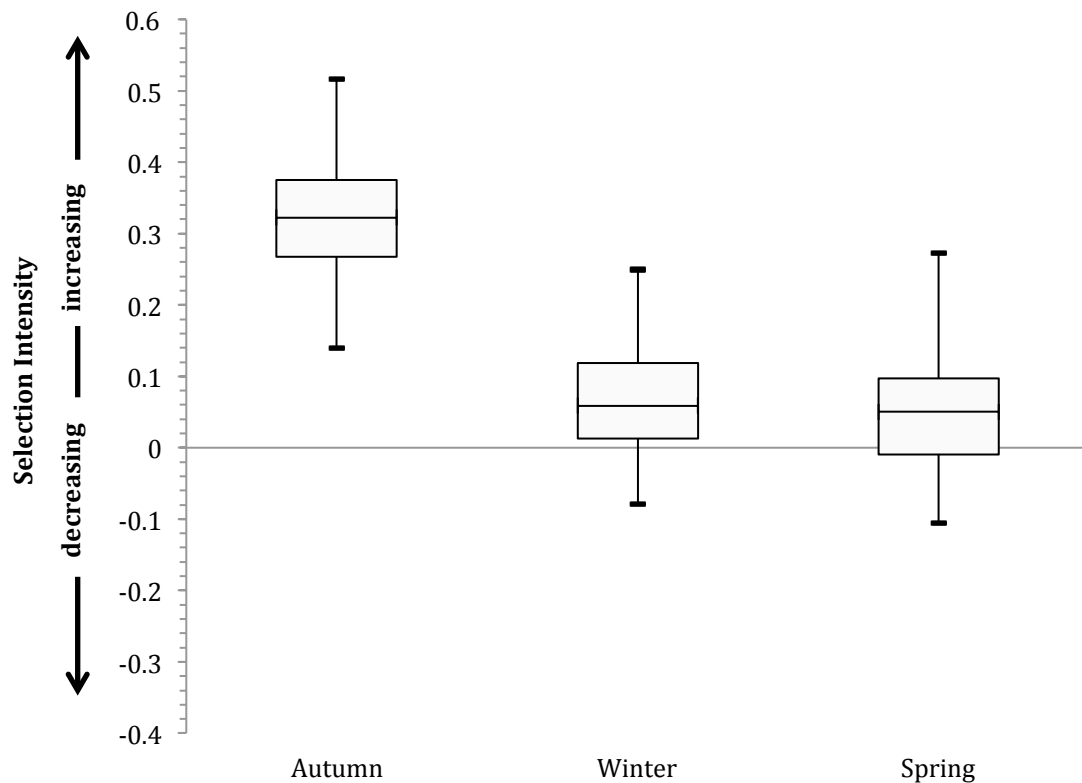


Figure 3.3 Boxplot of model predicted selection intensity for open water by season in the Atlantic Coast, Great Lakes and Prairies, autumn (n = 1045), winter (n = 1363) and spring (n = 1465).

The upper and lower limits of each box outline the areas where 25% of the data is greater than or lower than the median. The whiskers represent the maximum and minimum values observed (excluding outliers), and the line in the middle of the boxes is the median value observed.

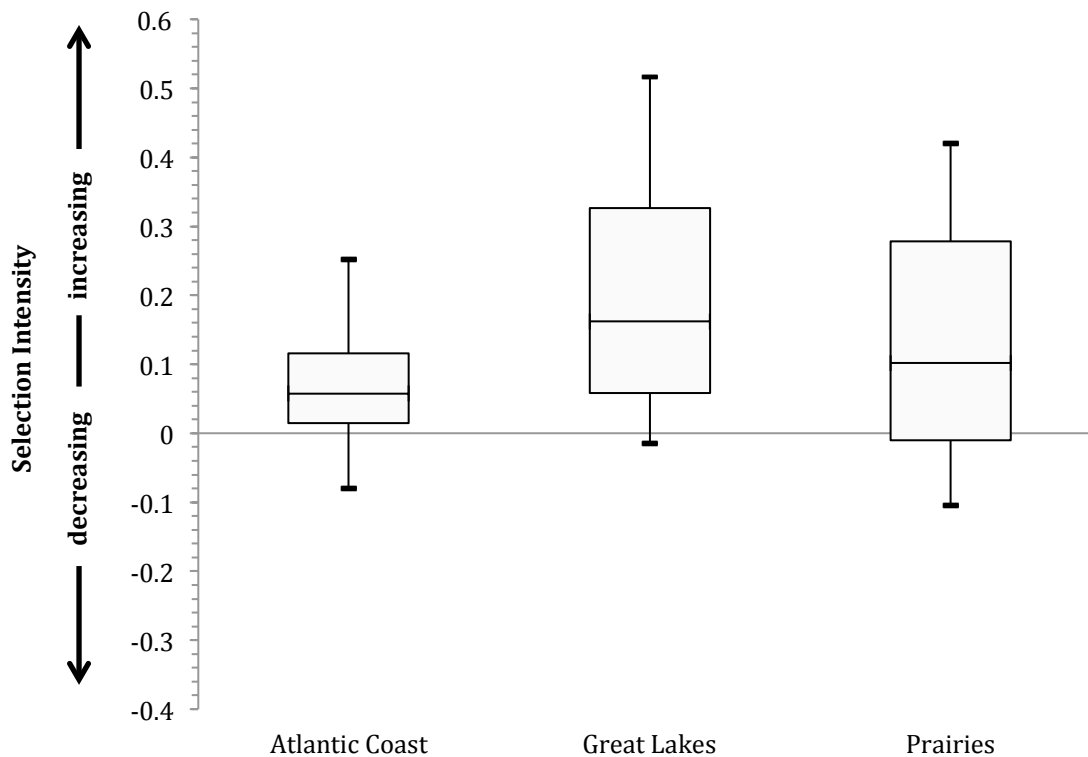


Figure 3.4 Boxplot of model predicted selection intensity for open water by region in the Atlantic Coast (n = 1344), Great Lakes (n = 1107) and Prairies (n = 1422).

The upper and lower limits of each box outline the areas where 25% of the data is greater than or lower than the median. The whiskers represent the maximum and minimum values observed (excluding outliers), and the line in the middle of the boxes is the median value observed.

