MOVEMENT ECOLOGY AND HABITAT USE OF CANADA GEESE USING MAJOR METROPOLITAN AREAS IN THE CONTEXT OF HUMAN-WILDLIFE CONFLICTS

BY

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DISSERTATION

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ABSTRACT

Canada geese (*Branta canadensis*) are economically and socially important due to their popularity as a game species and association with human-wildlife conflicts. The species' ability to adapt to human-altered agricultural and urban landscapes has contributed to the success of temperate-breeding Canada goose populations. Differences in habitat resources and predation risks across the rural to urban gradient of the upper Midwest shape the movement and behavioral ecology of Canada geese, requiring unique life history strategies to maximize survival through-out the annual cycle. Winter is an energetically costly period due to food limitation and increased thermoregulatory costs. Urban areas have altered these dynamics and facilitate northward shifts in wintering distributions by providing anthropogenic food sources, reduced predations risk, and thermal refugia for many avian species. Large abundances of Canada geese winter in highly developed, urban areas of Chicago, leading to concerns over risks to air traffic. Previous work indicates that safety due to hunting restrictions are driving these patterns rather than food availability or thermal refugia. We used global positioning system (GPS) transmitters equipped with tri-axial accelerometers to quantify factors influencing use of both urban and rural areas during two energetically costly portions of the annual cycle: winter and remigial molt. Pertaining to winter ecology, my research sought to examine, 1) differences in wintering strategies of geese in rural versus urban areas, 2) environmental and behavioral factors influencing goose movements and subsequent risk to air traffic, and 3) behavioral responses to targeted harassment. Regarding differences in wintering strategies, I found no differences in winter survival between rural- and urban-wintering geese but differences in cause-specific mortality indicating strong effects of temperature on survival in urban areas and alternatively harvest in rural areas. In addition, movements and behavioral time budgets suggest access to high-energy foods in rural areas may ameliorate energetic costs during extreme cold periods while geese in urban areas must rely on energetically conservative behaviors and endogenous reserves. Regarding movements and risks to air traffic, the risk of movements to air traffic varied by the juxtaposition of habitats relative to important air traffic areas but were associated with novel urban goose habitats including rooftops and railyards. In response to harassment, geese left the harassment site more often, were more alert, and flew more, but changes in habitat preferences during cold periods likely reduced discernible effects of harassment on survival or emigration from the area.

Remigial molt is the loss and regrowth of flight feathers and occurs simultaneously in waterfowl, rendering them flightless. Because of the energetic cost of replacing all remiges and risk of predation due to flightlessness, geese should select areas to undergo molt that provide high quality foraging environments and low predation risk. These decisions can occur at the landscape scale, involving the choice to molt near breeding areas or migrate to another area. This molt migratory behavior is common in temperate-breeding Canada goose populations, which undertake molt migrations of thousands of kilometers to the Subarctic. However, the trade-offs associated with molt migration may be altered by increased availability of novel molting habitat in temperate regions, in the form of urban greenspaces, and increased predation risk from hunting during migration. My research sought to determine 1) landscape factors influencing molt migration, 2) trade-offs in foraging environments between subarctic and temperate molting areas, and 3) differences in survival. My results demonstrate that the propensity to molt migrate decreases with the greater proportions of land uses that provide escape from predators (i.e. waterbodies), that foraging and alert behaviors indicate a better quality foraging environment in the subarctic, even when corrected for differences in day length, and that survival of molt migrants is greater than non-molt migrants until September when a large proportion were harvested on return migration. While nest removal to induce molt migration may serve as an important tool to indirectly decrease adult survival of urban-wintering geese. However, increased harvest of molt migrants is likely to affect breeding areas differentially and disproportionately decrease survival of geese nesting in more natural wetland and rural areas.

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TABLE OF CONTENTS

CHAPTER 1: GENERAL INTRODUCTION

The use of urban areas by wildlife requires species to adapt to novel resources and risks through unique behavioral and physiological adaptations (Marzluff et al. 2001, Møller 2008, Zuckerberg et al. 2011) but can confer increased survival and abundances (Shochat et al. 2010). Urbanization has been shown to decrease diversity in avian communities (Marzluff et al. 2001) as generalists are able to take advantage of resources in urban areas and sustain high population abundances (Blair 1996). Urban-adapted species are often viewed negatively, as many are non-native or associated with human-wildlife conflicts (Soulsbury and White 2016), yet urban adaptation has benefited species in their native range, including peregrine falcon (*Falco peregrinus*) and European blackbird (*Turdus merula*; Partecke et al. 2006, Caballero et al. 2016). The use of urban areas can provide thermal refugia (Wolf et al. 1996, Murthy et al. 2016), greater food availability due to supplemental feeding by humans (Jokimäki and Suhonen 1998, Zuckerberg et al. 2011), and reduced predation risk compared to surrounding landscapes (Møller 2008). However, the novel benefits provided by urban areas are often offset by novel risks (Evans et al. 2015). Available foods may be of lower quality (Shochat 2004), predation from human-subsidized predators (Crooks and Soule 1999, Loss et al. 2013, Magle et al. 2016), negative effects of human disturbance (Evans et al. 2009), and risks of collision with vehicles and buildings (Chace and Walsh 2006) can be high in some species, providing selective pressures against the use of urban environments (Evans et al. 2015).

Winter is a dangerous and energetically costly period for avian taxa as thermal constraints force birds to migrate to warmer latitudes or adapt to increased thermoregulatory costs and limited food availability (Newton 2007, Schummer et al. 2010). The ability to survive winter at northern latitudes is driven by complex interactions between physiology and the abiotic and biotic environment avian species inhabit (Canterbury 2002, Schummer et al. 2010). Wintering in the northern portions of a species' range (in the northern hemisphere) requires behavioral and physiological adaptations to survive periods of limited food availability and increased energetic costs (Biebach 1996, Pakanen et al. 2018). Optimal foraging theory dictates that animals should maximize survival during winter by balancing current energetic reserves and seeking out necessary resources, while avoiding predation (Brown 1988, Lima and Dill 1990, Hagy and Kaminski 2015, Palumbo et al. 2018). The distribution of resources and predation risk vary spatially and temporally across landscapes, requiring animals to move and select locations that maximizes survival and fitness (Madsen 1988). These predation-forage trade-offs are pervasive pressures in species' ecology, shaping most aspects of animal behavior (Werner and Anholt 1995, Frid and Dill 2013), especially during periods of increased risk or energetic requirements.

Geese have adapted well to human-altered landscapes across North America (Holevinski et al. 2007) and the world (Fox 2014, Atkins et al. 2017), contributing to increasing populations (Fox and Madsen 2017). Canada geese (*Branta canadensis*) are often associated with conflicts due to risks air traffic (Bradbeer et al. 2017), aggression towards people (Smith et al. 1999), and negative impacts of fecal deposition on greenspaces and water quality (Manny et al. 1994). While Canada geese are negatively associated with conflicts, they are also an economically and culturally important games species (Heinrich and Craven 1992, Berkes et al. 1994, Buij et al. 2017, Luukkonen et al. 2021) with an estimated 271,700 active goose hunters harvesting just around 1 million Canada geese annually in the Mississippi Flyway alone (Fronczak 2020).

Canada geese exhibit complex migratory and wintering strategies, that have made them well adapted to human-altered landscapes throughout the annual cycle (Guerena et al. 2014, Dorak et al. 2017, Clermont et al. 2018, Luukkonen et al. 2021). A clear understanding of the ecological interactions of Canada geese with the human-altered landscape is not only important for understanding and managing Canada goose populations (Dorak et al. 2017), but urban-adapted species in general (Evans et al. 2009). Selective pressures towards the use of urban areas will likely increase with increasing urbanization and warming climate trends, influencing the associated predation-forage trade-offs that shape animal behavior and distributions (Zuckerberg et al. 2011). The following four chapters investigate the behavioral and movement ecology of Canada geese with the goal of understanding how human-altered landscapes shape unique life history strategies.

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CHAPTER 2: UNDERSTANDING WINTERING STRATEGIES AND BEHAVIORAL ADAPTATIONS AT THE NORTHERN EXTENT OF A SPECIES' WINTERING RANGE

ABSTRACT

The ability to survive winter in northern portions of a species' range is driven by complex interactions between individuals and their abiotic and biotic environment. Urban areas have facilitated northward shifts in several species and changed predation-forage risk trade-offs, influencing avian movements and distributions (in the northern hemisphere). We used satellite telemetry and accelerometry to examine differences in movement, and behavior between Canada geese (*Branta canadensis*) wintering in rural and urban areas of northeastern Illinois. We modeled differences between rural and urban areas using known-fate survival models, examined sources of mortality, and quantified interacting effects of winter weather with landscape on various aspects of movement, energy expenditure, and behavior. Overall, there were no differences in survival between individuals that wintered in urban and rural areas, however sources of mortality differed. The probability of mortality due to non-harvest causes (i.e., exposure/starvation) increased with decreasing temperatures, while survival in rural areas were not affected by cold temperatures. Alternatively, survival of geese in rural areas decreased with increased proportion of rural area, due to harvest mortality. Rural-wintering geese also moved greater distances, expended more energy, and were 3.7 times more likely to move south during extreme cold periods than urban-wintering geese. We suggest differences in causes of mortality and movement reflect differing wintering strategies in which urban-wintering geese forego higher-quality food resources and assume greater risk of starvation in favor of safety from hunting, while rural-wintering geese assume greater risk of harvest mortality but access higher-quality forage. We found evidence that rural-wintering geese are more likely to move further

south, likely related to energetic condition or similarities in predation risk. While urban wintering strategies may confer higher survival during relatively mild winters, extreme weather events (i.e. “polar vortices”) may result in mass mortality events. Our results showed some plasticity in wintering strategies with rural-wintering geese more likely to switch to urban than vice versa. Large concentrations of urban wintering geese in urban areas reflect individual strategies to take advantage of these safe locations, while reducing energy expenditure, and waiting out periods of extreme cold.

INTRODUCTION

Winter is a dangerous and energetically costly period for avian taxa as thermal constraints force birds to migrate to warmer latitudes or adapt to increased thermoregulatory costs and limited food availability (Newton 2007, Schummer et al. 2010). The ability to survive winter at northern latitudes is driven by complex interactions between physiology and the abiotic and biotic environment species inhabit (Canterbury 2002, Schummer et al. 2010). Wintering in the northern portions of a species’ range (in the northern hemisphere) requires behavioral and physiological adaptations to survive periods of limited food availability and increased energetic costs (Biebach 1996, Pakanen et al. 2018). Optimal foraging theory dictates that animals should maximize survival during winter by balancing current energetic reserves and seeking out necessary resources, while avoiding predation (Brown 1988, Lima and Dill 1990, Hagy and Kaminski 2015, Palumbo et al. 2018). The distribution of resources and predation risk vary spatially and temporally across landscapes, requiring animals to move and select locations that maximizes survival and fitness (Madsen 1988). Urban areas have shifted predation-forage trade-offs by providing relatively novel pressures on species’ ecologies, negatively impacting many species relative to natural areas, but benefiting those capable of adapting to unique, urban environments (Jokimäki and Suhonen 1998, Zuckerberg et al. 2011).

Changes to predation-forage trade-offs in urban areas have facilitated poleward shifts in wintering distribution of many avian species by providing food subsidies, thermal refugia, and safety from predation (Root 1988, Jokimäki and Suhonen 1998, Murthy et al. 2016). Reduced predation risk relative to rural or natural areas likely drives the use of urban areas by a range of avian taxa (Shochat 2004, Hebblewhite and Merrill 2009, Fischer et al. 2012). Similarly, urban areas provide novel habitat resources that would not be available in natural areas at similar latitudes, including supplemental feeding and ice-free waterways (Jokimäki and Suhonen 1998, Zuckerberg et al. 2011, Dorak et al. 2017). However, predation risk and habitat resources in urban areas likely vary seasonally and are species-specific (Bolger et al. 2001, Fischer et al. 2012). While differences in predation risk and foraging environment vary spatially and temporally within urban areas and provide conflicting pressures for and against urban-adaptation in avian taxa, the use of urban areas provide game species with sanctuary from harvest mortality (Madsen and Fox 1995, Balkcom et al. 2010, Dorak et al. 2017).

Many species of ducks and geese have adapted to human-altered landscapes around the globe, providing opportunities to study differences in life history strategies along the rural-urban gradient (Fox and Leafloor 2018, Fox 2019). The adaptation of geese to urban areas is related to their large size, tolerance of human disturbance, and broad forage preferences that have adapted to modern agriculture and urban land uses (Fox 2019). This urban-adaptation has led to human-goose conflicts around the world (Dolbeer and Seubert 2014, Atkins et al. 2017, Fox 2019). Canada geese (*Branta canadensis*) are commonly associated with human-wildlife conflicts due to their abundance and extensive use of urban areas in North America and where introduced in Europe (Fox 2019). Canada geese are a popular game species and the effects of hunting, both direct and indirect, likely influence demographic rates and distribution of Canada geese, providing selective pressure towards the use of urban areas (Balkcom 2010, Dorak et al. 2017).

Despite the economic importance of Canada geese as a game species and negative human-goose conflicts, differences in overwintering strategies between rural and urban wintering geese is poorly understood. Turf lawns in urban greenspaces provide high-quality forage for geese during the breeding season but offer limited nutritional value in winter (Gates et al. 2001, Dorak et al. 2017). Spilt grain in railyards and supplemental feeding in parks may provide some energetic value, but availability is likely variable spatially and temporally and use of these food sources is not ubiquitous (Dorak et al. 2017). Conversely, rural areas present abundant and energy-rich forage items in the form of waste grains and other agricultural crop residues (Gates et al. 2001), but increased risk of mortality due to hunting (Holevinski et al. 2007, Balkcom 2010). While use of rural and urban areas by geese represent different predation-forage trade-offs for Canada geese (Cresswell 2008, Sansom et al. 2009), the use of both areas to overwinter at the northern extent of their winter range may be advantageous as it reduces costs of migration, allows geese to return to nesting areas earlier, or provide access to increased food availability (Alerstam et al. 2003, Clausen et al. 2018). The wintering strategies geese employ; in terms of home ranges and behaviors, are influenced by the winter severity (Clausen et al. 2018, Shirkey et al. 2018, Luukkonen et al. 2021) and faithfulness to these strategies is likely driven by the stability of environments in which individuals winter (Clausen et al. 2018).

Canada geese wintering in the Midwest originate from multiple breeding regions that exhibit relatively complex and variable life histories; differing patterns in migratory behavior and historical wintering areas (Gates et al. 2001) and varying degrees in use of urban environments. This variability makes Canada geese wintering in the upper Midwest an ideal model with which to understand trade-offs influencing wintering strategies at the northern portion of their range. The temperate-breeding population of Canada geese that commonly breed in urban areas across the Midwest and southern Canada (primarily large-bodied *B. c. maxima and B. c. moffitti*) are the result of reintroductions in order to recover the population and enhance hunting opportunities following near extinction in the first half of the 20th century (Hansen 1965, Sheaffer et al. 2007). Individuals in the temperate-breeding population vary widely in their migratory behavior and use of urban areas for breeding, from breeding in extremely urbanized areas (e.g. parking lots, rooftops) to the use of more natural wetland habitats. In contract to the temperate-breeding individuals, subarctic-breeding Canada geese (*B. c. interior*), which breed along Hudson Bay in Canada, nest in large wetlands areas that are extremely removed from urbanization. In addition, subarctic-breeding Canada geese historically wintered in rural areas south of northeastern Illinois, having shifted winter distributions from parts of Alabama and Kentucky, to southern Illinois, and most recently to northeastern Illinois (Gates et al. 2001).

We used advanced GPS telemetry and accelerometry (e.g. index of energy expenditures, behaviors) to compare the overwintering strategies geese employ between urban and rural landscapes. Our objectives were to: 1) quantify differences in survival, and factors influencing survival, 2) examine differences in movement distance, 3) quantify differences in time spent in foraging and flight, and 4) factors influencing departure and southward movement from primary wintering areas. We further discuss how understanding the strategies of overwintering birds can inform management and improve understanding of how species behave in intensive agricultural and urbanized areas. Additionally, our results provide valuable information on how climate change is likely to impact the strategies of birds wintering in urban and rural landscapes.

METHODS

Study Area

Our study focused on northeastern Illinois, including the Chicago Area in portions of Cook, DuPage, Kane, Kendall, and Will counties. The Chicago Area predominantly consists of urban land uses but includes a gradient of urban to suburban-rural land uses in outlying portions of the metropolitan area (Figure 1). Urban portions of Chicago are dominated by highly developed land uses including industrial areas, railyards, and residential areas interspersed with waterbodies and greenspaces (Dorak et al. 2017). Rural portions occur on the fringes of the Chicago Area where suburban areas interface with agricultural areas. Corn and soybeans are the predominant crop in northeastern Illinois with over 823,000 acres of corn and 735,000 acres of soybeans planted in 2019 (USDA Quick Stats 2019). The area averages 43 days annually below freezing, with 7 days below -18 °C and averages approximately 93 cm of snowfall annually. The estimated temperate-nesting Canada goose population in the area exceeds 30,000 individuals (Paine et al. 2003) with a human population of 9.7 million in 2010, including the city of Chicago and surrounding suburbs (Lichter et al. 2020). Northeast Illinois is located within the Mississippi Flyway, which is home to approximately 225,000 goose hunters that annually harvest around 1 million Canada geese (Fronczak 2020)

Field Methods

We captured geese in rural and urban areas during October 2015 – May 2020. During 2014 – 2018, captures occurred solely in urban portions of the Chicago area during fall and winter (Oct–Jan; n = 62). Starting in 2018, we captured geese during the breeding season (Apr-May; n = 28) and winter in urban and rural areas of northeastern Illinois (Fig. 2.1). We used animal net guns (Wildlife Capture Services, Flagstaff, Arizona, USA) for the majority of captures and rocket nets in rural areas where geese were difficult to approach. We affixed an aluminum leg band and Global Positioning System (GPS) transmitter on each goose prior to release (Castelli and Trost 1996, Coluccy et al. 2002, Caswell et al. 2012). We used either a Cellular Tracking Technologies (CTT) GPS-Global System for Mobile Communication transmitter (GPS-GSM; $n = 85$ Somerset, PA) attached to alphanumeric neck collars (Spinner Plastics, Springfield, IL) or neck collar-style, Ornitela GPS-GSM transmitter ($n = 21$, OrniTrack-N44, Vilnius, Lithuania) on captured Canada geese. Transmitters were < 2% of the body mass of Canada geese ($\bar{x} = 4{,}713$ grams, SE =10.6). We captured and handled all Canada geese using the approved methods detailed by the University of Illinois Institutional Animal Care and Use Committee (Protocol #14155). Work was conducted with all necessary permits, including institutional (IACUC #20039), Illinois state scientific (#6079), Chicago Parks District Scientific Research (#1839), Chicago Water Reclamation District (#P-557; 17-NE 014), and federal banding permits (USGS BBL #23923).

Survival

We estimated weekly survival using AIC model selection of known-fate models using Program MARK (White and Burnham 1999) implemented in package *RMark* in Program R (Laake et al. 2019, R Core Development Team 2013) and estimated winter survival from weekly survival estimates using the delta method (i.e. derived estimates; White and Burnham 1999). We then used AIC model selection to rank a suite the additive and interactive effects of time-specific covariates including weekly mean temperature, snow cover, proportion of rural land uses in the home ranges, and landscape groups (i.e. rural or urban) on weekly known-fate survival using generalized linear mixed effects models (Hedlin and Franke 2017). We used Pearson's product-moment correlation to test for correlation (P_r) between fixed effects and excluded those that were correlated ($P_r > 0.7$) from the same model. In addition, we examined factors contributing to cause specific mortality by modeling the interactive effects of cause-specific mortality with proportion of rural land uses and cause-specific mortality with mean daily temperature using generalized linear mixed effects models. We accounted for non-independence of survival by including nested random effects of individual ID. We determined cause of mortality as harvest mortality for geese that were harvested by hunters (i.e. direct contact, band reports, locations from homes) and non-harvest mortality for geese dying of other causes (i.e., predation, exposure/starvation, vehicle collisions). We excluded individuals with transmitters that apparently failed or for which fate could not be determined (n = 11). We used ancillary information, including location data, band recovery reports, and onboard sensors (i.e. temperature or accelerometer data) to determine cause of mortality. When possible, we physically located transmitters that were recording stationary GPS locations to confirm fate and cause of mortality. All recovered transmitters were from deceased birds and found no evidence of transmitter loss. Hunters typically contacted us directly, via phone numbers or email addresses printed on transmitters, shortly after harvest.