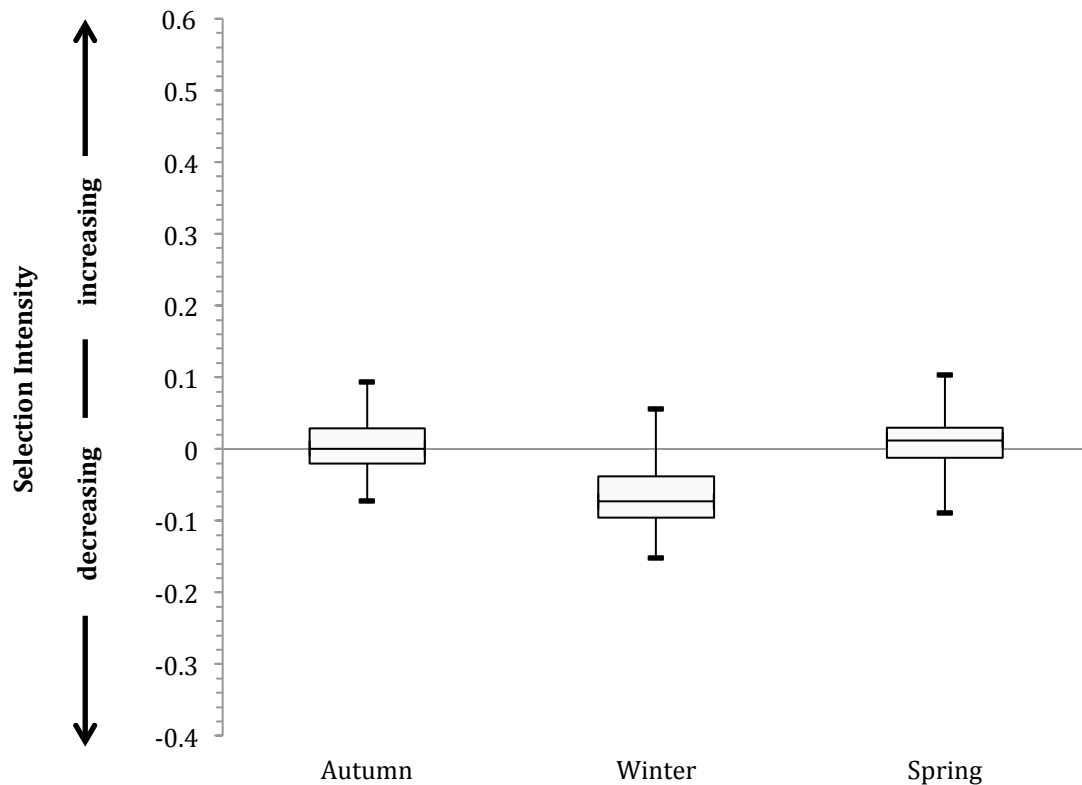


Figure 3.5 Boxplot of model-averaged predicted selection intensity for wetlands by season in the Atlantic Coast, Great Lakes and Prairies, autumn (n = 1045), winter (n = 1363) and spring (n = 1465).

The upper and lower limits of each box outline the areas where 25% of the data is greater than or lower than the median. The whiskers represent the maximum and minimum values observed (excluding outliers), and the line in the middle of the boxes is the median value observed.

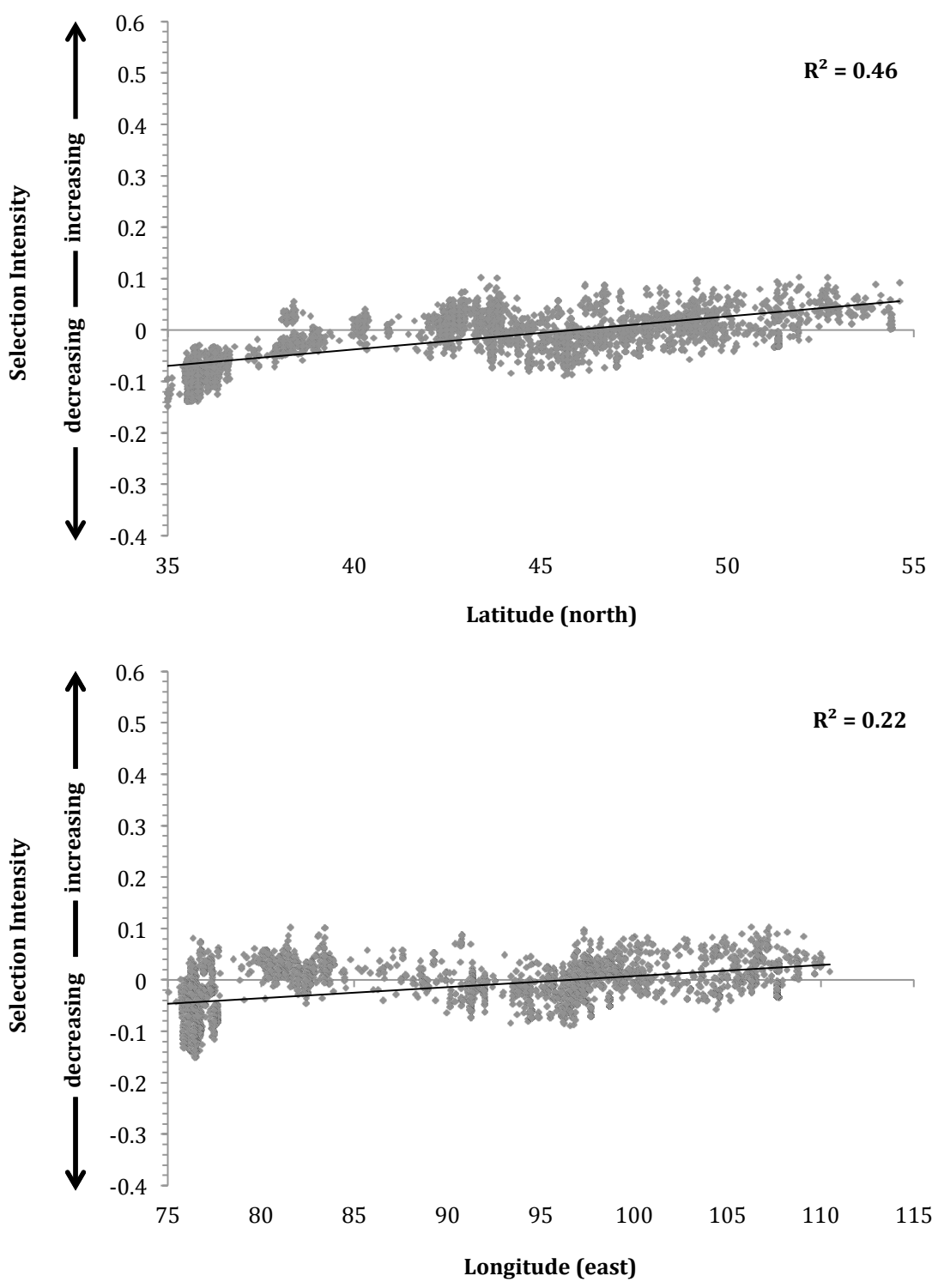


Figure 3.6 Scatterplot of model-averaged predicted selection intensity for wetlands by latitude and longitude (n = 3873) in the Atlantic Coast, Great Lakes and Prairies.

Aquatic Habitats in the Boreal Forest

Open Water. The model explaining the most variation in selection intensity for OPEN WATER included LATITUDE and LONGITUDE and was relatively strongly supported ($w_i = 0.87$; Table 3.3). Model-predicted selection intensity for OPEN WATER increased by 0.69% for each degree decrease in LATITUDE and increased by 0.15% for each degree decrease in LONGITUDE (Table 3.4, Figure 3.2).

Wetlands. The null model explained more variation in selection intensity for WETLANDS than any of the candidate models ($w_i = 0.94$). Because no models fell within 2.0 AIC units of the null model, no other models were retained. The null model-predicted selection intensity for WETLANDS was -2.99 ± 0.12 %.

Table 3.6 Mixed-effects models of selection intensity^a for aquatic habitats in the Boreal Forest based upon nonbreeding movements by 63 EP Tundra Swans, 1998 – 2003 (n = 363) and 2008 – 2011 (n = 806).

Habitat Type	Models ^b	K	ΔAIC^c	w_i
OPEN WATER	LATITUDE and LONGITUDE	6	0.0	0.87
	PERIOD, LATITUDE and LONGITUDE	7	4.6	0.09
	Null ^d	4	6.3	0.04
WETLANDS	PERIOD	5	0.0	0.06
	DATE	5	8.9	0.00
	Null ^d	4	-5.4	0.94

^aSelection intensity = difference between proportion of habitat used and available (0.0 – 1.0).

^bModels incorporated parameters of satellite telemetry error ratings (LC), diurnal and nocturnal selection differences, snow, and ice as fixed covariate effects. Individual Tundra Swans were identified and included, along with year, as random repeated effects.

^cModels are sorted Akaike Information Criterion (AIC), the top two models (models with the lowest AIC values) and null models are shown. The AIC values for top models were 1110.2 and 364.2 for OPEN WATER and WETLANDS, respectively.

^dNull model includes all covariates and the intercept.

K – number of parameters

ΔAIC – difference between AIC of the top model and AIC of model of interest

w_i – model weight, indicates probability that model is best among the candidate models

Table 3.7 Parameter estimates (θ), standard errors, and 95% confidence intervals derived from candidate models ($\Delta AIC \leq 2$) of selection intensity^a for agricultural and aquatic habitats in the Boreal Forest based upon nonbreeding movements by 63 EP Tundra Swans, 1998 – 2003 (n = 363) and 2008 – 2011 (n = 806).

Habitat Type	Parameter	θ	SE	95% CI
OPEN WATER	Intercept	1.09	0.172	0.704 to 1.484
	Latitude	-0.009	0.005	-0.019 to 0.001
	Longitude	0.002	0.002	-0.001 to 0.006
WETLANDS	Intercept	-0.078	0.021	-0.126 to -0.030

^aSelection intensity = difference between proportion of habitat used and available (0.0 – 1.0).

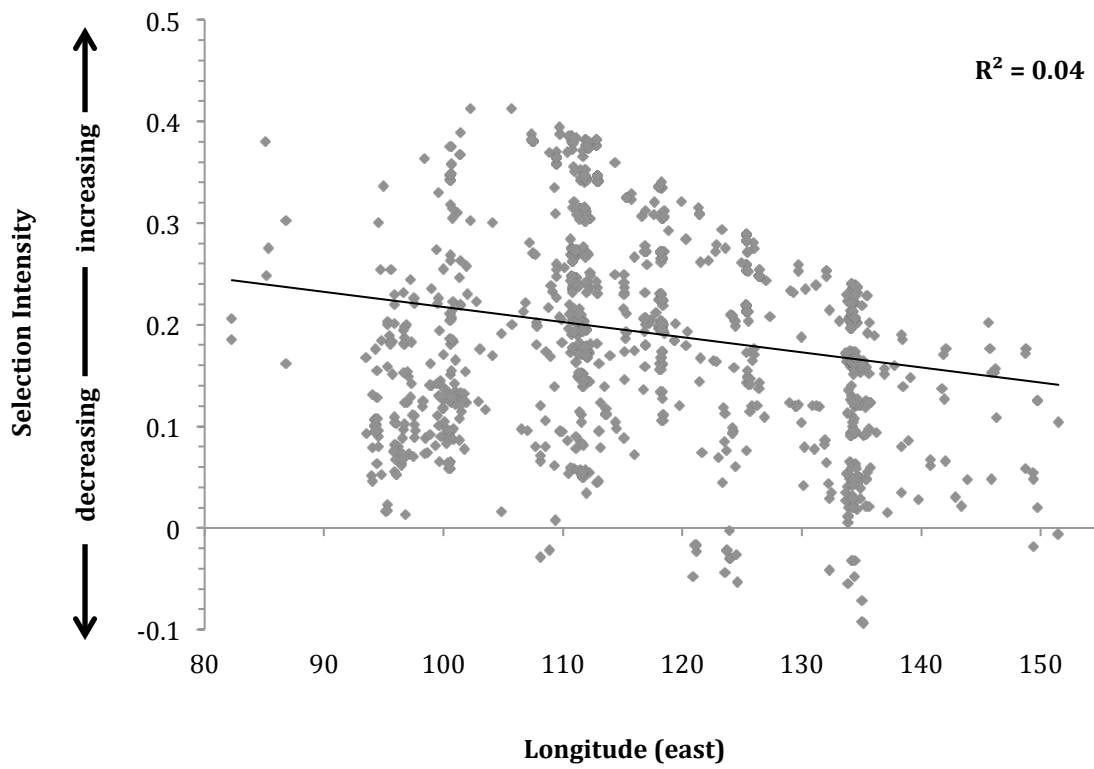
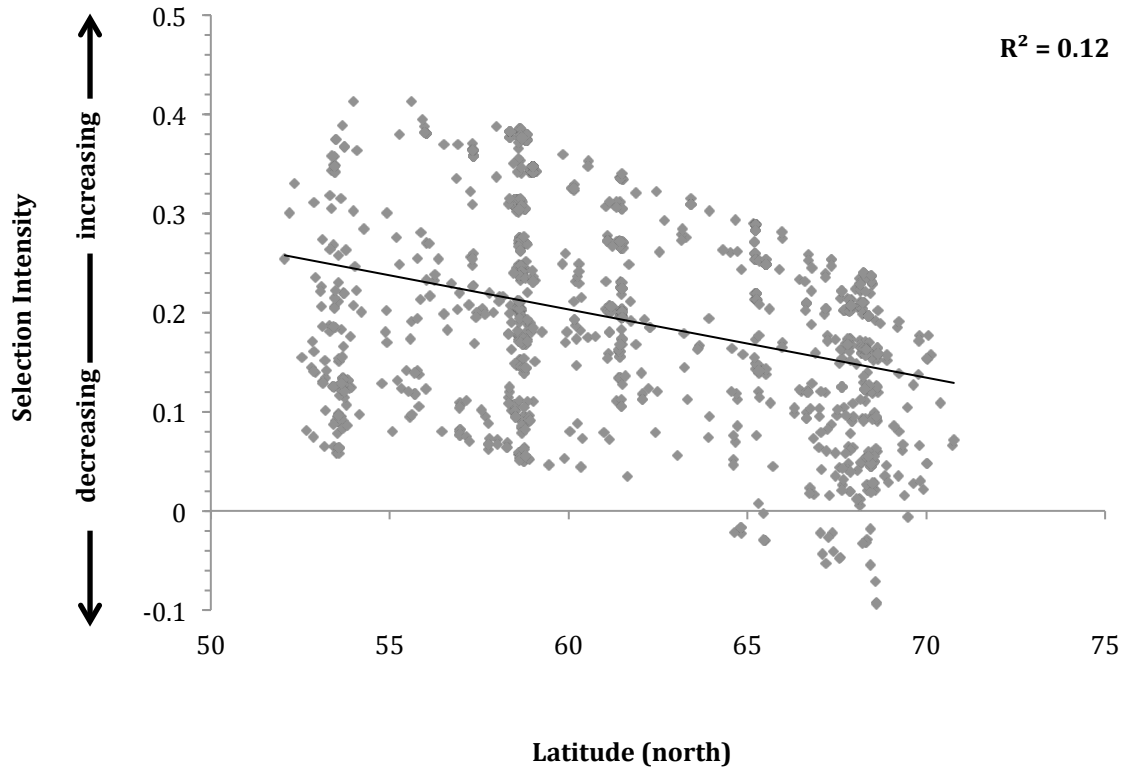


Figure 3.7 Scatterplot of model predicted selection intensity of open water by latitude and longitude in the Boreal Forest ($n = 3873$).

Chapter Four: Discussion

Habitat use and selection are inherently scale-dependent and involve making decisions on a hierarchy of temporal and geographic scales (Johnson 1980, Zhang and Yankuo 2005). Despite an abundance of site specific (i.e., local scale) habitat studies exist during snapshots of the annual cycle (e.g., habitat switching by Brant, *Branta bernicla* L., during winter in Norfolk, England, Vickery et al. 1995; cornfield use during spring by cranes and geese in Nebraska, Anteau et al. 2011), we do not know how these relationships relate to broad scale habitat selection. By understanding the temporal and geographic selection of habitats by Tundra Swans and the mechanisms driving these relationships, we can: 1) better predict how Tundra Swans respond to changing habitats and environmental factors, 2) make inferences about habitat selection at local scales based upon geographic location and time of year, and 3) refine conservation strategies to more appropriately match regional and seasonal requirements. Therefore, I used scientific theory to develop models in an observational study to investigate selection of agricultural, open water and wetlands habitats to better understand the ecology of large-bodied migratory waterfowl in autumn, winter and spring. I used multiple competing hypotheses and discovered that variables representing habitat availability, food availability and nutritional requirements all explain variation in selection intensity for agricultural and aquatic habitats in the Atlantic Coast, Great Lakes and Prairies, but, of the selection factors explored, only the representative variable for habitat availability appears to influence selection of aquatic habitats in the Boreal Forest. Moreover, the influence of habitat availability, food availability, or nutritional requirements on habitat selection intensities changed discretely with time and both discretely and continuously with location, depending upon the habitat type addressed. All conclusions drawn are based upon variables representing changes in habitat availability, nutritional requirements and seasonal food availability, as these factors could not be measured in my analysis.