To quantify the proportion of rural land uses, we modeled weekly home ranges for each goose using autocorrelated kernel density estimates using package *ctmm* (Fleming et al. 2015) and extracted the proportion of rural land uses from polygons of 95% probability of use using the extract function in package raster (Hijmans et al. 2015). For instances of missing data, caused by too few locations for computing home ranges or computational issues from extremely large home ranges, we extracted proportion of rural land uses from a 2.5 km buffer around the mean weekly location. We used an additive combination of corn field, soybean field, and idle crop land from the Cropland Data Layer (Boryan et al. 2011) to create geospatial layers representing varying composition of rural land uses across the rural-urban gradient at 30 m^2 resolution (Buxton and Benson 2015, Padilla and Sutherland 2019). We chose to use these land cover types as a proxy for harvest mortality risk as they are the dominate land covers in rural areas across much of the Midwest and represent land uses where goose hunting is most likely to occur (Beston et al. 2014). The Cropland Data Layer provides accurate and up to date data on land cover, including agricultural crop type, using a supervised, land cover, classification approach derived from remotely sensed satellite data (Boryan et al. 2011).

In order to simplify interpretation, we categorized individuals as urban or rural, by week and by season, using the function 'getJenksbreaks' in package *BAMMtools* to identify natural breaks in the distribution of weekly and seasonal proportional land uses determined by individual home ranges (Rabosky et al. 2014). We identified a break in the distribution of weekly proportion of rural land uses at 5% in weekly home ranges, and classified geese as urban if < 5% of their weekly home range consisted of rural land uses and rural if it was >5%. Likewise, we classified individuals as primarily urban wintering if home ranges contained < 5% rural land uses

Movement and Energetic Expenditure

We used AIC model selection to rank a suite of general linear mixed effects models that included the effects of proportion of rural land uses in weekly home ranges, weather variables, and week of season on daily movement distances and overall dynamic body acceleration as an index of energetic expenditure (Weegman et al. 2017). We calculated daily movement distances as the sum of Euclidean distances between sequential points.

Transmitters manufactured by CTT recorded acceleration in g-force (range -4 – 4 g) while Ornitela transmitters measured acceleration in millivolts (range -2049 – 2049 mV). Due to differences in measurements between the two transmitter types we used (Ornitela units bound to a range of values) we scaled the daily mean ODBA measurements to one standard deviation from the means for each transmitter type. In addition, we included transmitter type as a random effect account for differences in measurement units and bounding.

We included polynomial terms when fitting our candidate suite of linear mixed effects models as animal movement often has a curvilinear relationship with weather conditions and habitat use (Dorak et al. 2017, Holbrook et al. 2019). We used cubic (x^2) and quadratic (x^3), orthogonal polynomial terms on continuous variables using package stats in program R and evaluated models using likelihood ratio tests in package *lmertest* and visually by plotting the relationships (Holbrook et al. 2019, Fieberg et al. 2021, Von Bank et al. 2021).

Time spent Foraging and In Flight

We then quantified differences in the proportion of time spent in energetically costly behaviors (i.e., foraging and flight) by landscape composition, temperature, snow cover and interactive effects of landscape group with temperature (VonBank et al. 2021). We used acceleration data from on-board accelerometers to quantify behavioral time budgets of transmittered geese (Weegman et al. 2017, VonBank et al. 2021). Because of differences in measures of acceleration (i.e. Ornitela units bound data), we analyzed the CTT and Ornitela accelerometry data separately (see below). We built training datasets with which to train classification models by pairing observed behaviors from video of recorded geese in the field to ACC packets that could be unambiguously classified as head-up (i.e. alert), head tucked (i.e. resting), foraging, and in-flight behaviors. We chose these four behaviors, as they were the primary behaviors that could be differentiated using neck collar mounted accelerometers (Kölzch et al. 2016), and are commonly recorded in other behavioral studies of geese (Bélanger et al.

1989). Head-up behavior included any behaviors in which a gooses neck was erect, including alert and vigilance while walking, we considered head tucked as an individual with bill tucked under a wing typical of a resting goose, foraging as active pecking or grazing, including walking with head outstretched while actively feeding. Other behaviors that we did not uniquely identify included preening, drinking, swimming, or walking. We first calculated summary statistics for each ACC packet and translated these summarized ACC packets to instantaneous behaviors using a supervised machine learning approach and classification process (Shamoun-Baranes et al. 2012, Resheff et al. 2014, VonBank et al. 2021). Summary statistics include measures of overall acceleration among all axes, changes in acceleration in single axes, and relational measures between two axes following methods of Resheff et al. (2014). We used a workflow with an extreme gradient boosting algorithm (package XGboost; Chen and Guestrin 2016) to build separate classification models for CTT and Ornitela transmitters (due to their different data outputs) to predict unknown ACC packets (Shamoun-Baranes et al. 2012, Kölzch et al. 2016, VonBank et al. 2021). We ran 100 iterations of a train-test split using 75% of the data to train and 25% of the training data to test accuracy. The accuracy of the trained, extreme gradient boosting algorithm was 89.1% for CTT and 93.8% for Ornitela transmitters (i.e., how often the observed behavior was the same as the predicted behavior). We then used the trained models to predict the probability of an unknown ACC packet belonging to each of the focal behaviors and assigned the predicted label to the behavior class that had the highest probability. We assigned predicted behaviors to the nearest GPS fix (i.e., 30 minutes before or after a GPS fix) via timestamps of GPS and ACC packets, resulting in ~ 4 behaviors per locations per GPS fix.

We calculated the daily proportion of foraging and in-flight behaviors each transmittered goose and the weekly mean proportion of both behaviors. We used AIC model selection to rank a suite of models including the effects of proportion rural land uses, temperature, and the interactive effect of landscape groups with temperature on weekly proportion of foraging and in-flight behaviors using generalized linear mixed effects models in package *lme4* (Bates et al. 2014). We included an interactive, random effect of individual ID and transmitter type (e.g. 1|ID:Type) to account for differences in transmitter units and classification algorithms for each transmitter type.

Transitions Between Landscapes and Southward Emigration

In order to examine change in wintering strategies, we quantified transitions between wintering strategies (urban and rural) between weeks and seasons for each individual. We defined transitions as changes of an individual from occupying one landscape type (rural or urban) to the other in subsequent weeks and seasons. We report the mean proportion (± SE) of transitions between landscape groups. We modeled the effects of temperature and proportion of rural land uses on change in latitude and change in proportion of rural land uses. We calculated change in latitude as the difference between the mean latitude in the GCMA, over the entire winter period, from the mean weekly latitude. Similarly, we calculated change in proportion of rural land uses as the difference between season mean proportion of rural land uses and weekly proportion of rural land uses. We then modeled emigration (left or did not leave) from primary wintering areas using generalized linear mixed effects models in package lme4. We defined emigration as daily movements that were > 30 km south (~0.27° Latitude) from the individual's season mean location. This value was > 3 standard deviations from the mean of daily movement distance and thus indicated a considerable southward movement likely associated with a landscape-level relocation or migratory event (McDuie et al. 2019).

Differences in Breeding Origins

We classified the breeding region of individuals captured during winter, based on their locations during the first two weeks of May in previous or subsequent breeding season. Canada geese from all breeding areas are typically at or near nest sites during the first two week of May and failed or non-breeding Canada geese have not yet left on molt migration (Luukkonen et al. 2008). We did not observe any switching of breeding areas and assumed that breeding area in subsequent years represented prior breeding areas. During winter, we captured both temperate-breeding population Canada geese (n = 74) and subarctic-breeding population Canada geese (n = 7). Temperate-breeding Canada geese captured during winter nested in Illinois (n = 26), Wisconsin (n = 29), and southern Ontario (n = 12) while all subarctic-nesting Canada geese nested along southern Hudson Bay in Ontario (n = 7). We used generalized linear mixed effects models with collar ID as a random effect to model breeding area on weekly survival and probability of emigration.

RESULTS

Survival

We recorded 37 mortalities out of 95 geese (241 goose/winters) during winters 2015–2021. Sources of mortality included 17 harvest-mortalities and 20 non-harvest mortalities (i.e. vehicle collisions, exposure/starvation; Fig. 2.2). Mean harvest date was November 22nd (range = 5-October – 27-January) and mean date of non-harvest mortalities was January 13th (range = 30-October – 24-March). Most mortalities occurred in and around northeastern Illinois (26 of 37) but ranged as far as Minnesota and Tennessee (Fig. 2.3).

There were four competing models of winter survival of transmittered Canada geese which included the effect of landscape group (rural or urban), breeding population (temperate or subarctic), and season (i.e., winter period; Table 2.1). Based on the second best supported model (w_i), which included the additive effects of landscape group and breeding population, winter survival of Canada geese wintering in urban areas was greater (93.8%, CI = 73.5-98.8%) than rural areas (82.5%, CI = 50.8-95.6%) and temperate-breeding Canada geese had lower survival (86.1%, CI = 79.6-90.7%) compared to subarctic-breeding (93.8%, CI = 73.5-98.8%).

Five models representing weekly survival were competitive and included the effects of mean temperature, minimum temperature, and landscape group (Table 2.2). We reported the effects of the model including the interaction of mean temperature with landscape group as mean and minimum temperature were correlated ($P_r = 0.92, p < 0.05$). Weekly survival decreased as minimum temperature decreased ($\beta = 0.04 \pm 0.03$ SE) and geese using urban landscapes had lower weekly survival during weeks with minimum temperature below approximately -15° C compared to geese using rural areas (Fig. 2.4).

Movement and Energetic Expenditure

A model including the interactive effects of mean daily temperature (quadratic) with landscape group best represented daily movement distances (km; Table 2.2). The predicted daily movement distance of geese in urban areas was less than that of geese in rural areas except at extreme cold temperatures (Fig. 2.5). All other models were not competitive but performed well relative to the null model (Table 2.2).

Behaviors

The most supported model of proportion of time geese spent feeding included the interactive effects of minimum temperature (quadratic) with landscape group (Table.2.3). Geese using urban landscapes spent a greater proportion of their time foraging between -10 – 20° C compared to those in rural areas but less below -10° C (Fig. 2.6). There were three supported models of proportion of time in flight, and included the effects of minimum temperature and landscape group (Table 2.4). For ease of comparison, we present a figure of the interactive effects of mean temperature (cubic) with landscape group on proportion of time spent in flight (ΔAICc = 1.91; Fig. 2.7). The proportion of time geese spent in flight in rural areas was relatively constant across the range of temperature while those in urban areas decreased the proportion of time in flight during both cold and warm periods (Fig. 2.7).

Emigration and Rural-urban Switching

The interactive effects of snow depth (quadratic with landscape group best represented southward departure, indicated by change in latitude from the winter mean (Table 2.5). Geese that primarily wintered in rural areas moved south of mean wintering locations as snow depth increased while those in urban areas remained (Fig. 2.7). Likewise, a model including interactive effects of snow depth (quadratic) with landscape group on the probability of transmittered Canada geese leaving mean wintering locations was the best supported (Table 2.6). Geese wintering in rural areas were more likely to depart mean wintering areas and that probability increased with increasing snow depth (Fig. 2.8)

Geese that wintered in urban landscapes seldom switched to rural areas the following year ($\bar{x}$ = 8.0%, n = 88), while those in rural areas more frequently switched to urban landscapes ($\bar{x}$ = 33.3%, n = 18, G^{adj} = 6.59, p = 0.01). Within years, geese wintering in rural landscapes were more likely to move to urban landscapes ($\bar{x}$ = 13.7% ± 8.9 SE, n = 627) compared to geese moving from urban to rural ($\bar{x}$ = 2.6% ± 3.7, n = 2742, G^{adj} = 109.6, $p < 0.001$).

DISCUSSION

The ability of Canada geese to survive winter at the northern extent of the species' range in both urban and rural areas, with differing predation risk (i.e., hunting pressure) and resource availability, demonstrates adaptive wintering strategies that have contributed to the success of Canada goose populations. Urban versus rural wintering strategies represent risk-minimizing and resource-maximizing trade-offs that were reflected by survival and movement of geese in both areas. While winter survival was similar between urban and rural areas, the factors influencing survival differed. Extreme cold temperatures had a stronger effect on survival of urban-wintering geese due to increased risk of starvation and exposure during those periods than rural-wintering geese that can supplement endogenous reserves with waste grain. The greater risk of starvation/exposure by urban-wintering geese is likely the product of a wintering strategy that relies heavily on endogenous reserves in order to reduce risk of predation (Biebach 1996).

Animals living in areas where they rely on temporally variable food resources due to changes in weather or other factors, should maintain larger endogenous fat reserves to buffer against periods when food or access to food is limited compared to those with reliable food resources (Biebach 1996). Most geese do so during periods of increased energetic demand; including breeding, winter, and molt (Gates et al. 2001, Fondell et al. 2013, Hupp et al. 2017, Massey et al. 2020). This physiological trait likely facilitates the overwintering strategies of Canada geese in urban areas, despite poor-forage quality and little movement to rural areas, that we and others have documented (Dorak et al. 2017). However, sustained periods of increased thermoregulatory costs with no income of additional energetic resources can lead to death by starvation and exposure (Biebach 1996). We direct evidence of such an event during an extreme cold period (i.e., mean temperatures below -15° and minimum around -30° for ~7 days) in late January of 2018 during which none of 25 urban-wintering geese emigrated yet 4 urban-wintering individuals died from apparent exposure. During that same period, 2 of 13 rural-wintering geese emigrated and none died. Mortalities during this event were not limited to the transmittered geese in this study as dozens of other geese died due to apparent exposure/starvation (C. Pullins, USDA-APHIS personal communication). While rural-wintering geese were relatively unaffected during extreme cold periods, their predicted survival was lower at warmer temperatures than urban-wintering geese and risk of harvest was greater with increasing proportion of rural area.

Given the costs and benefits of wintering in urban vs. rural areas, we would expect urban-wintering geese to emigrate or switch to rural areas during periods of extreme cold weather and vice versa during warmer periods. However, very few geese left urban areas for warmer latitudes or access high-energy food resources in rural areas, while geese already utilizing high-energy food in rural areas were more likely to emigrate southward. This lack of switching between urban to rural areas may reflect a lack plasticity within season in overwintering strategies, likely related to physiological condition or differences in costs of staying versus costs of leaving. Rural-wintering geese likely perceived a lesser cost of moving south as they moved from one area of harvest risk to another and were already familiar with the risk to resource trade-offs associated with moving to another rural area. Likewise, urban wintering geese likely perceived the costs of leaving to be greater than the costs. This perception may be real, reflecting increased risk due to naïveté to hunting, or a misperception, as they had no previous knowledge to assess these risks. Alternatively, urban-wintering geese may be in poorer condition and not have the endogenous reserves necessary to move south.

The condition of geese at the end of the wintering period has important carry-over effects on fitness and survival in subsequent period (Sedinger et al. 2011, Clausen et al. 2015). Arctic- and subarctic-breeding geese, including Canada geese, use relatively large amounts of endogenous reserves for nesting (Jönsson 1997, Stephens et al. 2009, Sharp et al. 2013). Because geese use endogenous reserves, acquired prior to arrival, body condition during winter and spring migration influences energetic resources necessary for egg laying and incubation. (Sharp et al. 2013, Fowler et al. 2020). Subarctic-arctic breeding geese likely require greater endogenous reserves to meet the energetic need of a long migration (~1,500 km) followed by nesting attempts. These increased energetic demands likely provide stronger pressures to winter in areas where high-energy food resources are available while those nesting in temperate regions are likely to meet energetic needs locally, prior to nesting. While we found differences in the proportion of subarctic-breeding geese using rural land uses and greater probability moving southward, we caution drawing conclusions as our sample size of subarctic-breeding geese was limited (Lindberg and Walker 2010). Furthermore, our capture methods may have biased our capture of subarctic-nesting Canada geese if they were more wary as netguns required a relatively close approach to geese. Despite the limitations of our study, subarctic-nesting geese play an important role in harvest in northeastern Illinois and the wintering strategies they employ are of interest given their shift from historical distributions (Luukkonen and Leafloor 2017).

Understanding how and why some species can adapt to and thrive in urban areas is important for predicting how species respond to increasing urbanization. The observed overwintering strategies were influenced by complex factors including carry-over effects, familial or social dynamics, and prior knowledge, which were beyond the scope of this study (Clausen et al. 2018). However, our results provide important insights into the relationships between habitat resources and predation risks that shape urban adaptation in waterfowl species. The use of urban areas is fairly wide-spread across waterfowl species and are likely contributing to shifts in distributions of several including Black-bellied whistling-ducks (*Dendrocygna autumnalis*; James and Thompson 2001, Cohen et al. 2019), Mallards (*Anas platyrhynchos*; English et al. 2017), and Cackling geese (*Branta hutchinsii*; Ray and Miller 1997, Harrington 2016). This adaptation to urban areas may present difficult and sometimes conflicting managements goals as urban waterfowl abundances lead to increased conflicts while simultaneously providing unique recreational opportunities in and around major population centers for birdwatchers and hunters alike (Humberg et al. 2018).

Continued urbanization and climate change will likely to continue to provide suitable areas for geese, and other waterfowl species, to overwinter. Increased use of these areas will lead to northward shifts in wintering distributions and decreased hunting opportunities in areas where recreational hunting is socially and economically important. In addition, urban-wintering waterfowl will continue to be associated with human wildlife conflicts, further complicating management of waterfowl populations.

TABLES AND FIGURES

Table 2.1. Model comparison of season survival probability of Canada geese transmittered in Northeastern Illinois during winters of 2015 – 2020. We compared models using differences in Akaike's Information Criterion corrected for small sample sizes (ΔAICc), number of parameters (K), model weight (w_i), and log likelihood (LL).

Models	K	AICc	ΔAICc	w_i	LL
Landscape group	3	179.959	0	0.33	-86.92
Landscape group + breeding population	4	181.306	1.34714	0.17	-86.55
Season	7	181.35	1.39095	0.16	-83.37
Breeding population	3	181.848	1.88907	0.13	-87.86
Breeding population * landscape group	5	182.84	2.88126	0.08	-86.26
Landscape group + season	8	182.901	2.94137	0.08	-83.05
Breeding population + season	8	183.305	3.34574	0.06	-83.26
Breeding population * season	13	191.103	11.1437	0.00	-81.52
Null	1	238.502	58.5426	0.00	-118.24

Table 2.2. Model comparison of weekly survival probability of Canada geese transmittered in Northeastern Illinois during winters of 2015 – 2021. We compared models using differences in Akaike's Information Criterion corrected for small sample sizes (ΔAICc), number of parameters (K), model weight (w_i), and log likelihood (LL).

Model	K	AICc	ΔAICc	w_i	LL
Mean temperature	3	375.70	0.00	0.22	-184.84
Minimum temperature	3	376.16	0.46	0.17	-185.08
Mean temperature * landscape group	5	377.05	1.35	0.11	-183.51
Landscape group	3	377.36	1.67	0.10	-185.68
Mean temperature + landscape group	4	377.57	1.87	0.09	-184.78
Breeding population	3	377.97	2.27	0.07	-185.98
Minimum temperature * landscape group	5	378.40	2.70	0.06	-184.19
Mean snow depth * breeding population	5	378.67	2.98	0.05	-184.33
Mean temperature + landscape group + breeding population	5	379.17	3.47	0.04	-184.58
Mean temperature * breeding population	5	379.47	3.78	0.03	-184.73
Minimum temperature * breeding population	5	379.92	4.23	0.03	-184.95
Mean snow depth * landscape group	5	380.32	4.62	0.02	-185.15
Minimum temperature * mean snow depth	5	380.73	5.03	0.02	-185.36
Week of season	26	395.79	20.10	0.00	-171.69
Mean temperature * week of season	51	397.17	21.48	0.00	-146.82
Minimum temperature * week of season	51	410.54	34.85	0.00	-153.50
Null	1	559.83	184.13	0.00	-278.91

Table 2.3. Model comparison of daily movement distance of Canada geese transmittered in Northeastern Illinois during winters of 2015 – 2021. We compared models using differences in Akaike's Information Criterion corrected for small sample sizes (ΔAICc), number of parameters (K), model weight (*w*i), and log likelihood (LL).