Daily Movements by Tundra Swans

Knowledge of landscape mosaics within daily foraging distances is necessary to understand how wintering and migrating waterfowl may use landscapes surrounding roosting locations, wildlife refuges, and other managed and unmanaged habitats

(Ackerman et al. 2006). Mean daily foraging distance for Tundra Swans during the nonbreeding period was 6.5 km but individual foraging distances ranged from approximately 200 m to 50 km. Because of this variability, I used the upper CI for the daily foraging distance (8.0 km) to determine what habitats were available to 90% of Tundra Swans at any given location. The foraging distance used in my study is similar to those observed in other wintering waterfowl species in North America (e.g., geese 8.6 ± 7.6 km and dabbling ducks 5.7 ± 5.2 km; Johnson et al. 2013); therefore, selection intensities calculated in my study may be representative of other nonbreeding waterfowl species that regularly use agricultural habitats to forage. Understanding how waterfowl select habitats available in complex landscapes provides additional guidance to conservation planners charged with ensuring appropriate habitats are available at times when birds are selecting for specific resources (Arthur et al. 1996, Calvert et al. 2009).

Agricultural and Aquatic Habitats

The nonbreeding period is nutritionally demanding because it represents a time when adult Tundra Swans build and replenish nutrient stores and when juveniles continue to grow and develop (Bellrose 1980, Drent and Daan 1980, Sedinger 1992, Klaassen 2003, Petrie et al. 2002, Clausen et al. 2003, Studds et al. 2008, Reudink et al. 2009, Badzinski et al. 2011). Because aquatic foods provide balanced nutrient intake, and because increased consumption of submerged aquatic vegetation (SAV) has been linked to better body condition (Loesch and Kaminski 1989, Hoye et al. 2012), one would expect Tundra Swans to focus on aquatic habitats when available. However, foraging, senescence and ice can decrease the availability and accessibility of SAV over-winter and especially during spring migration (Alisauskas and Ankney 1992, Badzinski et al. 2006, Schummer et al. 2010). When investigating raw availability of habitats to Tundra Swans, the approximate make-up of regions was: 1) one third agriculture, one quarter wetlands and one quarter open water in the Atlantic Coast; 2) half agriculture, one quarter open water and one tenth wetlands in the Great Lakes; and 3) over three quarters agriculture in the Prairies with open water and wetlands making up only one tenth of the remaining habitat. Because Tundra Swans roost and feed in aquatic habitats overnight, it was possible that inclusion of nocturnal locations may have resulted in an overestimate of aquatic habitat

use and I controlled for this possibility by including diurnal or nocturnal classifications as covariates in my analysis. However, diurnal and overall raw habitat use data were not significantly different, indicating that inclusion of nocturnal data did not bias results in my study.

Overall, I detected the selection of investigated habitats by season to be: 1) during autumn, Tundra Swans selected open water most strongly, then wetlands, and agriculture was used substantially less than its availability; 2) during winter, selection intensity was greatest for agriculture, then open water, and wetlands were used less than their availability; and finally 3) during spring, selection intensity was greatest for open water, then wetlands, with Tundra Swans using agriculture slightly less relative to its availability. Because season had such a strong influence on the selection intensity of habitats, it appears that nutritional requirements, food availability, or both vary discretely with changing seasons, rather than continuously throughout the year. Discrete variance in habitat selection by season may be related to changes in nutritional requirements that evolved in relatively stable climates, enabling Tundra Swans to exploit habitat specific foods that change with the seasons throughout their annual life cycle.

Agriculture

Raw data indicated that availability of agriculture by region decreased as Tundra Swans moved south and east from the prairies to the Atlantic Coast. Selection for agriculture demonstrated an inverse relationship with agricultural availability by increasing with decreasing latitude and longitude, suggesting that availability of agricultural habitats had the greatest potential to be limiting as Tundra Swans moved toward wintering grounds. By investigating clusters on latitude and longitude scatterplots and pairing these results with a map of the nonbreeding period (Figure 4.1), I determined that selection intensity for agriculture during winter was greatest in North Carolina, with a slight decrease in intensity in Chesapeake Bay and again in Pennsylvania. Most Tundra Swans travel from Pennsylvania to Chesapeake Bay to North Carolina over-winter and then head back north just before spring migration, suggesting that selection for agriculture was strongest mid-winter. Outside the wintering grounds, selection intensity for agricultural habitats tended to be negative but was highly variable, suggesting that strategies among individual

Tundra Swans differed greatly during migration. An increased use of agriculture relative to its availability was detected in the Prairies at the eastern edge of North Dakota where the availability of agriculture is especially high (over 80% of available habitats) in comparison with other regions. Increased selection for agriculture in an area with such high agricultural availability may suggest an importance of agriculture for obtaining high-energy foods during spring immediately before travelling through the Boreal Forest where agriculture was unavailable and SAV may be reduced by senescence and ice cover. Obtaining lipid stores in the Prairies during spring migration would reduce the costs of migration prior to this point because Tundra Swans would have been travelling with a reduced body mass (Badzinski et al. 2011). However, the North Dakota relationship did not alter the overall negative trend and my results suggest agricultural habitats were more consistently selected for in the Atlantic Coast relative to the Great Lakes and Prairies.

Although agriculture was not selected during migration, it represented approximately 45% and 80% of habitats where Tundra Swans occur in the Great Lakes and Prairies, respectively. Therefore, it is likely that selection intensities in these regions were decreased by an oversaturation of agricultural habitats. Also, not all agricultural habitats are profitable to foraging Tundra Swans, either due to crop type (e.g., tobacco, pastures, cotton) or because of agricultural practices (i.e., harvest schedules and plowing of fields) and the inclusion of these habitats could have influenced my results. Moreover, the proportional availability of each crop type may vary by region, which would influence the nutritional profitability of each region and this must also be considered when interpreting results. Therefore, although agriculture was not selected for (in relation to availability) in the Great Lakes and Prairies during spring, it is likely still an important source of energy for migrating Tundra Swans when these carbohydrate needs cannot be met in natural aquatic habitats through consumption of SAV (Baldassarre and Bolen 1994).

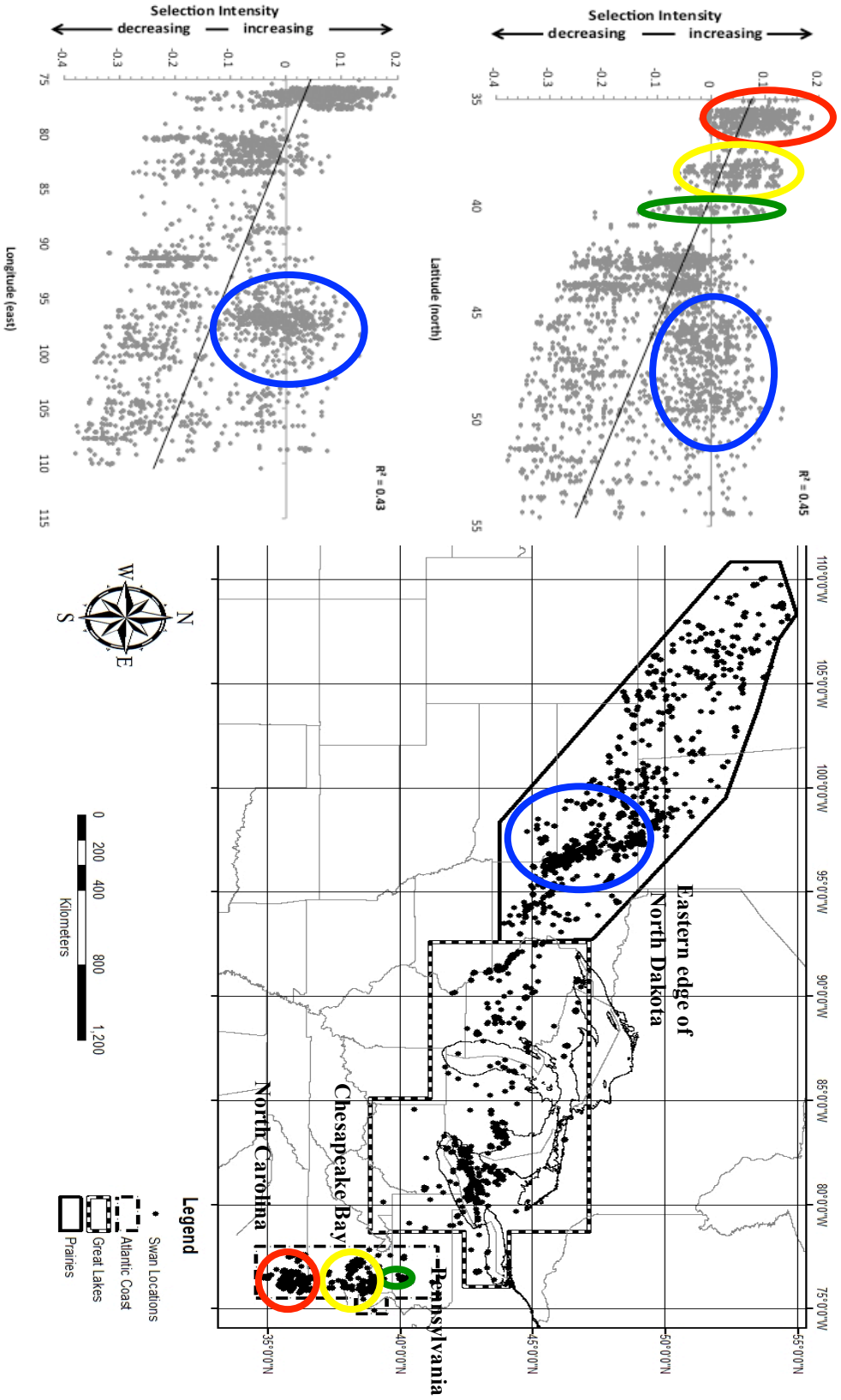


Figure 4.1 Grid-map Tundra Swan locations in the Atlantic Coast, Great Lakes and Prairies paired with latitude and longitude figures to address specific areas of interest for interpretation of agriculture selection results.

Variability in the results by latitude and longitude during migration may have been influenced by changes in seasonal selection intensity between autumn and spring. Even though Tundra Swans passed through the same regions during autumn and spring migration, my results indicate they used agriculture approximately 2× more during spring and they used agricultural areas substantially less during autumn relative to their availability. Avoidance of agricultural habitats during autumn does not appear to be a product of harvest schedules, because Tundra Swans arrive in each region after or during harvest when agricultural grains are most readily available (Table 4.1). Therefore, increased availability of SAV after the summer growth period (Alisauskas and Ankney 1992, Badzinski 2003, Badzinski et al. 2006) is likely linked to agricultural avoidance during autumn. Avoidance of agriculture in autumn, alongside greater selection intensities for open water during autumn than during winter and spring suggests that, when available, SAV and carbohydrate rich SAV tubers may be preferred over agricultural grains.

The consumption of agricultural grains is associated with cold temperatures (Jorde et al. 1983, Baldassarre and Bolen 1984) and may reduce use of lipid reserves during cold periods by increasing an individual's total energy balance (Calder and King 1974, Kendeigh et al. 1977, Baldassarre and Bolen 1984). In my study, Tundra Swans selected agricultural habitats during winter and used agriculture 2× more during spring migration than they did in autumn, suggesting that agricultural grains may be especially important as a high-energy supplement for winter and spring survival when Tundra Swans are exposed to cold temperatures and energy needs cannot be met through consumption of aquatic foods alone. Moreover, because selection of agricultural habitats during winter and spring was relatively greater than in autumn, it is possible that Tundra Swans increased lipid stores through consumption of agricultural foods during these periods in preparation for predictable future energetic requirements of migration and breeding.

Table 4.1 Agricultural harvest schedules and range of dates satellite tracked Tundra Swans were present in each region during the nonbreeding period.

Region	Tundra Swans Present	Crop	Harvest Date Range^a
Atlantic Coast	Nov 4 - Mar 28	Corn	Aug 25 - Dec 10
		Alfalfa	May 1 - Nov 30
		Oats	July 20 - Aug 30
		Sorghum	N/A
		Soybeans	Oct 4 - Dec 30
		Sugarbeets	N/A
		Winter Wheat ^b	Aug 30 - Dec 31
Great Lakes	Oct 13 - April 9	Corn	Sep 5 - Dec 10
		Alfalfa	May 20 - Oct 14
		Oats	July 19 - Sep 2
		Sorghum	N/A
		Soybeans	Sep 25 - Nov 13
		Sugarbeets	Sep 26 - Nov 11
		Winter Wheat ^b	Sep 22 - Oct 22
Prairies	Sep 26 - Dec 3	Corn	Sep 24 - Dec 6
		Alfalfa	May 1 - Oct 1
		Oats	July 14 - Sep 18
		Sorghum	Jun 30 - Nov 17
		Soybeans	Sep 17 - Nov 5
		Sugarbeets	Sep 16 - Oct 30
		Winter Wheat ^b	Sep 1 - Oct 16

^aData collected from USDA National Agricultural Statistic Service 2010 A.

^bDate range represents the planting dates rather than harvest dates because waterfowl forage on winter wheat new growth.

Open Water

Availability of open water ranged from just over 20% of Tundra Swan habitats in the Atlantic Coast and Great Lakes and only 5.5% in the Prairies, however, selection intensity did not vary directly with changes in availability as was observed with agriculture selection intensities. Rather, selection intensity for open water was lowest in the Atlantic Coast and greatest in the Great Lakes where overall availability of open water was approximately equal. Differences in selection intensities in these two regions suggests that some sort of regional difference, whether it was the stage within the annual cycle that Tundra Swans pass through the area or the different types of open water habitats available (i.e., in the Great Lakes and Prairies open water represents rivers and lakes but at the Atlantic Coast open water also includes estuarine and marine deep-water habitats), was strongly influencing selection of open water habitats.

During migration, selection for open water was approximately 7× greater in autumn than spring, likely due to the increased availability of SAV in autumn. Because many Tundra Swans travel with cygnets during autumn, and because the latter continue to grow and develop up to six months of age (Bowler et al. 1992), it is possible that aquatic habitats are especially important to provide nutritionally balanced foods (i.e., carbohydrates, proteins, minerals, essential amino acids) and predator protection for growing cygnets. Moreover, because agricultural forage was used more intensively during winter and spring, selection for open water may not need to be as intense at these times. Although I did not investigate other extrinsic factors such as the amount of field hunting or conspecific competition, these factors may influence accessibility and functional availability of agricultural forage during autumn, and thus necessitate increased use of open water habitats during the southward migration.