Models	K	AICc	ΔAICc	wi	LL
Mean temperature3 * landscape group	10	116368.59	0.00	0.99	-58174.29
Minimum temeprature3 * landscape group	10	116378.24	9.65	0.01	-58179.12
Mean snow depth3 * landscape group	10	116413.99	45.40	0.00	-58196.99
Mean snow depth2 * landscape group	8	116419.39	50.80	0.00	-58201.69
Minimum temperature2 * landscape group	8	116429.82	61.23	0.00	-58206.91
Mean temperature2 * landscape group	8	116433.22	64.63	0.00	-58208.61
Mean snow depth * landscape group	6	116434.31	65.72	0.00	-58211.15
Minimum temperature * landscape group	6	116478.13	109.54	0.00	-58233.06
Mean temperature * landscape group	6	116480.84	112.25	0.00	-58234.42
Mean temperature	6	116526.95	158.36	0.00	-58257.48
Landscape group	4	116528.71	160.12	0.00	-58260.35
Minimum temeprature3	6	116529.26	160.67	0.00	-58258.63
Mean snow depth3	6	116582.88	214.29	0.00	-58285.44
Mean snow depth2 * landscape group	5	116586.70	218.11	0.00	-58288.35
Mean snow depth	4	116599.58	230.99	0.00	-58295.79
Minimum temeprature2	5	116607.72	239.14	0.00	-58298.86
Mean temperature2	5	116610.66	242.07	0.00	-58300.33
Mean temperature	4	116628.37	259.78	0.00	-58310.19
Minimum temperature	4	116634.71	266.12	0.00	-58313.35
Null	3	116672.07	303.48	0.00	-58333.03

Table 2.4. Model comparison of daily proportion spent feeding by Canada geese transmittered in Northeastern Illinois during winters of 2015 – 2021. We compared models using differences in Akaike's Information Criterion corrected for small sample sizes (ΔAICc), number of parameters (K), model weight (w_i), and log likelihood (LL).

Models	K	AICc	ΔAICc	w_i	LL
Minimum temperature^3 * landscape group	10	-23878.93	0.00	1.00	11949.47
Mean temperature^3 * landscape group	10	-23831.66	47.27	0.00	11925.84
Minimum temperature^2 * landscape group	8	-23796.00	82.94	0.00	11906.00
Minimum temeprature^3	6	-23761.96	116.97	0.00	11886.98
Mean temperature^2 * landscape group	8	-23752.14	126.80	0.00	11884.07
Mean temperature	6	-23742.04	136.90	0.00	11877.02
Minimum temperature * landscape group	6	-23676.09	202.84	0.00	11844.05
Minimum temeprature^2	5	-23672.13	206.81	0.00	11841.07
Mean temperature^2	5	-23659.57	219.37	0.00	11834.79
Minimum temperature	4	-23594.35	284.58	0.00	11801.18
Mean temperature * landscape group	6	-23562.84	316.10	0.00	11787.42
Mean temperature	4	-23500.64	378.29	0.00	11754.32
Mean snow depth^3 * landscape group	10	-23235.79	643.14	0.00	11627.91
Mean snow depth^2 * landscape group	8	-23188.84	690.09	0.00	11602.43
Mean snow depth^3	6	-23128.79	750.14	0.00	11570.40
Mean snow depth^2 * landscape group	5	-23091.54	787.40	0.00	11550.77
Mean snow depth * landscape group	6	-22976.98	901.95	0.00	11494.49
Mean snow depth	4	-22897.37	981.57	0.00	11452.68
Landscape group	4	-22291.65	1587.28	0.00	11149.83
Null	3	-22255.87	1623.07	0.00	11130.93

Table 2.5. Model comparison of change in latitude from the winter mean by Canada geese transmittered in Northeastern Illinois during winters of 2015 – 2021. We compared models using differences in Akaike's Information Criterion corrected for small sample sizes (ΔAICc), number of parameters (K), model weight (w_i), and log likelihood (LL).

Models	K	AICc	ΔAICc	w_i	LL
Mean snow depth^3 * landscape group	10	2831.59	0.00	1.00	-1405.79
Mean snow depth^2 * landscape group	8	2879.42	47.83	0.00	-1431.71
Mean snow depth * landscape group	6	2960.75	129.16	0.00	-1474.37
Mean temperature^3 * landscape group	10	4431.04	1599.45	0.00	-2205.51
Mean temperature^2 * landscape group	8	4466.65	1635.06	0.00	-2225.32
Mean temperature * landscape group	6	4494.27	1662.68	0.00	-2241.13
Minimum temperature^3 * landscape group	10	4521.47	1689.88	0.00	-2250.73
Minimum temperature^2 * landscape group	8	4583.16	1751.57	0.00	-2283.58
Minimum temperature * landscape group	6	4591.96	1760.37	0.00	-2289.98
Landscape group	4	5102.11	2270.52	0.00	-2547.05
Mean snow depth^2	5	5911.23	3079.64	0.00	-2950.61
Mean snow depth	4	5911.76	3080.17	0.00	-2951.88
Mean snow depth^3	6	5911.89	3080.30	0.00	-2949.94
Mean temperature^3 * breeding population	10	6493.37	3661.78	0.00	-3236.68
Mean temperature^2 * breeding population	8	6507.22	3675.63	0.00	-3245.61
Minimum temperature^3 * breeding population	10	6527.21	3695.62	0.00	-3253.60
Minimum temperature^2 * breeding population	8	6529.10	3697.51	0.00	-3256.55
Minimum temperature * breeding population	6	6543.34	3711.75	0.00	-3265.67
Mean temperature	6	6545.04	3713.44	0.00	-3266.52
Mean temperature^2	5	6546.55	3714.96	0.00	-3268.27
Mean temperature * breeding population	6	6547.07	3715.48	0.00	-3267.53
Minimum temperature^3	6	6553.79	3722.20	0.00	-3270.89
Minimum temperature^2	5	6556.96	3725.37	0.00	-3273.48
Minimum temperature	4	6568.64	3737.04	0.00	-3280.32
Mean temperature	4	6573.05	3741.46	0.00	-3282.53
Null	2	6985.55	4153.96	0.00	-3490.78

Table 2.6. Model comparison of probability of departing from mean wintering locations by Canada geese transmittered in Northeastern Illinois during winters of 2015 – 2021. We compared models using differences in Akaike's Information Criterion corrected for small sample sizes (ΔAICc), number of parameters (K), model weight (w_i), and log likelihood (LL).

Models	K	AICc	ΔAICc	w_i	LL
Mean snow depth^3 * landscape group	10	-43405.29	0.00	0.67	21712.65
Mean snow depth^2 * landscape group	8	-43403.92	1.37	0.33	21709.96
Mean snow depth * landscape group	6	-43364.34	40.95	0.00	21688.17
Mean temperature^3 * landscape group	10	-42546.08	859.22	0.00	21283.04
Mean temperature * landscape group	6	-42534.07	871.22	0.00	21273.04
Mean temperature^2 * landscape group	8	-42533.68	871.61	0.00	21274.84
Mean snow depth^3	6	-42530.70	874.60	0.00	21271.35
Mean snow depth^2	5	-42528.62	876.67	0.00	21269.31
Mean snow depth	4	-42524.42	880.87	0.00	21266.21
Minimum temperature^3 * landscape group	10	-42507.85	897.44	0.00	21263.93
Minimum temperature^2 * landscape group	8	-42496.71	908.58	0.00	21256.36
Minimum temperature * landscape group	6	-42493.08	912.21	0.00	21252.54
Mean temperature^3 * breeding population	10	-42337.58	1067.71	0.00	21178.79
Minimum temperature^3 * breeding population	10	-42330.32	1074.97	0.00	21175.17
Mean temperature * breeding population	6	-42318.43	1086.87	0.00	21165.21
Mean temperature^2 * breeding population	8	-42315.63	1089.67	0.00	21165.82
Minimum temperature^2 * breeding population	8	-42310.88	1094.41	0.00	21163.44
Minimum temperature * breeding population	6	-42308.18	1097.11	0.00	21160.09
Landscape group	4	-42279.70	1125.60	0.00	21143.85
Mean temperature^2	5	-42278.84	1126.46	0.00	21144.42
Mean temperature	4	-42277.84	1127.45	0.00	21142.92
Mean temperature	6	-42277.52	1127.77	0.00	21144.76
Minimum temperature^3	6	-42269.25	1136.04	0.00	21140.63
Minimum temperature	4	-42268.27	1137.02	0.00	21138.14
Minimum temperature^2	5	-42266.62	1138.68	0.00	21138.31
Null	2	-42116.51	1288.78	0.00	21060.26

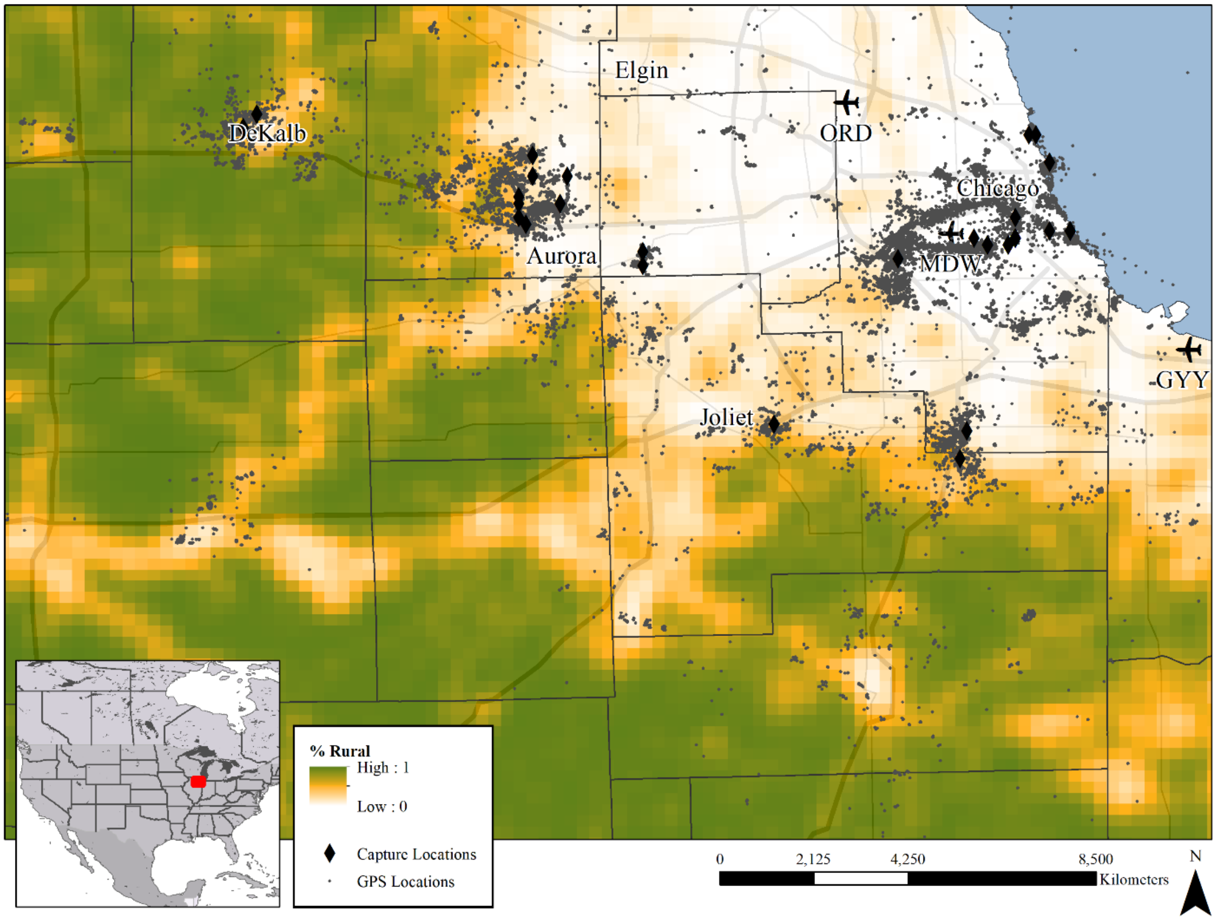

Figure 2.1. Map of the northeastern Illinois with a density map of rural land uses (e.g., corn, soybean, and idle agricultural fields) in green. We captured and deployed transmitters on Canada geese (*Branta canadensis*) in urban and more rural portions of the region (diamonds; n = 121) during winter of 2015-2017 and both winter and breeding season during 2018 – 2020.

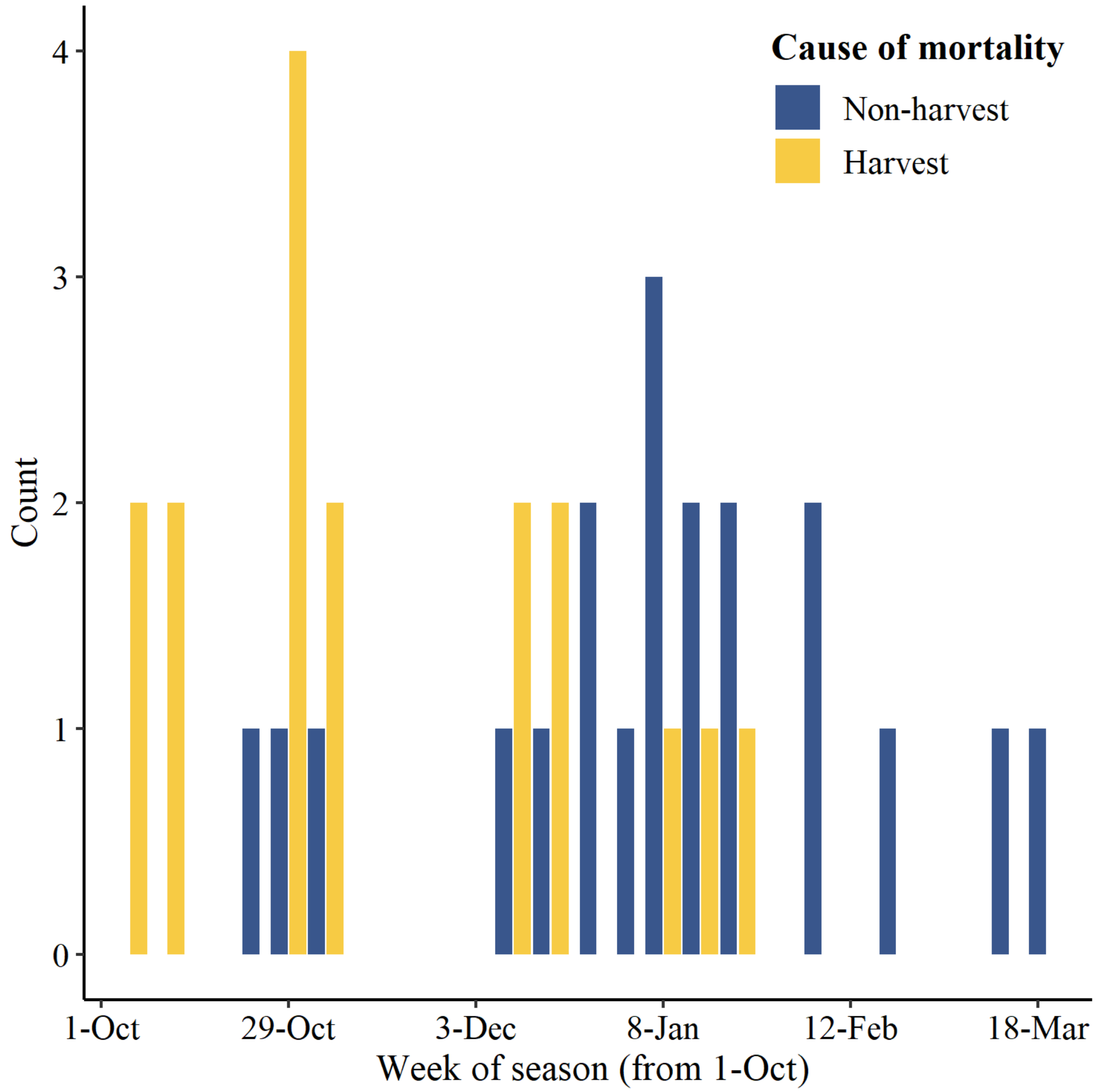

Figure 2.2. Comparison of timing of harvest and non-harvest mortalities of transmittered Canada geese (*Branta canadensis*) marked in northeastern Illinois during 1 October – 1 April, 2015 – 2021.

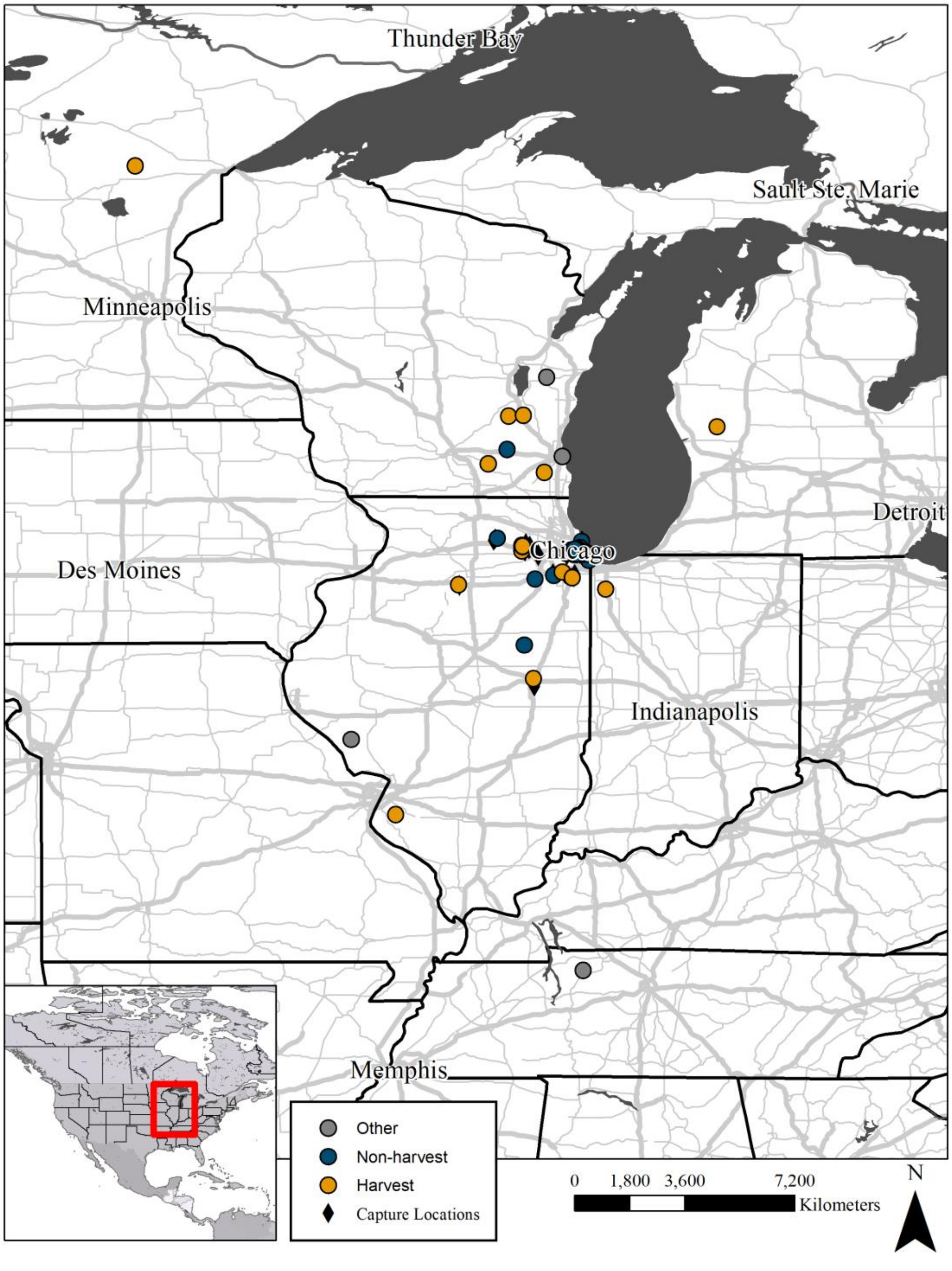

Figure 2.3. Locations of harvest mortalities, non-harvest mortalities, and transmitters that failed or cause was unable to be determined of Canada geese (*Branta canadensis*) transmittered in northeastern Illinois during 2015 – 2021.