Wetlands

Wetlands were most available in the Atlantic Coast (approximately 25% of Tundra Swan habitat), with availability decreasing to approximately 9% in the Great Lakes and 5% in the Prairies. As seen with agriculture, selection intensity for wetlands corresponded to changes in wetland availability and selection increased as Tundra Swans moved north and west in their range. Investigation of the latitude and longitude graphs suggests that

wetland use was greater than availability in the Prairies (in North Dakota and Canada), in the lower Great Lakes and along the Potomac and Rappahannock Rivers within the northern Chesapeake Bay, although wetlands were not selected at the Chesapeake Bay overall (Figure 4.2). As previously mentioned, wetland areas requiring protection are underrepresented during spring in the international network of protected wetlands (Arzel 2006) and my research has identified these four areas as potentially important for future research and management. Because Tundra Swans select for wetlands during the majority of autumn and spring, but do not during winter, it appears they may be responding to nutritional pressures such as growing cygnets, future egg production and the energetic stress of migration. However, it is also possible that variability in selection for wetlands was simply a function of decreased availability of wetlands during migration and increased availability over-winter.

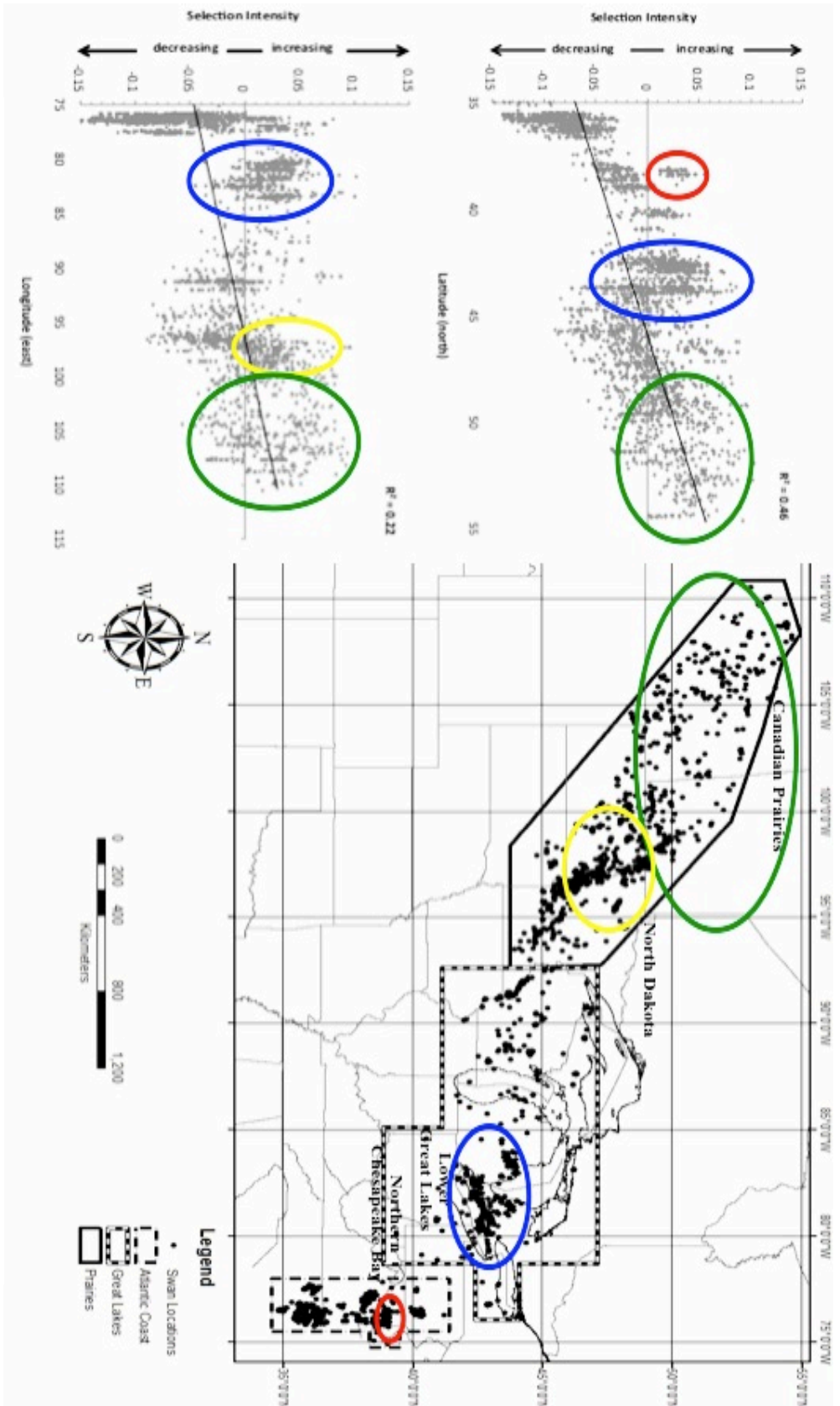


Figure 4.2 Grid-map of Tundra Swan locations in the Atlantic Coast, Great Lakes and Prairies paired with latitude and longitude figures to address specific areas of interest for interpretation of wetland selection results.

Aquatic Habitats in the Boreal Forest

I addressed the Boreal Forest separately because agricultural forage was not available and habitat relationships are likely to change when waterfowl must rely solely on aquatic foods. Boreal Forest aquatic systems are important to Tundra Swans and other Arctic-nesting waterfowl because they represent a final stopover before breeding and the first autumn stopover where cygnets continue to develop (Bowler 1992, Petrie and Wilcox 2003). Tundra Swans spend about 15% of spring migration and approximately 50% of autumn migration in the Boreal (Petrie and Wilcox 2003), suggesting the Boreal Forest is likely especially important to Tundra Swans during autumn.

Based upon the assumption that ice-cover during spring would influence habitat selection, I predicted that open water would be selected during spring and both open water and wetlands would be selected during autumn in the Boreal Forest. However, because season did not appear in the top habitat selection models, my results suggest that season did not have a strong influence on aquatic habitat selection in the Boreal Forest. Overall, the selection relationships indicated that open water was strongly selected and wetlands were used approximately equal to their availability. Although the relationship was weak, selection intensity for open water appeared to decrease as birds moved north and west from approximately 25% at the southern edge of the Boreal Forest to 15% near the breeding grounds. When exploring selection of wetlands by Tundra Swans in the Boreal Forest, I discovered that none of my proposed candidate models were better at explaining variation in selection intensities than my covariates alone. Weak support of my models suggests: 1) the Boreal Forest is so saturated with wetlands that I was unable to detect any selection relationships; 2) I did not capture the factor(s) driving selection for wetlands in the Boreal Forest; or 3) inaccuracy of land cover data in the Boreal Forest.

Overall, wetlands represented less than one fifth of habitats used in the Boreal while open water represented approximately half of the habitats used during spring and over three fifths of habitats used during autumn. Because of the extended amount of time spent in the Boreal Forest during autumn as compared with spring, it is likely that availability of suitable foraging habitats was more important than simply finding a place to rest, which may explain the increased use of open water during autumn. Although availability of

open water was between 1.5-2× greater than availability of wetlands in the Boreal Forest, selection intensity was greater for open water than wetlands. Increased selection for open water over wetlands may be explained by: 1) the gregarious nature of Tundra Swans during the nonbreeding period; 2) decreased accuracy of land cover data in the Boreal Forest (because it is difficult to distinguish between open water and wetlands without detailed depth information, it is possible that wetlands were underrepresented in my habitat analysis and were actually used more than results suggest); or 3) a potential association between Tundra Swan migration routes and river habitats (observed during habitat analysis in my thesis), which are classified as open water habitats. Tundra Swans may associate with rivers because they represent a landscape cue with which Tundra Swans can direct migration (Hochbaum 1955, Bellrose 1980), or because rivers contain moving water and therefore are likely one of the first aquatic habitats to thaw during spring migration. Given that river habitat was classified as open water in my analysis and that open water was so strongly selected for, a more detailed analysis of this relationship is warranted and may explain some of the patterns I observed.

As suspected, my results suggest that waterfowl researchers and habitat managers should be addressing the Boreal Forest separately from regions where agricultural habitats are available. Because previous literature on wetland selection by waterfowl is often obtained in regions where agricultural forage is available, it may not be applicable in the Boreal Forest. Moreover, because wetlands are especially vulnerable to climate change (Poiani and Johnson 1991, Poiani et al. 1996, Sorenson et al. 1998, Johnson et al. 2005), and because open water was so strongly selected in the Boreal Forest, further investigation into habitat characteristics that may influence selection intensities of wetlands and open water in this environment is suggested.

Satellite Telemetry: Advantages and Caveats

Local-scale habitat use patterns by Tundra Swans were generally supported by the broad-scale geographic and temporal selection relationships identified in this study, suggesting that selection of habitats by Tundra Swans is not scale-dependent. Habitat selection during spring differed from local-scale habitat use information in that selection intensity was greatest for open water and agricultural habitats were not selected for relative to their

availability. My results confirm that Tundra Swans use agriculture more during spring than autumn as observed, but it is likely that Tundra Swans were not documented to select agriculture during spring migration because it was so greatly available. Another possible explanation for differences between observational studies and satellite telemetry results is that, although Tundra Swans are habitat generalists at the population level, they may be habitat specialists at the individual level. That is, individual Tundra Swans may engage in a variety of foraging strategies from primarily aquatic to primarily agricultural, as documented for Bewick's Swan during autumn migration (Hoye et al. 2012). Because observation of Tundra Swans numbers within habitats does not identify the actions of individuals, this trend may not have been detectable prior to use of satellite telemetry data. Use of telemetry data removes observer biases and allows observation of individual animals at inaccessible locations and over broad geographic ranges (Wikelski et al. 2007). Moreover, pairing results with land cover data allows easy comparison between habitats used and available (Minton et al. 2003, Aarts et al. 2008), and my results suggest that use of satellite telemetry and land cover data is an important tool for habitat management.

Use of satellite telemetry allowed analysis of habitat selection throughout the entire nonbreeding range, however, it also introduced error and potential bias into the analysis. The main issue caused by use of satellite telemetry data in my study was the inaccuracy of Tundra Swan locations, which necessitated that I consider proportional use of habitats within a used polygon rather than identifying specific habitats used (Minton et al. 2003). By using habitat mosaic information I may have reduced the accuracy of my results for comparison between agricultural and aquatic habitats when Tundra Swans were located on edges between habitats. With respect to agricultural habitats specifically, use of satellite telemetry data may have resulted in an underestimate of their nutritional contribution to Tundra Swan diets. Waterfowl can obtain nutrients from agricultural fields during very short periods of time because it is a high-energy food that is easily accessible and because their esophagus morphology allows them to carry more food than they could consume at one time (e.g., dabbling ducks averaged 20 to 45 minute foraging periods in fields over-winter; Baldassarre and Bolen 1984). Because satellite telemetry does not report locations continuously throughout the day and because I chose to include

only one location per day for individual Tundra Swans to reduce temporal autocorrelation, it is possible that I may have missed short flights to agricultural fields.

Without the use of land cover data, I would not have been able to address my research questions; however, it is possible that certain habitat selection relationships may not have been identified because of the broad land cover habitat classification system. For instance, agricultural habitat encompasses many types of agriculture that are not nutritionally profitable to Tundra Swans, such as tobacco, cotton, fruits, and pasture land. Specifically in North Carolina, where Tundra Swans were most strongly selecting for agriculture, tobacco and cotton accounted for 18.4% and 15.6% of all field crops planted in 2004 and 2010, respectively (U.S. Department of Agriculture National Agricultural Statistics Service). By obtaining detailed information on crop type availability, it is possible that more intense selection of nutritionally profitable agricultural habitats may be detected during winter and spring. Use of land cover data may also explain why there was no selection relationships identified for wetlands in the Boreal Forest and it is likely that more detailed information on wetland characteristics is needed.

Chapter Five: Thesis Summary

Conclusions

Aquatic vegetation is a nutritionally balanced food source and my results support the notion suggested by Baldassarre and Bolen (1984) that, if SAV were abundantly available in aquatic habitats, it would be advantageous to forgo energetically expensive flights to agricultural fields and forage solely in aquatic habitats. However, loss and degradation of aquatic habitats has necessitated the consumption of high-energy agricultural foods (Baldassarre et al. 1983, Delnicki and Reinecke 1986, Loesch and Kaminski 1989). For the most part, local-scale habitat trends transferred to the broad spatial and temporal scales investigated in my thesis. As predicted, selection intensity was greatest for aquatic habitats during autumn, and agriculture was avoided. Also fitting with predictions, agriculture and open water were the habitats most strongly selected during winter, suggesting Tundra Swans may forage in agricultural fields to increase lipid stores and rest in open water, as observed by Pearse et al. (2013) in Greater White-fronted Geese, *Anser albifrons frontalis* Scop., and Lesser Snow Geese, *Chen caerulescens caerulescens* L., in Nebraska. However, during spring I had predicted Tundra Swans would select both aquatic and agricultural habitats and, although aquatic predictions were supported, agriculture was not selected relative to its availability. Expectations for springtime agriculture selection stemmed from evidence of increased use of agriculture by Tundra Swans during spring migration. Although agriculture represented 68% of habitats used during spring in my study, agriculture was so greatly available (71.5%) that it was not selected. Important caveats of my study design that must be recognized when interpreting agricultural selection results are: 1) short flights to agricultural fields may have been missed due to the nature of satellite telemetry and my study design and, 2) availability of agricultural foods to foraging Tundra Swans may have been overestimated. Overall, it appears that Tundra Swans are using agriculture during spring to supplement more nutritionally balanced aquatic diets with a quick source of energy.

Wetlands were not selected on the wintering grounds as a whole; however, Tundra Swans do appear to select wetlands along the Potomac and Rappahannock Rivers in the Chesapeake Bay. As Tundra Swans moved further from the wintering grounds, selection

intensity values followed an overall positive trend, resulting in slight selection of wetlands in the lower Great Lakes and most of the Prairies. Increased selection for aquatic habitats near breeding grounds suggests that Tundra Swans may be selecting for habitats with more balanced nutrient availability immediately prior to and following reproduction. By increasing consumption of aquatic vegetation, Tundra Swans would be able to replenish nutrients and gain weight rapidly, which would be important for building stores for reproduction during spring and replenishing reserves during autumn (Loesch and Kaminski 1989, Jorde et al. 1995). Similarly, Northern Pintails, *Anas acuta* L., selected agricultural and aquatic foods relative to their availability in late autumn and early winter, but prior to spring migration they actively selected foods with balanced nutrient availability (Miller 1987). In my study, selection of open water, wetlands and agriculture all fell within 10% of each other during winter and spring, yet the difference exceeded 50% during autumn. These results may suggest a diverse diet during winter and spring was important to obtain adequate nutrient stores for breeding. Although, it is likely that Tundra Swans were using aquatic habitats to rest during winter and using them to obtain a balanced diet in late winter and spring. However, because agriculture was so highly available, and because I was not able to quantify what Tundra Swans were doing in each habitat through satellite telemetry, I am unable to make any conclusions on the importance of nutritional requirements in the selection of habitats.

Important geographic and temporal selection relationships for agriculture, open water and wetlands were identified in this study and have opened the door to many important microhabitat selection studies in the future. Understanding habitat use is essential to assess a species' biological requirements, justify protection of key areas, predict effects of habitat change, and test hypotheses underlying ecological processes (Holbrook and Schmitt 1988, Andren 1990, Carey et al. 1992, Crist and MacMahon 1992, Lubin et al. 1993). By investigating habitat selection and accounting for the availability of habitats I increased the utility of my results for conservation planning and promoted a more realistic understanding of the influence environmental features may have on abundance and distribution of large-bodied waterfowl (Johnson 1980, With and Crist 1995). Variability in the results was likely due to a combination of individual variation in foraging strategies (Hoye et al. 2012) and error introduced from satellite telemetry and

land cover data. Overall it appears that habitat and food availability have the strongest influence on selection of habitats, with nutritional requirements also appearing to be important. Based upon my results, I suggest that habitat managers interested in increasing roosting and foraging habitat for large-bodied waterfowl focus on conservation and restoration of aquatic habitats and food sources while ensuring availability of supplementary agricultural forage within 8 km of known roosting locations during winter and spring.