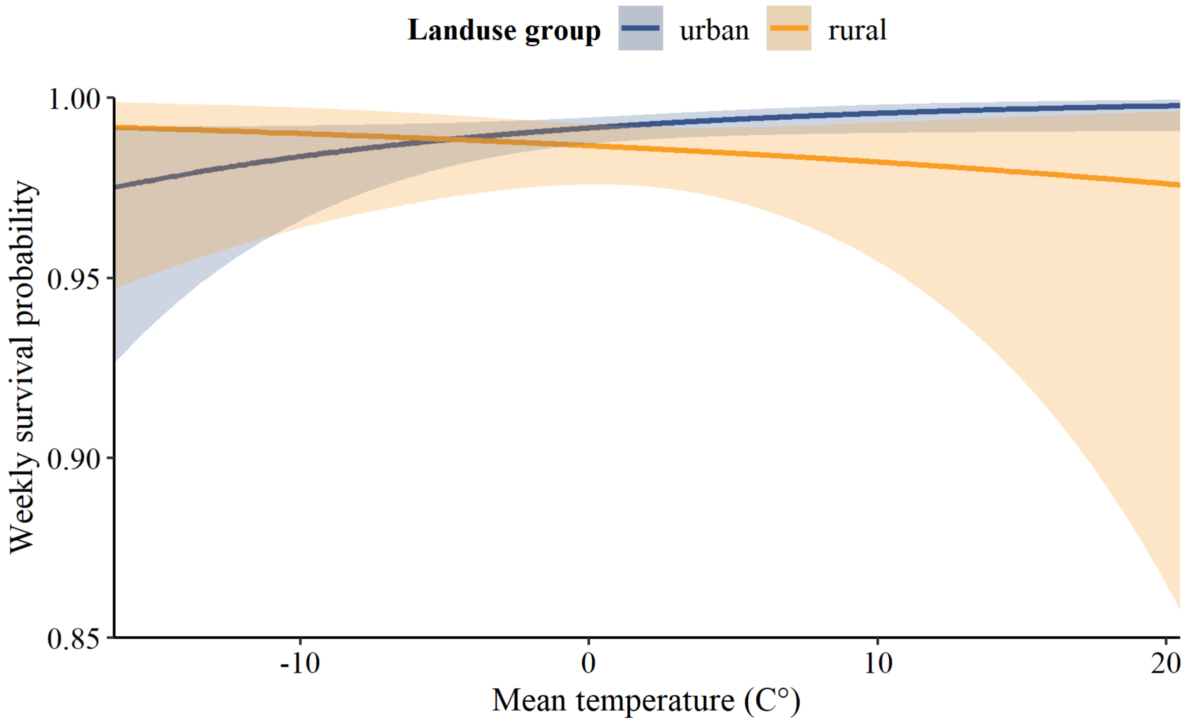

Figure 2.4. Interactive effects of landscape (rural and urban) with mean weekly temperature (°C) on weekly survival estimates of Canada geese (*Branta canadensis*) in the northeastern Illinois during winters (October – March) of 2015-2021.

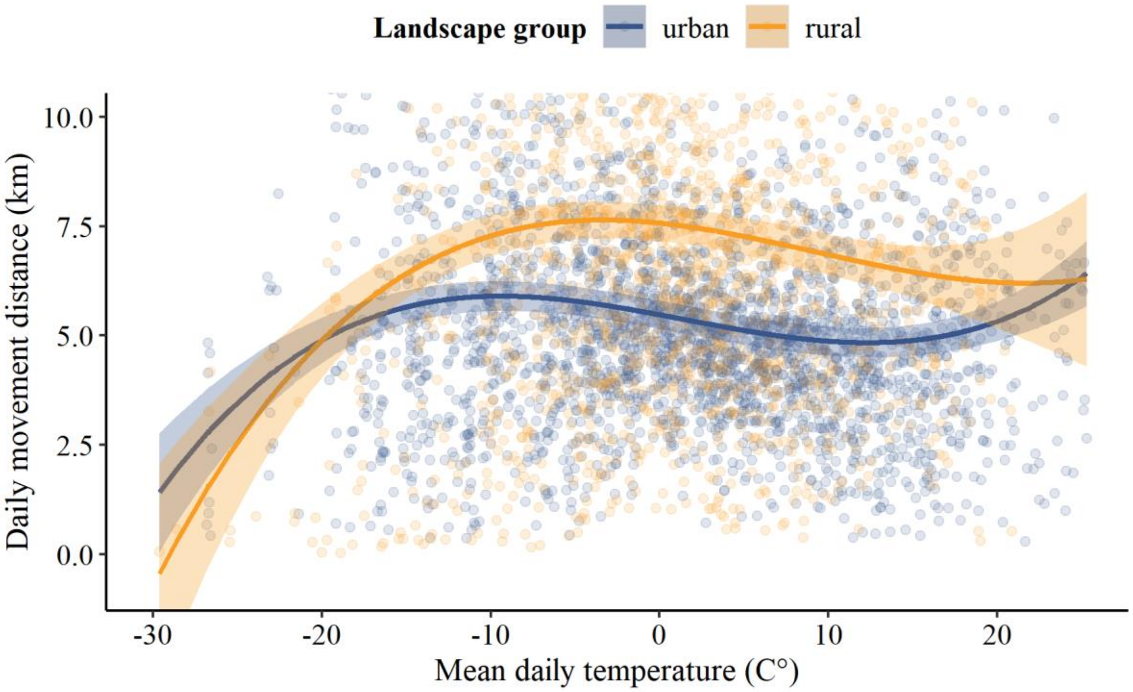

Figure 2.5. Model results of linear mixed effects models with interaction between landscape group (rural or urban) with quadratic polynomial terms of mean temperature on daily movement distance (km) of Canada geese (*Branta canadensis*) wintering in northeastern Illinois during winter of 2015 – 2021.

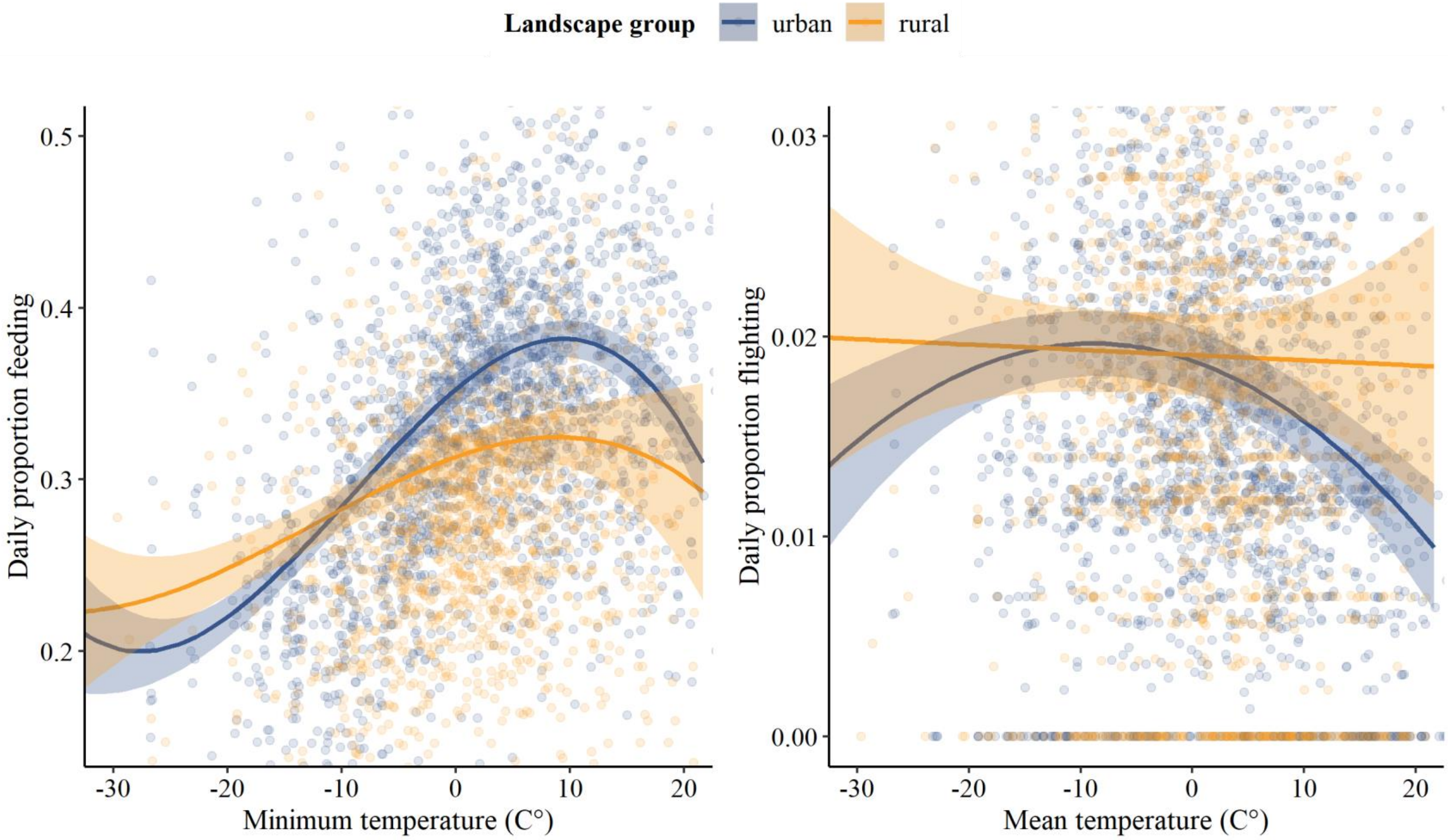

Figure 2.6. Model results of linear mixed effects models with interaction between landscape group (rural or urban) with quadratic polynomial terms of minimum temperature on daily proportion of time spent feeding (left) and cubic polynomial terms of mean temperature on daily proportion of time spent in flight of Canada geese (*Branta canadensis*) wintering in northeastern Illinois during winter of 2015 – 2021.

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CHAPTER 3: TRACKING MOVEMENTS OF CANADA GEESE NEAR AIRPORTS: THE IMPORTANCE OF HIGH-RESOLUTION SPATIAL DATA IN INFORMING MANAGEMENT1

ABSTRACT

The adaptation to urban environments by birds has created direct hazards to air transportation with potential for catastrophic incidents. Bird strikes involving Canada geese (*Branta canadensis*) pose greater risks to aircraft than many bird species due to their size and flocking behavior. We modeled environmental and behavioral factors influencing the intersection of goose movements (i.e., transition from one location to another) with air operations areas (i.e., aircraft flight paths). We deployed 31 transmitters on Canada geese near Midway International Airport in Chicago, Illinois during November 2015 – February 2016. Of 3,008 goose movements recorded, 821 intersected a 3-km buffer around the airport representing FAA recommended distances from wildlife attractants, and 399 intersected flight paths for approaching and landing aircraft. No environmental factors (i.e., snow cover, temperature, wind speed) had a strong effect on the probability of geese flying through air operation areas; however, the movements between certain habitat resources greatly increased the probability of intersection. For example, the juxtaposition of foraging (railyards with spilled grain) and loafing areas (rooftops) near the airport led to a higher probability of movements intersecting important air operations areas. The average altitude of flying geese was 29.8 m above the ground, resulting in the greatest risk of collision being within 0.5 km of the edge of runways. We suggest management actions such as decreasing suitability of habitat near the airport using focused harassment or physical modifications might be effective ways to mitigate risks when guided by animal movement data in an area.

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INTRODUCTION

Canada geese are among the largest and most frequently struck birds by aircraft in North America (Dolbeer 2011). More than 1,400 recorded strikes between geese and civil aircraft occurred from 1990 to 2012, although more strikes likely went unreported (Dolbeer and Eschenfelder 2003, Dunning 2008, Dolbeer et al. 2014). Since 1988, wildlife collisions with aircraft have led to 262 human fatalities worldwide (FAA 2016). In 1995, 24 crewmembers lost their lives in the crash of a military aircraft following the ingestion of Canada geese (*Branta canadensis*) into both engines during take-off from Elmendorf Air Force Base in Alaska (USAF 1995, Dolbeer et al. 2000, Richardson and West 2000). In 2009, the ditching of US Airways 1549 into the Hudson River following take-off from LaGuardia Airport captivated national attention and was attributed to a collision with Canada geese shortly after takeoff (Marra et al. 2009, NTSB 2010). Aircraft-Canada goose strikes result in greater monetary loss than any other species due to their size and flocking behavior (FAA 2016). Given the risks Canada geese pose to air traffic, a clear understanding of goose behavior is needed to reduce risk of aircraft-Canada goose strikes.

The abundance of Canada geese wintering in the Greater Chicago Metropolitan Area (GCMA) and the large volume of air traffic at two international airports pose considerable risk of bird-aircraft strikes (Dorak et al. 2017). In particular, thousands of Canada geese use parks, wetlands, river corridors, rooftops, and other urban habitat near Chicago's Midway International Airport (hereafter Midway) during winter (Dorak et al. 2017). The resident breeding population exceeds 30,000 individuals, joined by migrants from other areas in the United and Canada in winter, resulting in even greater numbers in winter (Paine et al. 2003). Midway is a hub for major commercial airlines, averaging 1,010 flight operations daily in 2016 (FAA 2017). Although there are active mitigation procedures in place at Midway to help prevent bird-aircraft strikes, Canada geese commonly use areas near Midway and pose a risk to aircraft (Dorak et al. 2017).

Information on factors driving movements of geese near airports and within aircraft arrival/departure areas are limited (Rutledge et al. 2015). Advancements in GPS transmitter technology can provide insights to movements and distribution of birds in relation to air operations previously unattainable (Avery et al. 2011, Rutledge et al. 2015). For example, only a small proportion of goose movements pose risk to aircraft so understanding what specific locations and conditions do pose risks can help wildlife managers implement more tailored management approaches. Typically, there are two broad categories of management used to mitigate risks of bird strikes at airports – habitat modification and harassment. If specific locations or habitat resources that result in birds flying across air operation areas can be identified, managers can implement management to make sites less attractive to geese without using lethal methods. Secondly, harassment with pyrotechnics, dogs, and human disturbance (Castelli and Sleggs 2000, Marra et al. 2009) can be used to increase perceived risks or increase energy expenditure associated with particular locations and in turn reduce movements that intersect focal departure and arrival areas for aircraft (Rutledge et al. 2015). An understanding of how specific habitat use patterns, times of year, and weather conditions influence movements of geese across focal air operations areas will allow wildlife managers to best accomplish the goal of reducing bird strike risk to aircraft.

We investigated the movements of Canada geese in the vicinity Midway to understand the frequency at which their movements intersect air operation areas. Our objectives were to 1) quantify the intersection of goose movements (i.e., transition from one location to another by flight) with 4 focal air operations areas (e.g., runways), 2) determine the altitude at which geese are flying when crossing runways, and 3) identify environmental (e.g., temperature, snow cover, wind) and behavioral factors (the habitats/locations) that influence the probability of movements intersecting focal air operations areas. The ultimate goal of the study was to identify the reasons why geese fly through areas near Midway, and if there were key locations or habitat resources that could be managed differently to provide a disproportionately greater impact on the probability of geese moving through focal air operation areas.

METHODS

Study Area

Our study focused on the area surrounding Midway International Airport (41º47'6.5"N, 87º45'6"W), a major commercial airline hub with more than 22.5 million travelers in 2016 (CDA 2016). Midway is located in Cook County within the GCMA of northeastern Illinois. The area surrounding Midway consists mostly of dense residential areas, commercial buildings, factories, large railyards. Within 8 km of Midway, less than 2% of the landscape consist of water (i.e. rivers, ponds, canals) while less than 5% consist of greenspaces (i.e. city parks, cemeteries). The GCMA averages 43 days annually below freezing, with 7 days below -18 °C. The average high temperature in November is 9 °C with a low of 0 °C. December has an average high of 2 °C with a low of -6 °C, and January has an average high of 0 °C and a low of -9 °C. February has an average high of 2 °C and low of -7 °C (NOAA 2015). Chicago, IL averages approximately 93 cm of snowfall annually (NOAA 2015). The GCMA has a human population of 9.4 million, including the city of Chicago and surrounding suburbs (USCB 2013). The GCMA has a breeding population of Canada geese exceeding 30,000 individuals (Paine et al. 2003).

Field Methods

We captured Canada geese (hereafter, geese) from 14 November 2015 through 29 February 2016 at parks, cemeteries, housing complexes, and a water treatment plant within 12 km of Midway. We chose these sites due to the abundance of geese and their proximity to the Midway (Fig. 3.1). Geese were captured using cast nets, commonly used for baitfish, and MagNet small animal net-guns (Wildlife Capture Services, Flagstaff, Arizona, USA). We attached an aluminum leg band and Global Positioning System- Global System for Mobile transmitters (GPS-GSM; Cellular Tracking Technologies, Somerset, PA) on neck collars (Spinner Plastics, Springfield, IL) with unique alphanumeric codes on geese selected for transmitter marking. Transmitters were solar-powered CTT Generation 3 transmitters (CTT-1000-BT3; $\bar{x}$ = 62.2 grams, *SE* = 0.2). Transmitters were remotely programmable, scheduled to record a GPS location and altitude (meters above ground level [AGL]) every hour, and connected to GSM network to upload location data 3 times a week.

Transmitters (n = 31 in 2015–2016) were deployed during four times periods each year (mid-November, early- December, mid-December, and early-January) and across the seven different capture locations that were an average of 7.2 km from Midway (range = 3.7 – 12.0 km; Fig. 3.1). We excluded data from 4 transmitters that failed within 10 days of deployment and redeployed 3 transmitters obtained from hunters. Transmitters were <2% of the body mass of geese ($\bar{x}$ = 4,713 grams, *SE* =10.6) and all geese were captured and handled using methods approved by the University of Illinois Institutional Animal Care and Use Committee (Protocol no. 14155) and Illinois Department of Natural Resources (Permit no. W17.6079).

Data Analyses

We quantified intersections of goose movements with air operation areas at Midway during winter from 16 November 2015 to 28 February 2016. We defined movements as the straight line between two consecutive GPS locations in which a change in habitat occurred and the distance moved was such that flight would have occurred. Movements between locations of the same habitat resource type (e.g., moving across a park) were not analyzed because we assumed altitude would have been low and flight time nonexistent or limited. Movements with a start or end location with fixes derived from 1 satellite or with a horizontal dilution of precision of > 4 were removed in order to maintain locational accuracy (CTT 2015). We removed movements that included a location with a speed value of >25 km/h to exclude in-flight locations for our models of intersecting movements.

We classified movements by the habitat resource types in which they originated and ended. Habitat resource types included greenspace, open water, rooftop, railyard, or miscellaneous and were classified using available aerial imagery and ancillary information following Dorak et al. (2017). Greenspaces were typically large parks, cemeteries, and other large areas that contained a mixture of trees and shrubs, large sports fields, and golf courses offering foraging and loafing sites as well as ponds that may be used as roost areas within their boundaries. Our observations suggest that greenspaces were used primarily for foraging and loafing. Water included large, permanent waterbodies that remained ice free throughout the year (shipping canals and rivers) as well as smaller wetlands and impoundments that froze during cold periods. Our observations indicated that these areas were primarily used as roosting and loafing locations. Rooftops were the tops of large commercial buildings including retail stores, factories, distribution centers, and other commercial buildings with flat roofs. Our observations indicated that rooftops were used as loafing locations during winter (Dorak et al. 2017). Railyards included areas used for railroad operations such as switching yards, loading yards, and depots. Our observations indicated that railyards likely served as foraging sites due to the existence of grain spilled from train cars loaded with corn (Dorak et al. 2017). Miscellaneous area mostly consisted of paved or gravel lots associated with industrial areas.