Future Directions

Trends observed in this study about habitat selection by EP Tundra Swans on regional and seasonal scales can be applied to large-bodied waterfowl species in a suite of studies. Because satellite telemetry error and land cover limitations reduced the utility of my results to broad-scale analysis, further analysis using radio-telemetry or Global Positioning System devices to address aspects of local ecosystems movements is suggested to correct for any potential inaccuracies in my study. Fine scale assessment of forage availability, quality, and use in agricultural, open water and wetland habitats by region and season would help explain temporal and geographic trends observed in my study and lend assistance to habitat managers. Moreover, body condition studies and isotopic analysis of Tundra Swans during autumn, winter and spring would determine relative consumption of different aquatic and agricultural foods, thereby identifying how and where Tundra Swans are acquiring nutrients for migration and reproduction, and identifying the importance of each habitat to seasonal nutrition. Information such as crop type selection, quality of available aquatic foods, and selection of aquatic system characteristics would also be beneficial. Further, because disturbance has the ability to limit accessibility and profitability of aquatic and agricultural habitats considered available, future research on the influence of these exogenous factors is suggested. Finally, the association observed between rivers and Tundra Swan migration routes should be further investigated.

The potential influence of weather has been addressed throughout this thesis, specifically in regards to its influence on accessibility of habitats, increased selection of agriculture at colder temperatures, and the sensitivity of wetlands to changing weather. However,

weather also has the ability to decrease the nutritional quality of post-harvest agricultural grain in fields from autumn to spring due to moisture related damage (Warner et al. 1989, Barney 2008). When flooded for 90 days rice loses 19% of metabolizable energy, and corn and soybean decrease by 50% and 86%, respectively (Ringelman 1990). In more northern latitudes, a “freezer effect” can preserve the nutritional content of grains (Barney 2008), which may make agricultural habitats with frequent snow and freezing temperatures important foraging areas during winter and spring (Schummer et al. 2010). However, a warming climate has the potential to reduce the profitability of agricultural forage due to above freezing temperatures and subsequent increased decline in nutrient availability (Barney 2008, Schummer et al. 2010). While I controlled for the influence of ice and snow on habitat selection in my modeling procedure, it may be important to further explore the potential influences of weather on habitat selection. Moreover, because a warming climate may encourage shortstopping in the Great Lakes (i.e., stopping and spending winters in the Great Lakes rather than continuing on to traditional wintering grounds; Greene and Krementz 2008, Brook et al. 2009, Nevin et al. 2010, Schummer et al. 2010), understanding the impact of intraspecific and interspecific shortstopping on nutritional availability in the Great Lakes staging areas also warrants further attention.

Management Implications

Waterfowl managers use information from food and habitat selection studies to set conservation goals and to conserve and manage foraging habitat at staging and wintering areas for waterfowl and other wildlife (Bolen 2000, Callicutt et al. 2011). Because Tundra Swans select different habitats depending on location and timing within the annual cycle, it is possible that landscapes that remain unchanged with regards to habitat availability through time and location may not be ideal when managing Tundra Swan habitats. Rather, one must consider availability and accessibility of habitat, seasonal availability of food and current and predictable future physiological requirements (Baldassarre and Bolen 1994).

My overall habitat recommendations are as follows. First, protect open water habitats during the nonbreeding period because open water was the most strongly selected habitat

during migration and was selected for over-winter. Second, manage for quality, abundant SAV at times when open water is most strongly selected (i.e., during autumn and spring in the Boreal Forest and during autumn in the Prairies, Great Lakes and Atlantic Coast). Third, protect and enhance wetland habitats in the lower Great Lakes, North Dakota, Canadian Prairies, and the northern Chesapeake Bay; and fourth, because changing cropping practices and increased harvester efficiency has the potential to greatly decrease the carrying capacity of many waterfowl species, monitor the availability of agricultural foods through time (especially during winter and spring) to ensure that they remain profitable locations for waterfowl to supplement nutrition acquired in aquatic habitats. Overall, managers should consider time of year and proportional availability of open water, wetlands and agriculture within 8 km of managed land when making decisions pertaining to habitat designations. Also, because selection for wetlands and agriculture changed continuously throughout the landscape, habitat management should be unified across flyways and political borders.

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Appendices

Appendix A. Crosswalk Chart describing Habitat Analysis Classification System used to combine three different land cover datasets (Hybrid Wetland Layer (HWL), Circa 2000, and National Land Cover Database 2001 (NLCD)) for analysis.

Habitat Analysis Classification System	Land Cover Classification Systems	
Open Water	NLCD	Open Water
	HWL	Water
	Circa	Water (rivers too)
Wetland	NLCD	Woody Wetlands Emergent Wetlands
	HWL	Bryoids Wetland Wetland – Treed Wetland – Shrub Wetland – Herb
	Circa	Bryoids Wetland Wetland – Treed Wetland – Shrub Wetland – Herb Wet sedge
Perennial Ice/Snow	NLCD	Perennial Ice/Snow
	HWL	Snow/Ice
	Circa	Snow/Ice
Developed	NLCD	Developed – Open Developed – Low Intensity Developed – Medium Intensity Developed – High Intensity
	HWL	Developed
	Circa	Developed
Barren Land	NLCD	Barren Land (Rock/Sand/Clay)
	HWL	Exposed/Barren Land Rock/Rubble Non-Vegetated Upland Cloud Shadow
	Circa	Barren/Non-vegetated Rock/Rubble Exposed Land Sparsely vegetated bedrock Sparsely vegetated till-colluvium Bare soil Cloud Shadow
Deciduous Forest	NLCD	Deciduous Forest
	HWL	Broadleaf Broadleaf – Dense Broadleaf – Open Broadleaf – Sparse

	Circa	Deciduous Forest Broadleaf – Dense Broadleaf – Open Broadleaf – Sparse
Coniferous Forest	NLCD	Evergreen Forest
	HWL	Coniferous Coniferous – Dense Coniferous – Open Coniferous – Sparse
	Circa	Coniferous Forest Coniferous – Dense Coniferous – Open Coniferous – Sparse
Mixed Forest	NLCD	Mixed Forest
	HWL	Mixedwood Mixedwood – Dense Mixedwood – Open Mixedwood – Sparse
	Circa	Mixed Forest Mixedwood – Dense Mixedwood – Open Mixedwood – Sparse
Shrub/Scrub	NLCD	Dwarf Scrub * Alaska Only Shrub/Scrub
	HWL	Shrubland Shrub – Tall Shrub – Low
	Circa	Shrubland Shrub – Tall Shrub – Low Prostrate Dwarf Shrub Tussock Graminoid Tundra Non-tussock/Dwarf Shrub Tundra Dry Graminoid Dwarf Shrub Tundra
Agriculture *Agriculture in the Boreal Region represents Sedge/Herbaceous and includes Dwarf Shrub in Alaska*	NLCD	Grassland/Herbaceous Pasture Cultivated Crops
	HWL	Herb Native Grassland Agriculture Cropland Pasture/Hay
	Circa	Herb Grassland Cultivated Agricultural Land Annual Cropland Perennial Cropland/Pasture

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Presentations:

Weaver, K., M. L. Schummer, S. A. Petrie, and H. Henry. 2013. Habitat selection during the non-breeding period by Eastern Population Tundra Swans (*Cygnus columbianus columbianus*). (Oral Presentation). Biology Graduate Research Forum, October 2013, London, ON.

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