We chose four areas to represent focal air operations areas in the proximity of Midway. The Federal Aviation Administration (FAA) recommends separation distances between land use practices that attract wildlife (i.e. parks, waterbodies) and airports to reduce risks to air traffic (FAA 2007). The FAA recommended separation distances is 1.6 km from the edge of Midway's (i.e., perimeter) area serving piston-powered aircraft and 3 km for those serving turbine-powered aircraft (FAA 2007). The FAA also recommends a separation distance of 8 km (5 mile) between airports and habitat resources that cause wildlife movement across approach and departure paths (Cleary and Dolbeer 2005). However, given the majority of geese captured in this study were within 8 km of Midway, we focused on the smaller buffers recommended by the FAA. We analyzed the intersection of goose movements with thresholds based on these separation distances and runway headings extending for 3.2 km (2 mi) from the ends of runways 13/31 and runways 4/22 (hereafter, runway extensions) as an approximation for aircraft approach and departure paths (Fig. 3.1). We estimated the altitude of aircraft per kilometer from the end of runways based on approach charts for runway 31 center (i.e. the most used runway; https://aeronav.faa.gov/d-tpp/1902/00081ILD31C.PDF) to evaluate if the altitude of geese in-flight would pose a risk to air traffic. We used an estimate of 51.5 m AGL per kilometer from the end of runways to compare aircraft altitudes to all in-flight GPS location of transmittered geese.

We examined the number of daily movements as a function of month using a one-way analysis of variance (Program R, R Foundation for Statistical Computing, Vienna, Austria). The binary outcome of movements, intersection or no intersection, were modeled using mixed effect, logistic regression modeling (GLMER) in package lme4 in Program R (Bates et al. 2014). We tested for correlation between predictor variables using a Pearson pairwise correlation (r) analysis and excluded one variable in the pair if correlation existed ($|r| \geq 0.7$). We used a suite of biologically plausible predictor variables based on existing literature which included habitat resource type, temperature (C°), wind speed (km/hr), and snow cover (cm). Continuous predictor variables (i.e. snow depth, temperature, wind speed) were standardized to two standard deviations from the mean values (Gelman 2008). We designated individual goose ID as a random effect to account for subject-specific effects. We ranked biologically plausible models against a null model using Aikaike's Information Criterion (AIC) to identify the most parsimonious model from the candidate model set (Burnham and Anderson 2002) using package MuMIn in Program R. We reported model outcomes for our top ranked model as odds ratios, which approximates the relative probability of a movement intersecting with one unit change in the predictor variable. We used predicted probabilities for fixed effects to explore the influence of a specific variable on the probability of a movement intersection by holding all other variables at their means (Muller and MacLehose 2014). We did not fit a model for intersections of runway 4/22 extensions because too few intersections occurred, while too many intersected the 8.05 km buffer for model convergence. We detected no correlation between parameters; thus, all parameters were included in models (Pearson, $P < 0.15$).

RESULTS

We recorded 3,008 movements from 24 transmittered geese (Fig. 3.2). Geese made an average of 1.48 (±0.20 SE, range 0.07 – 3.69) movements per day. The average number of movements varied by months ($F_{3, 2.7} = 17.27$, $p < 0.001$) and was greatest in January (1.91 movements ± 0.21 SE), followed by February (1.71 ± 0.22 SE), December (0.76 ± 0.20 SE), and November (0.22 ± 0.12 SE). Across individuals and months, 821 (27.3%) movements intersected the 3-km buffer and 225 (7.5%) movements intersected the 1.6-km buffer around Midway. Extensions of runways 13/31 were intersected more frequently (13.3% of movements, n = 399) than extensions of runways 4/22 (2.52% of movements, n = 76). We recorded an average of 0.23 (± 0.05 SE, n = 1,824) intersections with extensions of runway 13/31 per bird per day. Only 18 instances of movements intersecting the Midway airfield were recorded during our study (0.6% of movements).

Greater than 70% of intersections with each air operations area stemmed from movements associated with greenspaces (Table 3.1). Movements between greenspaces and railyards had the most intersections with the 3-km buffer (30.8%, n = 253), followed by movement between greenspaces and rooftops (22.3%, n = 183), and greenspaces and water (11.9%, n = 98; Table 3.1). For runway 13/31 extensions, movement between greenspace and railyards contributed the highest percentage of the intersecting movements (47.4%, n = 189), followed by movement between greenspace and rooftops (28.8%, n = 115; Table 3.1).

We report model results for extensions of runways 13/31 and the 3-km buffer as too few intersections of runway 4/22 extensions and 1.6-km buffer occurred for model fitting. The global model including the effects of temperature, snow depth, wind speed, and habitat types was the most supported models for the 3-km buffer (ΔAIC ≤ 2; Arnold 2010; Table 3.2). The top supported model for runways 13/31 was similar except for the exclusion of snow depth, however the global model was closely ranked so we report those results for ease of interpretation (Table 3.2). The log odds ratios can be interpreted as change in likelihood based on one unit increase in the parameter with all other variables held at their mean. For example, movements between water and rooftops were 1.78 times more likely to intersect the 3-km buffer than not (Fig. 3.3). Movements associated rooftops and railyard are more likely to intersect both the 13/31 runway extensions and the 3-km buffer (Fig. 3.3). Conversely, many of the movements associated with water to miscellaneous habitat and greenspace to water lead to movements are less likely to intersect with air operation areas (Fig. 3.3). Increased wind speed had a negative effect on the intersection of movements for both 13/31 runway extensions a 3-km buffer while increased snow cover had a positive effect but confidence intervals overlapping zero.

Altitudes of geese (*n* = 23) in-flight ranged from 1.0 to 149.0 m AGL, with an average altitude of 29.8 m (*n* = 377; Fig. 3.4). We estimated altitude of commercial aircraft at 0.5 km from the end of runway at 25.7 m AGL; at 1.0 km from the end of the runway an aircraft would be approximately at an altitude of 51.5 m AGL, and the aircraft would be at an approximate altitude of 102.9 m at 2.0 km from the edge of the runway. Therefore, at 2.0 km from runway 31, only 1.1% of flying geese would be at an altitude to pose a risk of a bird strike, whereas 13.3% of flying geese would pose a risk 1.0 km, and 49.9% of flying geese at 0.5 km from the end of the runway.

DISCUSSION

Despite ongoing harassment efforts to dissuade geese from using areas within and nearby of Midway during our study, more than a quarter of movements between habitat resource types potentially intersected focal air operations areas around the airport. Our results suggest a 22.5% chance that an individual goose would intersect the 3-km buffer on given day, equating to around 4 intersections by transmittered geese per day. We did not estimate goose abundances at our capture locations or surrounding habitats, however a conservative estimate of 10,000 geese present throughout our study area (C. Pullins, USDA - Wildlife Services, personal communication) would result in 2,250 potential intersections of geese with air operations areas associated with runways 13/31 each day. Fortunately, the number of probable overflights of the main airfield itself was low and altitude of most flights appears to be below the flight paths of most aircraft using Midway. However, the growing number of geese in the area surrounding Midway and the number of potential intersections documented in our project indicate that additional management may be necessary to reduce risk of goose-aircraft collisions at Midway.

One of the encouraging results in the context of risk is that less than one percent of the intersections were over Midway. Another way to evaluate these data is to compare the number of intersections within an area controlling for the size of the area. The 3-km buffer comprises 51.4 km^2, with 821 intersections there are 16.0 intersection/km^2. The 1.6-km buffer (21.1 km^2) has 10.7 intersections/km^2, whereas Midway, which comprised 2.7 km^2, had less than half the intersections per area compared with the 3-km buffer, with 6.8 intersections/km^2. We attribute the relatively low number of intersections with Midway to on airport management to reduce conflicts. Goose movements during this study suggest the greatest risk to aircraft is in the runway extension areas. Although more than 2,000 geese may be intersecting the extension of runway 13/31 each day, most geese are flying at an altitude below commercial aircraft. The risk obviously increases as an aircraft is nearer to the runway and the aircraft's altitude is lower. At 0.5 km, we estimated the altitude of an aircraft at 25.7 m, and the average altitude of geese was 29.8 m, thus areas 0.5 km from the runways is where the greatest risk occurs. Previous descriptions of altitude distribution of resident geese report a slightly lower average altitude with only 9.0% of movements occurring above 30 m AGL (Rutledge et al. 2015), compared to 38.0% in our study. Regardless of goose flight altitudes, we suggest the modeling the influence of nearby habitats to understand why geese are flying through specific air space is the best approach to prioritize management.

Confidence intervals of temperature and snow cover overlap zero making conclusions on their effect uncertain. However, wind speed had a clear, negative relationship to intersections. The relationship between climate variables and the intersection of goose movements with important airspaces is complex and likely interrelated to landscape composition, food availability, and levels of disturbance in the vicinity of Midway (Dorak et al. 2017). Geese wintering near Midway are remaining north of their traditional wintering grounds (Gates et al. 2001) and may become energetically stressed during cold weather, especially if food is limited. Scarcer resources (i.e., waterbodies freezing, snow cover decrease food availability) likely force geese to move more and to habitats where resources remain accessible. This is supported by a greater number of movements in January and February. In our study area, spilled and waste grain in the railyards and the ice-free waterbodies of the Chicago Shipping and Sanitation Canal seem to concentrate geese during colder periods. The movement associated with railyards appears to increase the probability of intersections with air operations areas, whereas those movements associated with water reduce the probability of intersecting air operation areas. Future research should incorporate more complex modeling of habitat-specific movements associated with different environmental factors. Incorporating finer scale information may provide a better understanding of the impact of environmental factors on movement between habitats.

While environmental variables likely have a complex relationship with movements, our analysis suggests that movements between specific habitat resource types have a clear effect on the probability of intersecting air operation areas at MDW. Several locations commonly used by geese were close proximity to Midway, particularly a large railyard just south of the airport.

Nearly 50% of intersections of the 3-km buffer and greater than 50% of intersection with runway extensions of runways 13/31 are associated with this railyard. Railyards have not traditionally been considered to provide habitat for geese and are relatively limited on the landscape compared to greenspaces and permanent water. However, some geese likely use railyards to forage on spilled grain highlighting the adaptability of geese under limited resource conditions. Therefore, management to decrease accessibility to these food resources by either harassing the geese or removing the spilled grain is likely to reduce the risk of bird-aircraft collisions. It is likely mutually beneficial for railyard and airport managers to reduce abundances of geese in the railyard.

Geese use of large, industrial rooftops that are abundant in the vicinity of Midway has only recently been described (Dorak et al. 2017). Geese appear to use rooftops as roosting and loafing sites, taking advantage of safety and limited disturbance. Thirty-five percent of the intersections with the 1.6-km buffer were birds moving to or from rooftops. Given the large number of rooftops available for geese in the area, it would be difficult to effectively manage each rooftop. However, movements that intersect important air operations areas appear to be associated with a limited number of rooftops south and northwest of Midway. By identifying rooftops used by Canada geese near the airport managers might be able to use various harassment or habitat modification (i.e. wire grids; Smith et al. 1999) to make rooftops less hospitable for geese. Similar to rooftops, geese appear to use the Chicago Shipping Canal during cold periods in order to avoid disturbance and conserve energy. Harassment there could potentially reduce movements originating from the canal but is unlikely to be as effective due the use of a large area by Canada geese, and the fact that relatively fewer movement to and from water intersected with air operation areas than other locations.

While this study is limited to a single study site and season, Canada goose pose a risk to many airports in North America. Midway International Airport likely has a lower proportion of goose habitat in the surrounding area than many other airports in the northern United States. Differences in habitat composition could lead to the level of risk geese pose and make management more or less difficult. However, our results highlight how high-resolution data on the movements and behaviors of geese (or other wildlife) can improve our understanding of the factors that contribute to a higher probability of movements intersecting air operations areas. Other studies have suggested that effective large-scale management would require sustained effort in an 8 km radius of airports to reduce goose abundances that pose risks to air traffic (Holevinski et al. 2007, Seamans et al. 2009, Rutledge et al. 2015). Given all geese in our study were marked within 12 km of the Midway, movements between locations within 8 km of the airport were extremely common. Management of geese in an 8 km radius around Midway would be extremely challenging despite the relatively discrete patches of goose habitat, highlighting the need for movement data to conduct focused management in critical areas.

Our findings highlight the need for ongoing harassment or other management techniques to reduce risk of intersections of geese with air operations areas near Midway. Management should non-traditional urban habitat resources, such as rooftops and railyards, as these accounted for the majority of intersections with focal air operation areas. We argue advanced transmitter technology is useful to pinpoint key locations where management may have the greatest effect. Harassment and habitat management has potential to mitigate the risk of goose-aircraft strikes, but continued collection of movement data in conjunction with harassment is paramount to determine if geese disperse to new locations that reduce risks or simply move to other locations that maintain or increase potential intersections with air operations areas.

TABLES AND FIGURES

Table 3.1. Percentage of intersecting movements by associated habitat types of transmittered Canada geese (*Branta canadensis*; *n* = 24) intersecting air operations areas at Midway International Airport, Chicago, IL, USA during 16 November 2015 – 28 February 2016.

		Intersecting				Movements
Habitat type	*n*	1.61 km	3.05 km	Runway 13/31	Runways 4/22	Total
Greenspace/Miscellaneous	24	4%	6%	2.8%	21.1%	168
Greenspace/Railyard	22	32%	30.8%	47.4%	9.2%	557
Greenspace/Rooftop	24	34.7%	22.3%	28.8%	14.5%	340
Greenspace/Water	17	12%	11.9%	6.5%	30.3%	1331
Railyard/Miscellaneous	17	2.2%	7.3%	1.8%	1.3%	67
Railyard/Water	21	8.9%	10%	6%	9.2%	213
Rooftop/Water	20	4%	5.2%	3.5%	7.9%	90
Water/Miscellaneous	23	2.2%	6.5%	3.3%	6.6%	242
Total Intersections	24	225	821	399	76	3008

Table 3.2. Logistic regression models of the effects of time of day, snow cover (cm), temperature (C°), habitat resource types, and wind speed (km/hr) on the probability of Canada goose (*Branta canadensis*) movements intersecting extensions of runways 13/31 at Midway International Airport in Chicago, IL, USA between 16 November 2015 – 28 February 2016. Models are ranked from best to worst based on Akaike's Information Criteria (AIC), delta (Δ*i*), and Akaike weights (w_i); AIC is based on -2 x log likelihood (L) and the number of parameters in the model (K).

Area	Models	AIC	ΔAIC	*w*i	K	Log-likelihood	Evidence Ratio
3-km Buffer	snow cover + temperature + types + wind speed	1045.94	0.00	0.73	12	-510.92	0
	temperature + types + wind speed	1047.98	2.04	0.26	11	-512.95	2.78
	types	1054.70	8.76	0.01	9	-518.32	79.91
	types + temperature	1056.50	10.56	0.00	10	-518.21	196.64
	null	1266.56	220.62	0.00	2	-631.28	8.06×10^{47}
Runways 13/31	temperature + types + wind speed	908.49	0.00	0.69	11	-443.20	0
	snow cover + temperature + types + wind speed	910.15	1.66	0.30	12	-443.02	2.29
	types + temperature	919.36	10.87	0.00	10	-449.64	229.47
	types	920.94	12.45	0.00	9	-451.44	504.5
	null	1002.14	93.65	0.00	2	-499.07	2.17×10^{20}

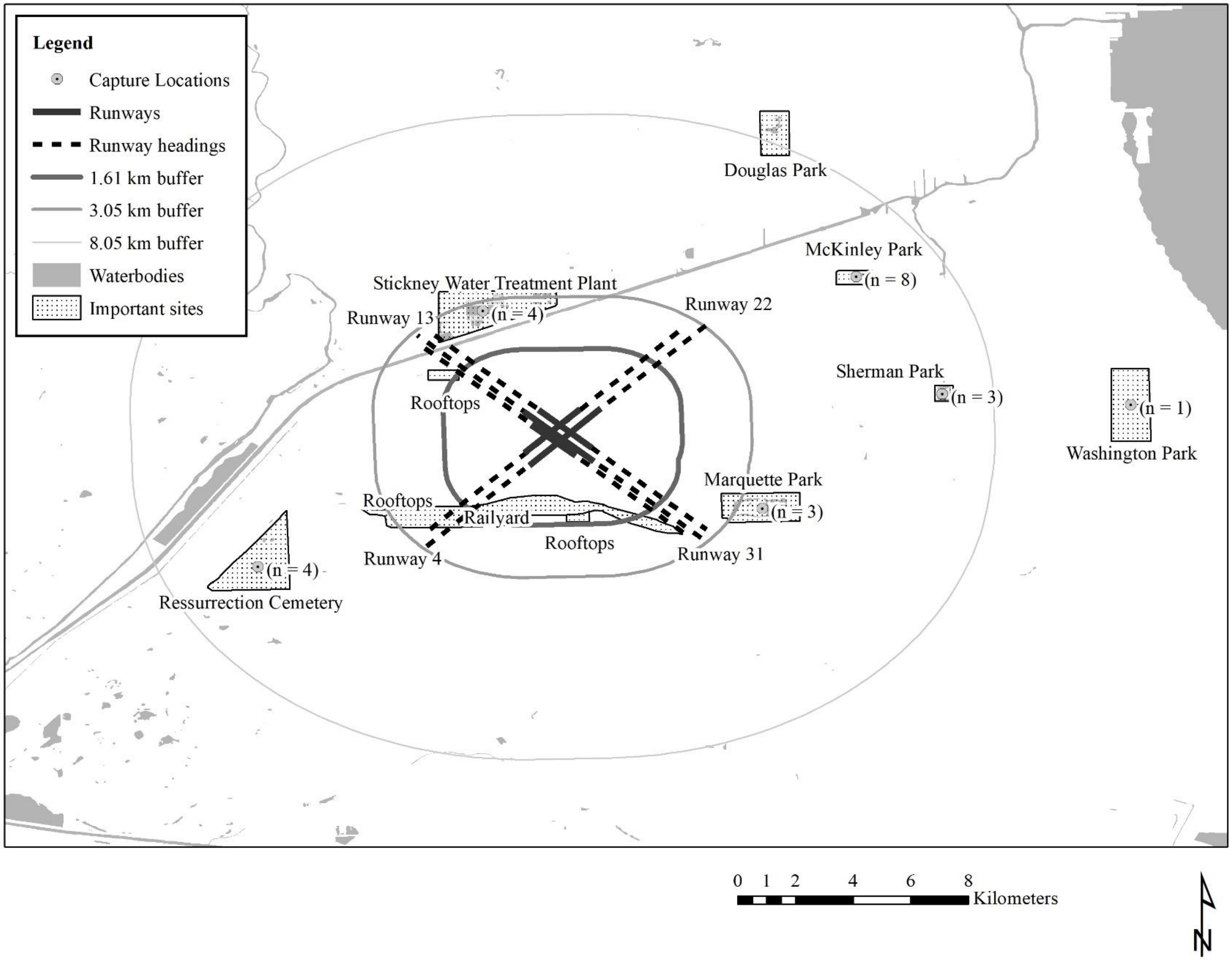

Figure 3.1. Map of study area surrounding Midway International Airport in Chicago, Illinois, USA with important sites used by Canada geese (*Branta canadensis*) in winter, water bodies, and capture sites.

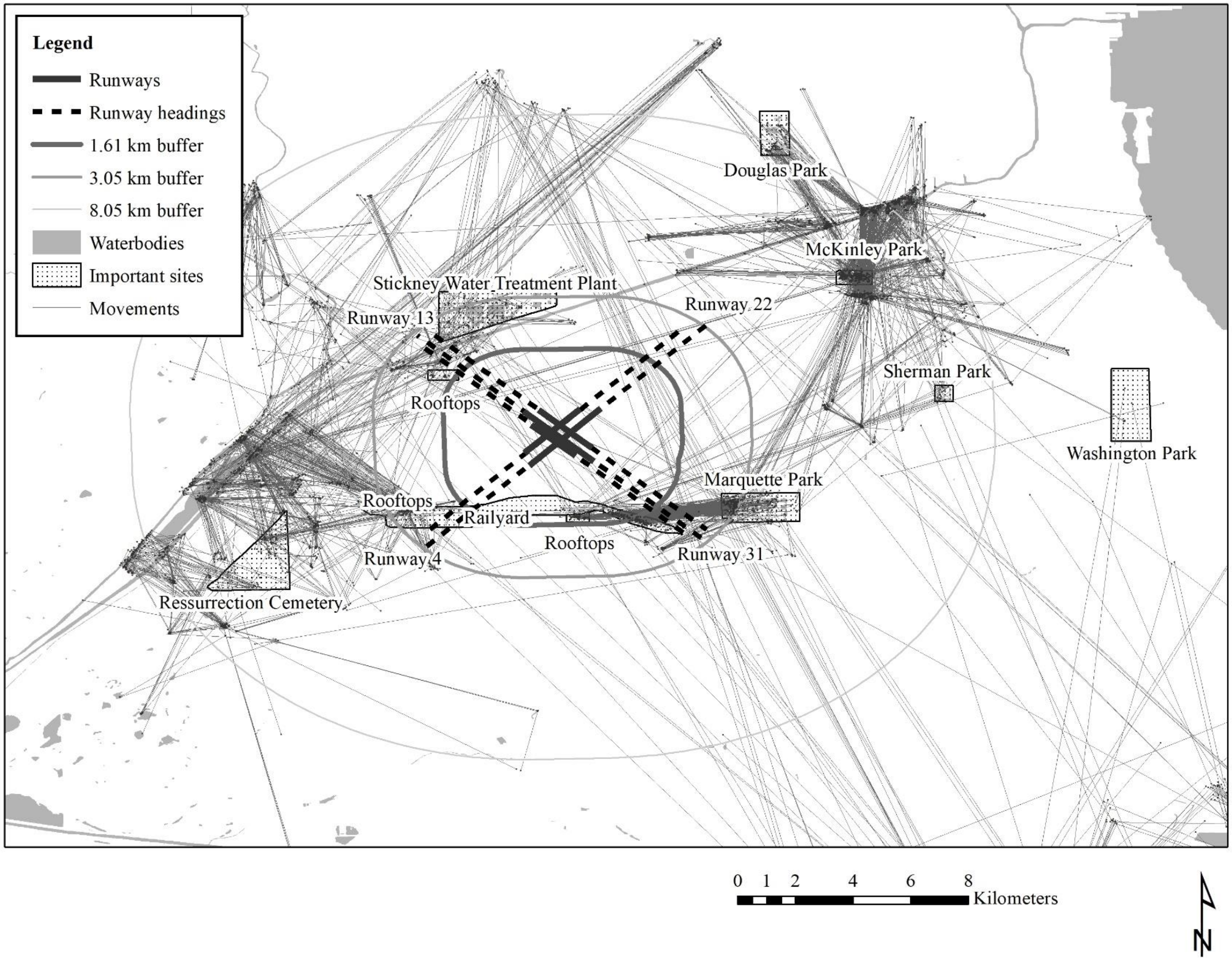

Figure 3.2. Movements of Canada geese (*Branta canadensis*) in relation to Midway International Airport and runway headings in Chicago, Illinois, USA during November 2015 – February 2016.

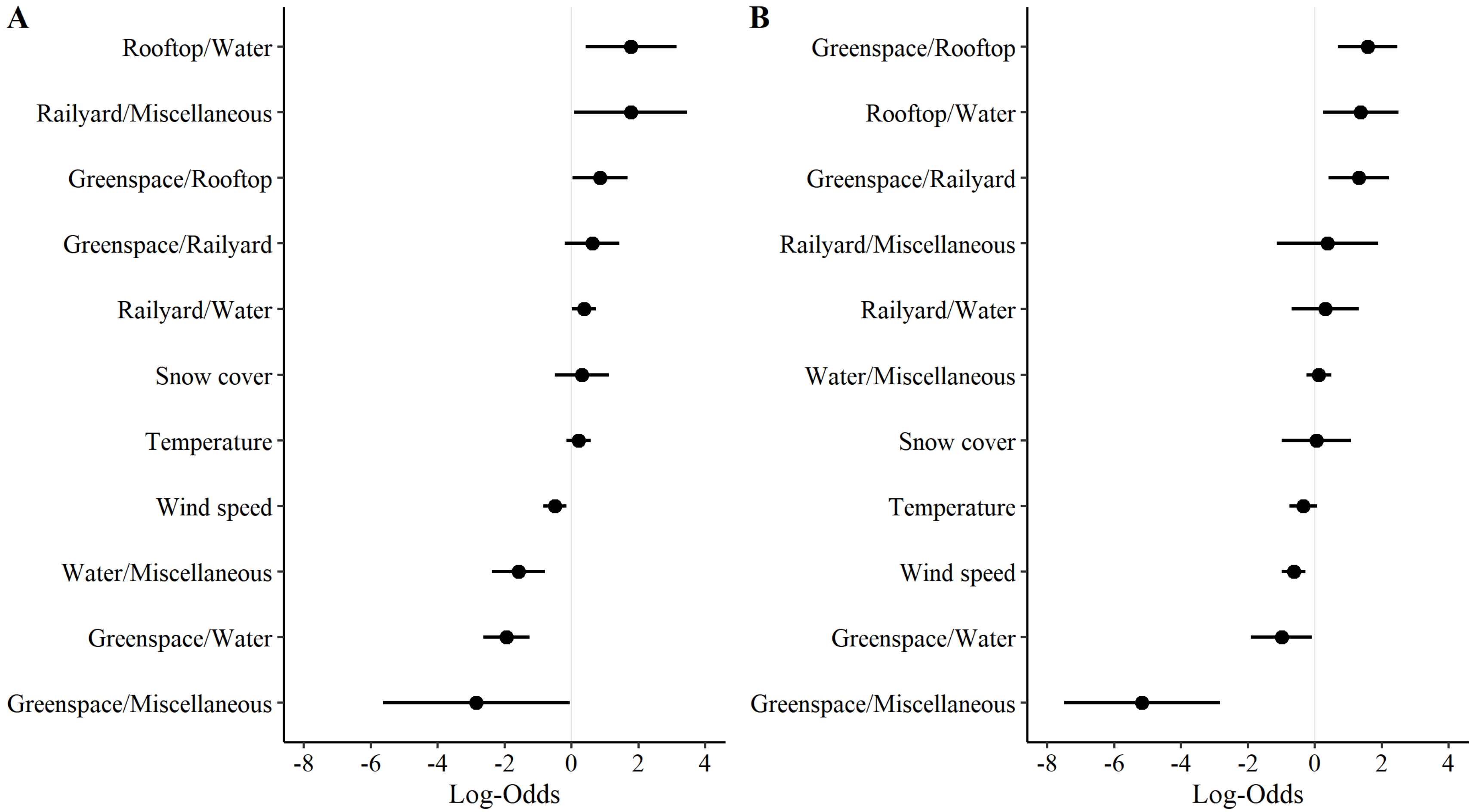

Figure 3.3. Log-odds of fixed effects in logistic regression mixed models of Canada geese (*Branta canadensis*) movements intersecting (A) 3.05 km and extensions of runway headings (B) 13/31 at Midway International Airport in Chicago, IL, USA during November 2015 – February 2016.

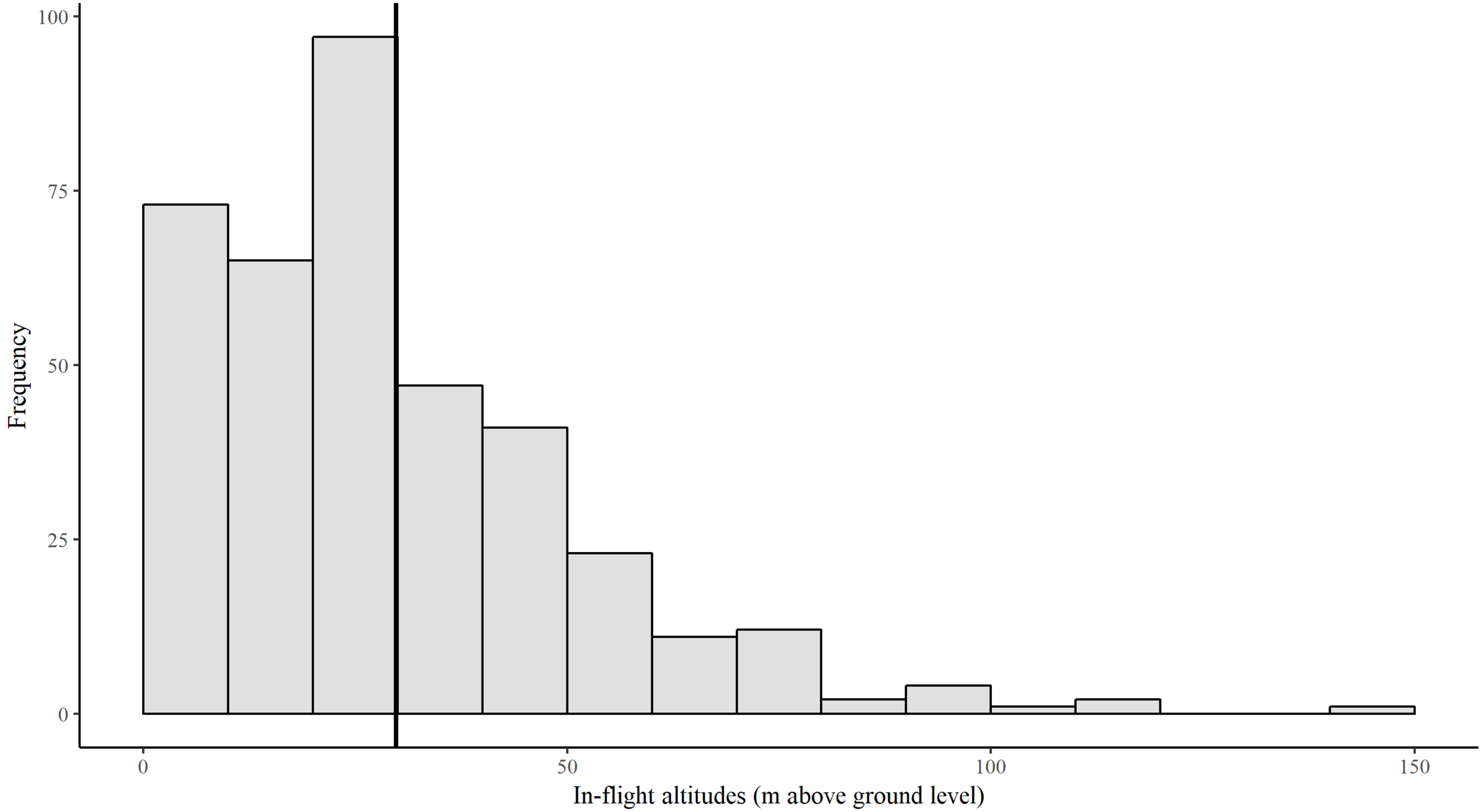

Figure 3.4. Frequency distribution of in-flight altitudes (m AGL) from GPS fixes (*n* = 377) of transmittered Canada geese (*Branta canadensis*) during 16 November 2015 – 28 February 2016 in Chicago, Illinois. The mean altitude of in-flight GPS fixes ($\bar{x}$ = 29.8 m AGL) is denoted by the vertical black bar.

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CHAPTER 4: BEHAVIORAL RESPONSES OF CANADA GEESE TO WINTER HARASSMENT IN THE CONTEXT OF HUMAN-WILDLIFE CONFLICTS[1]

ABSTRACT

Wildlife harassment (i.e., intentional disturbance by humans) is a common non-lethal management approach employed to reduce human-wildlife conflicts but is often ineffective. We evaluated the effect of harassment on Canada goose (*Branta canadensis*) behavior in an urban area during winter. Winter is a challenging period for waterfowl given limited food availability and greater thermoregulatory costs; thus, we expected that harassment in winter may be more effective than during other portions of the year. We used GPS transmitters equipped with accelerometers to evaluate the behavioral responses to harassment and whether harassed individuals left the area or died. We investigated the effects of harassment, weather conditions, and breeding origin on goose movements, land cover use, and behavioral time budgets. Harassment caused geese to leave the harassment site more often (3.5 times more), but geese returned quickly (1.9 times faster). Harassment of geese affected specific goose behaviors (foraging, resting, flying, and alert), but effects were relatively small compared to the effects of weather conditions. Changes in land covers used were impacted by weather conditions, independent of harassment. Our findings suggest that harassment was ineffective at significantly changing site use or behaviors of geese and repeated harassment has diminishing returns. Geese moved to specific land cover resources that serve as sanctuaries (e.g., open waterbodies) during periods of extreme cold to engage in energetically conservative behaviors (i.e. resting). Harassing geese in areas that provide sanctuary during extreme cold periods or the use of lethal management in coordination with targeted harassment are likely more effective than harassment alone in an urban greenspace.

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INTRODUCTION

Human disturbance can adversely affect wildlife by altering behavioral time budgets (Beale and Monaghan 2004, Atkins et al. 2017), increasing energetic costs as animals flee (Bélanger and Bédard 1990, Nolet et al. 2016), displacing animals from high-quality habitat resources (Seamans and Gosser 2016), and imposing sublethal effects on fitness and reproduction (Beale and Monaghan 2004, Beale 2007). Human disturbance can be used to reduce human-wildlife conflicts by intentionally altering animal behavior and distribution (Kloppers et al. 2005). The use of intentional disturbance (hereafter referred to as harassment) has included use of pyrotechnics to disrupt double-crested cormorant (*Phalocrocorax auratus*) roosts near aquaculture operations (Tobin et al. 2002), the use of noise-making cannons to scare birds away from crops and airports (Seamans and Gosser 2016), use of falcons to scare/kill geese around golf courses (Atkins et al. 2017), and many other applications (Bishop et al. 2003). Although many studies have investigated the effectiveness of harassment in terms of accomplishing management goals (York et al. 2000, Sherman and Barras 2004, Holevinski et al. 2007), few have examined how harassment affects the behavior of targeted animals (*but see* Nolet et al. 2016, Atkins et al. 2017).

For harassment to influence the behavior of a targeted animal, it must first be perceived as a threat of injury or death. Animals generally respond to human disturbance as if it were a predation risk as many species have evolved with human hunting or have evolved responses to generalized predator behaviors such as direct approach (Frid and Dill 2002, Beale and Monaghan 2004). One of the underlying principles of non-lethal harassment is that it increases the perceived risk at a site, manipulating behaviors in a way that makes the cost of staying at that site greater than the costs of moving to a new site (Frid and Dill 2002, Kloppers et al. 2005). However, animals can become habituated to disturbance, reducing the energetic cost to respond to harassment (Conomy et al. 1998, Baudains and Lloyd 2007). Even if harassment is perceived as a predation risk, the perceived risk may still be outweighed by the perceived cost of moving elsewhere. This decision involves weighing the conditions of the site (i.e. resource availability versus perceived risk) as well as condition at alternative sites (Frid and Dill 2002, Hagy et al. 2017). Harsh winter weather also has potential to limit resource availabilities and affect behaviors of animals as they cope with increased thermoregulatory costs. Thus, the factors affecting response to harassment are interrelated with climatic conditions, as these conditions impact the resources available, particularly in winter when resources may be limited.

We investigated the effects of harassment on behavior of Canada geese (*Branta canadensis*) during winter in city parks of Chicago, IL, USA. Canada geese are one of the most conspicuous wildlife species in urban areas across North America and parts of Europe (Groepper et al. 2008, Fox 2019, Groom et al. 2020). The adaptability of Canada geese to city and suburban landscapes has contributed to population increases and brought about human-wildlife conflicts on the ground and in the air (Conover and Chasko 1985, Paine et al. 2003). Urban Canada geese are associated with conflicts including aggression towards people when nesting, fecal and feather deposition leading to decreased aesthetic values of greenspaces, and risks to air traffic (Smith et al. 1999). More than 1,854 recorded goose-aircraft strikes from 1990– 2018 have been attributed to Canada geese (Dolbeer and Eschenfelder 2003, Dunning 2008, Dolbeer et al. 2021). Large open turf lawns and waterbodies in city parks can support large concentrations of geese throughout the winter in areas that pose risk to air traffic (Askren et al. 2018). The Chicago area supports a large breeding population of Canada geese that is supplemented by birds from northern breeding area during winter that likely match or exceed those breeding locally. These winter abundances of Canada geese have caused concern over risk to air traffic using major airports in the area.

Harassment is a common tool used by wildlife managers to reduce human-goose conflicts in urban areas but is often ineffective at achieving management goals (Smith et al. 1999, Sherman and Barras 2004, Holevinski et al. 2007, Dorr et al. 2010). Few studies have examined the effects of harassment on behavior during winter, an energetically taxing period during which man species of waterfowl exhibit reduced survival rates (Gates et al. 2001, Massey et al. 2019). Many species of waterfowl exhibit decline in endogenous nutrient reserves over the winter period (Loesch et al. 1992, Massey et al. 2019), including Canada geese (Joyner et al. 1984, Gates et al. 2001). This phenomenon is likely a facultative strategy that balance the costs of maintaining endogenous nutrient reserves with the energetics needs to survive winter (Gates et al. 2001). The loss in endogenous nutrient reserves in Canada geese is likely influenced by limited food availability, decreased food quality and increased costs of thermoregulation during cold periods (Joyner et al. 1984, Loesch et al. 1992, Gates et al. 2001). Geese in Chicago do not leave urban areas to access high-energy, agricultural grains (Dorak et al. 2018) and remained in areas where available forage is limited to low-quality, turf grasses (Conover and Chasko 1985, Conover 1991, Petrie et al. 1998). For Canada geese wintering in Chicago where nutrient rich food resources are limited, the inability to spend time in energetically conservative behaviors could result in a negative energy balance leading to death from starvation and/or exposure during extreme cold periods (Biebach 1996) and may be more likely to change their behaviors when harassed.

In this study, we explored the effects of harassment on Canada goose behavior, as a means to reduce human-wildlife conflict. We sought to determine how harassment affected 1) whether geese remained in a location, 2) distances geese moved following harassment, 3) the use of multiple land cover types, 4) behavioral time budgets, and 5) interactive effects of weather and breeding region on these aspects of Canada goose behavior. We expected that harassed Canada geese would leave the harassment site more frequently and for longer periods, have greater daily movement distances on days when harassed, and spend greater amounts of time in alert behavior and less time in foraging behavior when at the harassed site. We expected that harsh weather conditions might increase the effect of harassment on these behaviors and that movement and behavior of local-and non-local-breeding geese would differ due to differences in habituation. In addition to investigating how harassment impacts goose behavior, we investigated whether harassment achieved the ultimate wildlife management goals of causing geese to avoid the harassment site and disperse from the broader area.

METHODS

Study Area

I studied parental behaviors at three sites in east-central Illinois and seven sites in northeastern Illinois, USA during 2012 and 2013. Sites contained open areas interspersed with both clusters and individual shrubs. Shrubland habitats were comprised primarily of herbaceous vegetation such as blackberry (*Rubus* spp.) and common goldenrod (*Solidago canadensis*) as well as woody vegetation such as autumn olive (*Elaeagnus umbellata*), honeysuckle (*Lonicera* spp.), eastern red cedar (*Juniperus virginiana*), multiflora rose (*Rosa multiflora*), hawthorn (*Crataegus* spp.), and dogwood (*Cornus* spp.).

Our study area consisted of the south and central portions of the Chicago, Illinois, USA metropolitan area in Cook County (Fig. 4.1). This area includes Midway International Airport (41°47'6.5"N, 87°45'6"W), a major commercial airline hub with thousands of flights landing and departing daily (Chicago Department of Aviation 2020). The Greater Chicago Metropolitan Area has a human population of 9.4 million, including the city of Chicago and surrounding suburbs (United States Census Bureau 2012). The area consists of dense residential areas, commercial buildings, factories, large railyards, cemeteries, lawns, and parks. Rivers, ponds, and other waterbodies are interspersed throughout. The Greater Chicago Metropolitan Area has a Canada goose breeding population exceeding 30,000 individuals (Paine et al. 2003) that is supplemented by geese from more northern breeding areas in winter (Dorak et al. 2017).

Field Methods

We captured and deployed transmitters on Canada geese (*n* = 47) from 14 November 2015 through 16 November 2018 at parks, cemeteries, housing complexes, and water treatment plants (Fig. 4.1). Of those 47 transmitters, 18 were active in both winters of the study resulting in 65 goose/winter seasons for analysis. Canada geese were captured using MagNet small animal net-guns (Wildlife Capture Services, Flagstaff, Arizona, USA). We attached an aluminum leg band and either a Cellular Tracking Technologies (CTT) Global Positioning System, Global System for Mobile Communication transmitter (GPS-GSM; *n* = 44 Somerset, PA) attached to alphanumeric neck collars (Spinner Plastics, Springfield, IL) or an Ornitela GPS-GSM transmitter (*n* = 3, OrniTrack-N44, Vilnius, Lithuania) on captured Canada geese. Work was conducted with all necessary permits, including institutional (IACUC #20039), Illinois state scientific (#6079), Chicago Parks District Scientific Research (#1839), Chicago Water Reclamation District (#P-557; 17-NE 014), and federal banding permits (USGS BBL #23923).

Transmitters recorded GPS fixes every hour and uploaded data via the GSM network at least three times per week. We included only daylight locations (i.e., 30 min before and after sunrise) using R package *suncalc* (package *suncalc*, cran.r-project.org/package=suncalc, accessed 20 Nov 2019). We excluded locations with a horizontal dilution of precision > 4, to reduce location error, and excluded locations collected more frequently than 30 minutes to keep from biasing estimates of distance moved. We compared all geese located in the study area as well as a subset of geese that primarily used the harassment site.

Harassment was conducted by United States Department of Agriculture (USDA)-Wildlife Services employees (usually one person) during 4 December 2017 to 3 March 2018 and 7 December 2018 to 1 March 2019 at Marquette Park (41.7686°, -87.7032°). Marquette Park is 127.5 ha and consists of a mix of waterbodies, sports fields, forested areas, and open turf lawn. We chose Marquette Park as our harassment site due to its proximity to Midway International Airport (2.7 km at the nearest points) and previous work showing movements associated with the park conflicted with air traffic using Midway International Airport (Askren et al. 2018). Geese were harassed by approaching them on foot or an all-terrain vehicle and by clacking 2 in x 4 in lumber boards together, until all or most of the flock flushed and left the vicinity (i.e., that half of the park). At each harassment event, Wildlife Services personnel recorded time and location to observations of geese present (e.g. observation of transmitters, # of geese observed).

Data Analyses

We used Gaussian generalized linear mixed effects models to test the effects of harassment (was or was not harassed that day), use of the harassed site (did or did not use), breeding region (local or non-local), average daily temperature, and average daily snow depth on daily movement distance with individual ID as a random effect in Program R (GLMERs; package *lme4*, cran.r-project.org/package=lme4, accessed 20 Nov 2019; Table 4.1). We assigned geese as associated with the harassed site if > 10% of their locations occurred there in order to quantify effects of behaviors outside of the site boundaries. We classified the breeding region of individuals as local or non-local based on their locations during the first two weeks of May in previous or subsequent springs. At this time of year, most Canada geese breeding in northern regions have reached their breeding destination and have not left on molt migration (Luukkonen et al. 2008). In addition, we investigated the interactive effects of harassment on individuals from different breeding regions (Table 4.1).

We classified a goose as harassed if an individual's GPS location occurred within the harassment site and within 30 minutes (both before and after) of harassment occurring and determined the land cover type (package *spatialEco*, cran.r-project.org/package=spatialEco, accessed 20 Nov 2019). We then used this variable to quantify if an individual was harassed in a given day to compare effects on daily movements of just geese associate with the harassed site. We also included a variable of day of harassment, if harassment occurred in a given day regardless if an individual was affected or not, to account for spurious correlations. We calculated distance moved as the Euclidean distance between one location to the following location and daily distance moved as the summed distances between sequential diurnal points.

We calculated the daily proportion of GPS locations that occurred in specific biologically relevant land cover types (e.g. park, rooftop) using reclassified data from Open Street Maps (OpenStreetMap Contributors 2019, planet.openstreetmap.org, accessed 15 November 2019) and manually digitizing areas of missing data using high resolution aerial imagery (~1-m, Cook County Geographic Information Systems, https://hub.arcgis.com/datasets/, accessed 3 September 2020) and used this information to quantify land cover use. We checked accuracy and desired land cover classifications by visually comparing the classified land cover type to aerial imagery at 100 random locations in Cook County. We grouped land covers into three generalized classes; greenspaces, water bodies, and developed (appendix of specific-generalized land covers). We used binomial GLMERs to model the effects of harassment, breeding region, temperature, snow depth, and week of season on daily proportion of time in parks and daily proportion of time in different land cover types. Daily average temperature and snow depth was downloaded from the National Oceanic and Atmospheric Administration – National Centers for Environmental Information for the weather station at Midway International Airport within our study area (www.ncdc.noaa.gov/cdo-web/datatools/records; accessed 3 September 2020). We modeled the effects of average daily temperature and average daily snow depth on time budgets of geese during daylight hours using GLMMs with a logit link and binomial error distribution (Bates et al. 2015).

The use of accelerometer-equipped GPS transmitters allows researchers to quantify complex behavioral patterns at large spatial and temporal scales (Weegman et al. 2017, VonBank et al. 2021). We used tri-axial acceleration data (*hereafter* ACC packets) recorded by transmitters at 10 Hz frequency for 3 seconds at 15-minute intervals to quantify behavioral time budgets of transmittered geese. CTT transmitters recorded acceleration in g-force (range -4 – 4 g) while Ornitela transmitters measured acceleration in millivolts (range -2049 – 2049 mV), therefore we analyzed the CTT and Ornitela accelerometry data separately (see below). We built training datasets with which to train classification models by pairing observed behaviors from video of recorded geese in the field to ACC packets that could be unambiguously classified as head-up (i.e. alert), head tucked (i.e. resting), foraging, and in-flight behaviors. We chose these four behaviors as they were the primary behaviors that could be differentiated using neck collar mounted accelerometers (Kölzch et al. 2016) and are commonly recorded in other behavioral studies of geese (Bélanger et al. 1989). Head-up behavior included any behaviors in which a gooses neck was erect, including alert and vigilance while walking, we considered head tucked as an individual with bill tucked under a wing typical of a resting goose, foraging as active pecking or grazing, including walking with head outstretched while actively feeding, and flight as an individual actively airborne. Other behaviors that we did not uniquely identify included preening, drinking, swimming, or walking. We first calculated summary statistics for each ACC packet and translated these summarized ACC packets to instantaneous behaviors using a supervised machine learning approach and classification process (Shamoun-Baranes et al. 2012, Resheff et al. 2014, VonBank et al. 2021). Summary statistics include measures of overall acceleration among all axes, changes in acceleration in single axes, and relational measures between two axes following methods of Resheff et al. (2014). We used a workflow with an extreme gradient boosting algorithm (package *XGboost*; Chen and Guestrin 2016) to build separate classification models for CTT and Ornitela transmitters (due to their different data outputs) to predict unknown ACC packets (Shamoun-Baranes et al. 2012, Kölzch et al. 2016, VonBank et al. 2021). We ran 100 iterations of a train-test split using 75% of the data to train and 25% of the training data to test accuracy. The accuracy of the trained, extreme gradient boosting algorithm was 89.1% for CTT and 93.8% for Ornitela transmitters (i.e., how often the observed behavior was the same as the predicted behavior). We then used the trained models to predict the probability of an unknown ACC packet belonging to each of the focal behaviors and assigned the predicted label to the behavior class that had the highest probability.

As the training dataset consisted of "clean" behavioral observations that represented only one of the four focal behaviors, we allowed for behaviors that could not be distinguished (e.g. preening, bathing) or ACC packets that had multiple behaviors within the 3 second window (Kölzsch et al. 2016). We reclassified predicted labels to "other" if the probability for that ACC packet was below the 1st quartile of the probability distribution of each behavior and excluded those packets from subsequent analyses. This class likely includes preening behaviors, that we were unable to accurately classify as the behavior includes a wide range of motions, and ACC packets that captured switching more than one behavior in the 3 second period (Kölzsch et al. 2016). We assigned predicted behaviors to the nearest GPS fix (i.e., 30 minutes before or after a GPS fix) via timestamps of GPS and ACC packets, resulting in ~ 4 behaviors per locations per GPS fix. We calculated the hourly proportion of alert, foraging, resting, and in-flight behaviors per hour for each transmittered goose using accelerometer data. We modeled the effects of harassment on time budgets of geese during daylight hours using GLMMs with a log link and Gaussian error distribution (Bates et al. 2015).

Dispersal from the study area was defined as departure from a 25-km radius from harassment site. This distance was related to the distance to agricultural dominated landscapes and the extent of Cook County where harassment and captures were conducted. We used a G-test of independence to compare the proportion of geese that dispersed by breeding regions, primarily used parks, and the geese that had been harassed. We estimated seasonal, known-fate survival of transmittered Canada geese in Program MARK (White and Burnham 1999) implemented in package RMark (Laake and Rexstad 2018) using a staggered entry design (Cooch and White 2005). We determined mortality during the study period based on hunter reports of harvested geese or GPS locations indicating mortality. We assumed stationary GPS locations for extended periods indicated a deceased bird, as we had no evidence of transmitter loss, and attempted to confirm all mortality. We used a G-test of independence to test if harassment explained variation in the survival of transmittered geese.

RESULTS

Of 47 geese tracked during this study, 17 bred within the study region (Chicago Area), while 30 bred in other parts of the upper Midwest and Canada. We recorded 99,919 locations (n = 47 geese), consisting of 44,333 daytime locations and 55,586 nighttime locations. We conducted 359 harassment events during 4 Dec 2017 – 3 Mar 2018 and 268 harassment events during winter of 7 Dec 2018 – 1 Mar 2019. An average of 25.6 (±18.7 SE) harassment events were conducted each week in 2017–2018 and 20.6 (±12.3) in 2018–2019. In both years, 12 individual geese were harassed, resulting in a total 105 goose/harassment days in 2017–2018 and 123 goose/harassment days in 2018–2019.

Departures and Movement Distance

The probability that a goose left the park where harassment occurred on a day when no harassment occurred was 6.3% (± 5.6 SE, n =19) compared to 21.8% (± 9.6, n = 19) on days when harassment occurred. Geese that were harassed returned to the location where they were harassed faster (return time = 40.6 hours ± 0.24, n = 349) than when not harassed (return time = 78.8 hours ± 0.21, n = 146, $t = -3.9$, $p < 0.005$). The daily distance moved by geese in the park where harassment occurred was greater (5,907.5 m ±1,336.6 SE, n = 13) than geese in the parks without harassment (4,040 m ±667.8 SE, t23.18 = 3.37, $p < 0.01$). Furthermore, geese using the harassment site where harassment occurred moved 1.61 times further on days when harassment occurred than days that it did not (4,282 m ± 0.09 versus 6,433.22 m ± 0.09, $t = 8.64$, $p < 0.01$). There was an immediate effect of harassment as the hourly average distance moved of harassed geese (531.7 m) was greater than the average distance moved without harassment (429.0 m, $t = 1.94$, $p = 0.05$). The number of harassment events in a day had diminishing returns, with a negative correlation between with the number of harassment events and distance moved ($t = -4.47$, $p < 0.01$).

There was no difference in the daily distance moved of local breeding vs. non-local geese in parks without harassment (3,969 m ± 0.11 vs. 4,269 m ± 0.08, $p = 0.58$) or with harassment (5,864 m ± 0.13 vs. 5,209 m ± 0.11, $t = -0.74$, $p = 0.46$). Overall, geese that bred locally departed parks at similar rates (0.39 departures/day ± 0.24) to geese that bred in other regions (0.31 departures/day ± 0.31, $z = -0.74$, $p = 0.458$). However, when harassed, local breeders departed a park more often (harassed = 1.68 departures/day ± 0.25) than geese that bred in other regions (harassed = 0.86 departures/day ± 0.25; $p < 0.01$, $z = 3.15$).

Land Cover Use

There was no long-term effect of harassment resulting in geese spending less time in the harassed site compared to geese in other parks during the study period ($z = -0.10$, $p = 0.92$; Fig. 4.5). During daylight hours, 57.4% (± 17.1 SD) of locations occurred in greenspaces (including 21.1% (± 35.2) in large city parks), 14.4% (± 14.6) in developed land covers (including parking lots, industrial areas), and 28.4% (±10.6) on waterbodies (e.g., rivers, ponds). Of locations recorded immediately following harassment (1 hour later), 71.4% remained in the harassment site, meaning they left the park but returned within the hour or simply flew to another portion of the park. Geese that left the park after harassment used commercial rooftops (23.9%, $n = 6$), railyards (20.2%, $n = 7$), other parks (16.5%, $n = 8$), water treatment ponds (12.0%, $n = 5$), and sports fields (11.0%, $n = 4$). Weather appeared to have the greatest impact on land cover use (Fig. 4.6). Use of water ($z = -40.1$, $p < 0.01$) and developed resources decreased ($z = -9.2$, $p < 0.01$) while use of greenspace increased ($z = 49.7$, $p < 0.01$) with increasing temperatures (Fig. 4.6). Use of water ($z = -29.0$, $p < 0.01$) and developed resources increased ($z = 24.9$, $p < 0.005$) and use of greenspace decreased ($z = -50.8$, $p < 0.01$) with increasing snow depth (Fig. 4.5). As temperature declined and snow depth increased, geese tended to leave greenspace for open water, unrelated to harassment.

Behavioral Time Budgets

On average, geese in this study spent 31.0% (± 4.6% SE) in alert behavior, 35.0% (± 4.7%) in foraging behavior, 3.5% (± 1.5%) in resting behavior, and 20% in other behaviors. Geese that primarily used the harassment site spent 4.7% more time in alert behavior (± 7% SE, $z = 2.8$, $p < 0.01$) and 1.6% more time in flight (± 20%, $z = 3.61$, $p < 0.01$) on days when harassment occurred but there was no effect on foraging ($z = -1.46$, $p = 0.14$) or resting ($z = -0.50$, $p = 0.62$) behaviors. Prior to harassment, proportion of time spent in the 4 focal behaviors by geese located in the harassment site did not differ from geese in other parks, but geese in the harassment site spent more time alert and in flight and less time foraging an hour after harassment than times when harassment did not occur (Table 4.2). Geese spent more time in alert and resting behavior and less time foraging in waterbodies and developed land covers compared to greenspaces (Table 4.2). We investigated the impact of temperature and snow depth on behavioral time budget, as well as the interactive effect of harassment and weather. Increasing temperature had strong positive effect on the foraging ($z = 15.82$, $p < 0.005$) behavior of geese, moderate negative effects on alert ($z = -5.14$, $p < 0.005$) and resting ($z = -3.96$, $p < 0.005$) behaviors, and no effect on flight ($z = -0.16$, $p = 0.87$; Fig. 4.2) behavior. Snow depth had similar but inverse effects on foraging ($z = -11.03$, $p < 0.005$), alert ($z = 6.17$, $p < 0.005$), and resting ($z = 3.34$, $p < 0.005$) behaviors, but it differed in its effect on flight ($z = -5.16$, $p < 0.005$; Fig. 4.2). For geese that used the harassment site, there was an interactive effect of harassment and temperature on alert ($z = 2.63$, $p = 0.008$) and foraging behaviors ($z = -2.21$, $p = 0.03$), but not resting behavior ($z = -0.45$, $p = 0.66$) or flight ($z = 0.00$, $p = 1.0$). Likewise, there was an interactive effect of harassment and snow depth on foraging behavior ($z = -102.95$, $p < 0.005$) but not alert ($z = -0.72$, $p = 0.47$), resting ($z = 0.11$, $p = 0.92$), or flight behaviors ($z = 0.00$, $p =$

1.0).

Dispersal and Survival

Most geese that wintered in the Chicago area survived (*Ss* = 86.2%, *n* = 65 goose/winters) for the duration of the study period. The proportion of geese that departed the area did not differ between seasons (2017, 6 of 34 goose/winters; 2018, 4 of 31; $G^{adj} = 0.27$, p = 0.60). Local breeders left the study area during winter at a similar rate (3 of 28 goose/winters, *n* = 17) as geese from other breeding regions (7 of 37 goose/winters, *n* = 30; $G^{adj} = 0.81$, p = 0.37). Geese that were harassed left at a similar rate (5 of 19, *n* = 13) to geese that were not harassed (5 of 46, *n* = 34; $G^{adj} = 2.14$, p = 0.14). Only 5 birds died during the study and there was no difference in the percentage that died that were harassed (2 of 19) compared to those that were not harassed (3 of 46; $G^{adj} = 0.25$, p = 0.63). Mortality events occurred during periods of colder temperatures and deeper snow [average temperature of -5.8° C (± 2.28) and snow depth = 8.0 cm (± 3.8)] compared to the study period (1 December – 1 March 2017 – 2019) means of -2.8° C and 3.0 cm.

DISCUSSION

Winter harassment in an urban park influenced geese to spend more time in alert behavior and flight both at the daily and hourly scale, following our predictions and previous studies (Nolet et al. 2012, Atkins et al. 2017). However, harassment resulted in short-term behavioral changes that may not have significantly affected energetic costs of using the site and did not accomplish the management goals of causing individuals to leave the area or avoid a specific location for more than 48 hours. We suggest the success of harassment in this study was limited by two broad themes. First, harassment did not affect the perceived cost of staying versus the perceived cost of leaving the site; and second, weather affected use of the harassment site and other greenspaces, regardless of harassment. The use of unique locations (open waterbodies and developed areas) resulted in the inability of us being able to harass individuals during these extreme cold periods and likely provided some spatial sanctuary for the geese within the study area.

The effectiveness of our harassment may have been limited by the ability of geese to discern our harassment as a simple disturbance rather than a real threat of predation (Frid and Dill 2002, Atkin et al. 2017). Avian species have evolved the ability to recognize and respond to different predators according to the threat they pose (Curio et al. 1983). For harassment to increase the cost of staying at a site, it must be perceived as a real risk and if it is, should affect changes in vigilance behavior (Atkins et al 2017). The amount of time geese spent in alert behavior was greater on days when harassment occurred and in the hour after harassment, however, these differences were relatively small and variable. Additionally, the social behavior and flock dynamics of geese may have mitigated the behavioral effects of harassment (Atkins et al. 2019). Many species of animals share duties of watching for predators and the proportion of those spending time watching for predators decreases as the number of animals increase (Cresswell and Quinn 2011, Atkins et al. 2019). Geese in this study were harassed while part of a flock (mean flock size = 99.6, range = 2 – 1,500; R. Askren, unpublished data). Because of the flock size and dynamics of geese, it is possible that we increased the amount of time spent in vigilance behavior of some individuals within a flock without affecting measurable changes to the behaviors of the entire flock or the transmittered individuals.

Similarly, habituation to human disturbance can moderate the impacts of harassment on behaviors of animals (Kloppers et al. 2005, Fox 2019). Habituation is a decreased response to stimulus and can vary temporally and spatially (Blumstein 2016). While we didn’t explicitly test for habituation to harassment, we were interested in differences in the response to harassment by geese from different breeding regions. Local breeding geese in this study nested in greenspaces and industrial areas within the city, exposed to human disturbance year-round. Non-local breeding geese nested where human disturbance was likely light or non-existent, along Hudson Bay and southern Ontario in Canada or large marshes in rural Wisconsin. We expected that local breeding geese would be more tolerant of harassment compared to non-local geese. However, harassment was more effective in causing local individuals to move and leave the park compared to non-local individuals. It might be that local geese had previous knowledge of other parks that likely provided the same resources as the park where harassment occurred and thus perceived little cost of relocating compared to non-local breeding geese. This suggests that habituation to general human disturbance did not have a major impact on goose movements but the perceived cost and trade-off with harassment likely did.

The ability of Canada geese to overwinter in the upper Midwest, especially in urban areas, is facilitated by their ability to buffer against periods when access to food is extremely limited, such as in deep snow cover or extreme cold temperatures (Gates et al. 2001). The ability of geese to survive the winter period, largely by using energy reserves, is well described yet the importance of these reserves for geese wintering in urban areas is unknown. Even the temporary effects of harassment on behaviors is energetically costly and likely leads to the metabolism of some endogenous reserves. Flight is generally the most energetically costly behavior in flying animals (Bryant 1997), estimated to be 11.5 times more costly than resting behaviors in snow geese (*Chen caerulescens*; Bélanger and Bédard 1990). While alert behavior is not as energetically costly (3 times more so than resting; Bélanger and Bédard 1990), it does reflect missed opportunity costs, meaning that an individual must forego foraging or resting behavior. In addition, increased foraging by harassed geese in this study reflect the costs incurred by behavioral changes caused by harassment are likely reflected in the amount of time spent foraging as geese compensate for lost energy (Nolet et al. 2016). While there was some evidence that foraging increased following harassment, it was not biologically significant enough to suggest that geese were working to make up energetic costs. While we harassed geese daily it may be that the type of harassment did not result in the behaviors that greatly impact the energy balance of wintering geese. Future work examining the relationship between habitat resources and the energy balance of geese wintering in urban and exurban/rural areas could shed more light on the ability to change goose behavior and achieve management objectives.

The effects of harassment on goose behaviors were likely reduced during harsh weather as geese reduced their use of greenspaces, including the harassment site. While we predicted harassment would have the greatest effects on geese during extreme cold periods, harassment in a greenspace had little effect as geese selected other land covers during those periods. Transmittered geese spent twice as much time resting and resting in developed land covers and waterbodies compared to greenspaces. The use of these land covers for energetically conservative behaviors is likely driven by either the thermal characteristics or disturbance levels. Dorak et al. (2017) used anemometers to record temperature and wind speed at canals and rooftops in our study area but did not find any evidence of thermal benefits of these sites. Because of this, we suggest that site use during cold periods is driven by land cover characteristics that allow geese to avoid disturbance and energetically costly behaviors. If a lack of disturbance at these resources allows geese to maintain a positive energy balance during winter, harassment at these sites may be more effective at incurring greater energetic costs and persuading geese to disperse from those land covers and the broader area.

TABLES AND FIGURES

Table 4.1. List of generalized linear mixed effects models included in analyses of aspects of Canada goose movement and behavior relative to harassment at an urban park in Chicago, Illinois during 2017 – 2019.

Independent	**Fixed effect**	**Error distribution**	**Time scale**	**Data subset**
Departures and Movement Distances				
Departure	Day of harassment	Binomial (logit)	Hour	Individuals - Harass site
Return time	Harassment	Gaussian (log)	Hour	Individuals - Harass site
Distances moved	Associated with harassed site/not	Gaussian (log)	Day	All transmitters
	Day of harassment	Gaussian (log)	Day	Individuals - Harass site
	Breeding region	Gaussian (log)	Day	All transmitters
	Harassment	Gaussian (log)	Hour	All transmitters
	Harassment	Gaussian (log)	Day	All transmitters
# of park departures	Breeding Region	Poisson (log)	Day	Locations - Harassed site
	Breeding region*Harassment	Poisson (log)	Day	Individuals - Harass site
Land Cover Use				
% Locations in parks	Harassment	Binomial (logit)	Day	All
% Water, % Developed, % Greenspace	Average daily temperature	Binomial (logit)	Day	All
	Average snow depth	Binomial (logit)	Day	All
Behavioral Time Budgets				
% Alert, % Feed, % Fly, % Rest	Day of harassment	Binomial (logit)	Day	Individuals - Harass site
	Harassed site - in/out	Binomial (logit)	Hour	All
	Day of harassment	Binomial (logit)	Day	Locations - Harassed site
	Average daily temperature	Binomial (logit)	Day	All
	Average snow depth	Binomial (logit)	Day	All
	Harassment*Average daily temperature	Binomial (logit)	Day	Individuals - Harass site
	Harassment*Average snow depth	Binomial (logit)	Day	Individuals - Harass site

Table 4.2. Mean proportion (± SE) of alert, foraging, resting, flight, and other/unclassified behaviors. Statistical differences from the harassed site – no harassment occurred to parks without harassment, and the harassed site – hour after harassment to harassed site – no harassment occurred based on binomial, generalized linear mixed effects models denoted by • < .1, * < 0.05. Greenspaces – Not parks consisted of any area of vegetation not contained in city parks (ex. golf courses, cemeteries), developed include any constructed surfaces (ex. rooftops, parking lots, industrial areas), and waterbodies are any area of open water (ex. ponds, rivers, wetlands).

	Hourly - In parks			Hourly - Land cover types		
	Parks without harassment	Harassment site - Not harassed	Harassment site – Hour after harassed	Greenspaces - Not parks	Manmade	Waterbodies
Alert	27.3 (± 5.0)	24.0 (± 6.7)	30.1 (± 7.8)•	23.2 (± 3.9)	33.8 (± 4.9)	42.7 (± 5.1)
Feeding	44.4 (± 5.6)	40.6 (± 7.5)	37.8 (± 7.8)*	47.6 (± 4.7)	25.7 (± 4.2)	18.5 (± 3.6)
Resting	6.7 (± 3.0)	16.4 (± 6.9)	13.1 (± 6.7)	7.2 (± 2.7)	14.8 (± 4.4)	14.1 (± 4.0)
Flight	4.0 (± 1.9)	2.3 (± 1.8)	4.2 (± 2.7)*	4.2 (± 1.7)	3.5 (± 1.6)	2.2 (± 1.1)

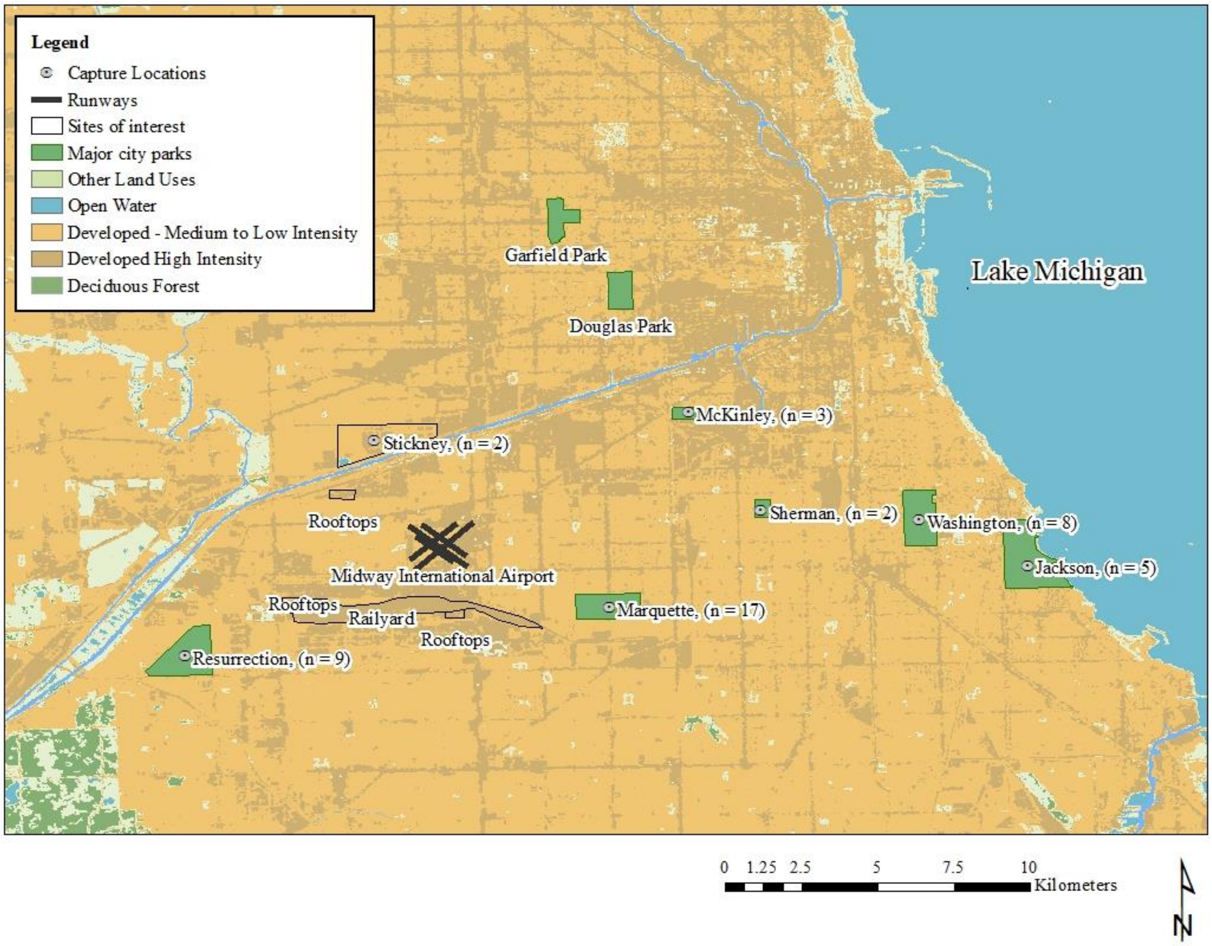

Figure 4.1. Map of the study area in Chicago, Illinois, US, sites of interest relevant to this project, and capture locations of Canada geese (*Branta canadensis*) transmittered during winters of 2016 – 2018.

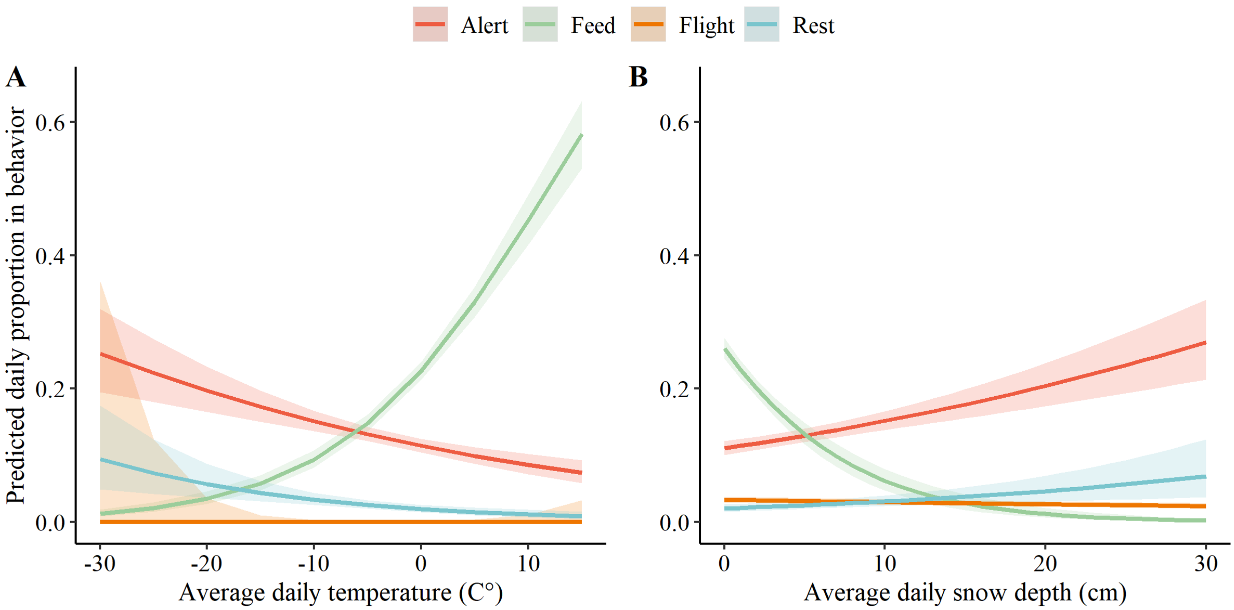

Figure 4.2. The effect of temperature (A) and snow depth (B) on daily proportion of time spent in alert, foraging, flight, other, and resting behaviors by Canada geese (*Branta canadensis*) in the Chicago area during 1 December – 1 March during 2017–2018 and 2018–2019.

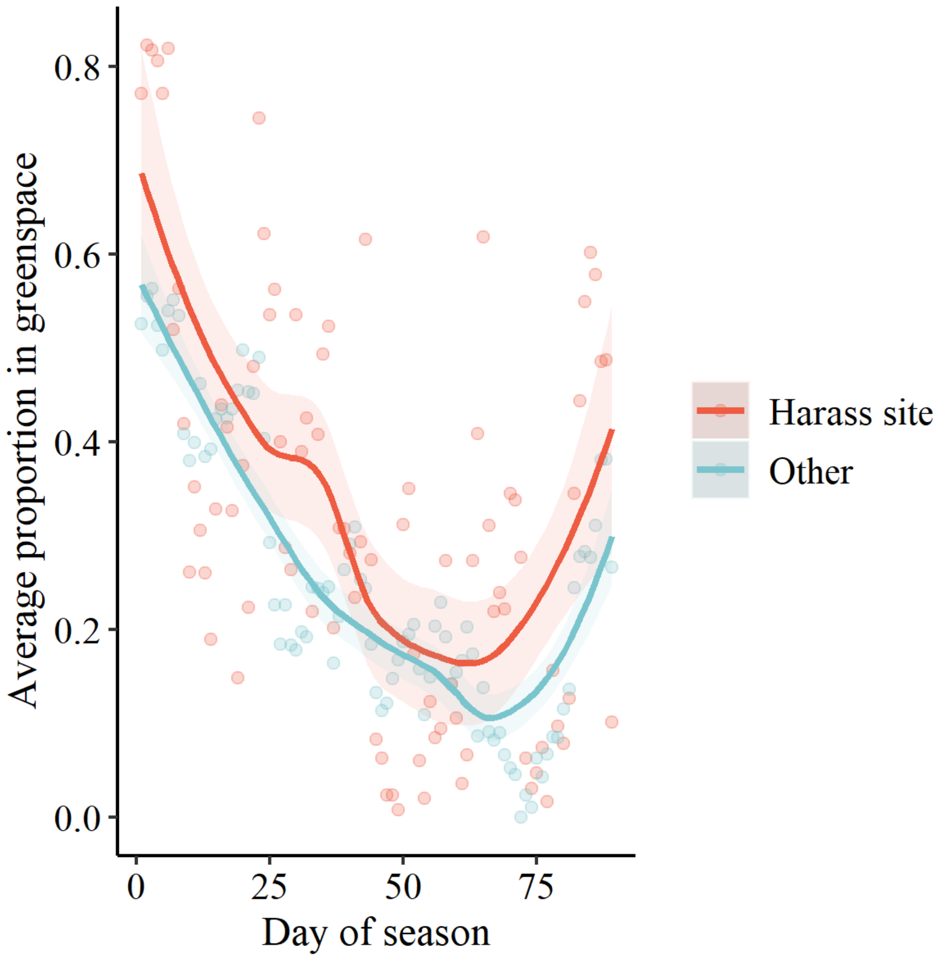

Figure 4.3. Average daily proportion in the park for Canada geese (*Branta canadensis*) assigned to Marquette Park by day of season in Chicago, Illinois during 1 December – 1 March during 2017–2018 and 2018–2019.

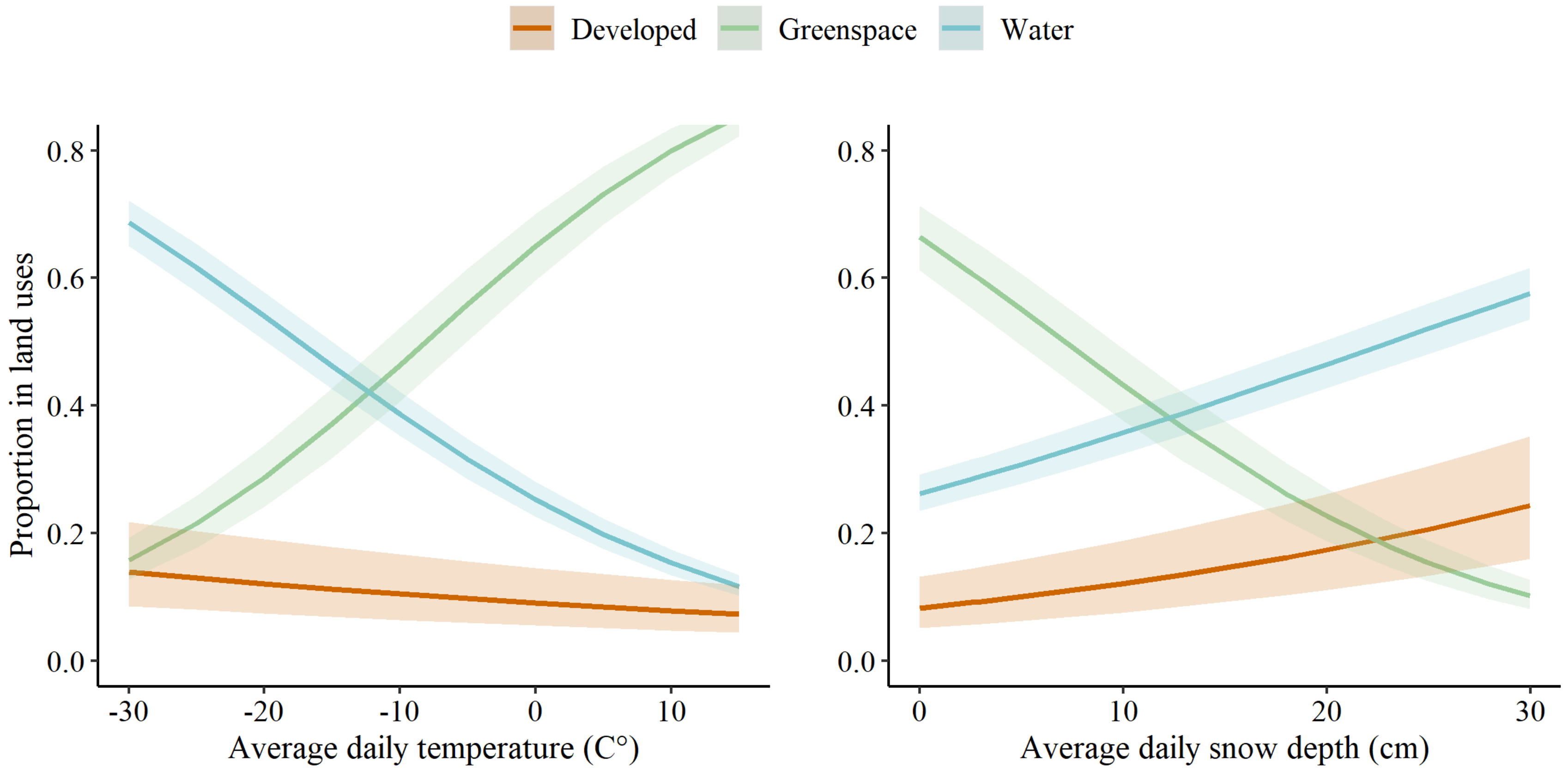

Figure 4.4. The effects of average daily temperature and average daily snow depth on proportional use of developed, greenspaces, and water land covers by Canada geese (*Branta canadensis*) in the Chicago area during 1 December – 1 March during 2017–2018 and 2018–2019.

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CHAPTER 5: INFLUENCES AND TRADE-OFFS ASSOCIATED WITH LONG-DISTANCE MOLT MIGRATION IN CANADA GEESE

ABSTRACT

Molt migration is a unique life history strategy representing the decision to undergo costly flight-feather molt in areas with relatively higher-quality forage and reduced predation risk. This strategy is well documented in non-breeding and failed-nesting Canada geese (*Branta canadensis)* breeding across much of North America but varies spatially among and within populations. We used satellite telemetry and accelerometry to quantify the propensity of temperate-breeding Canada geese to molt migrate and examine trade-offs associated with this strategy. We fitted 157 Canada geese with GPS transmitters mounted to neck collars on nesting females in Toronto, Canada and nesting females and both sexes during winter in northeastern Illinois, USA. We monitored movements and recorded subsequent breeding status, nest attempts, and nest success. In addition, we removed 69 nests in Toronto and northeastern Illinois ensure nest failure. We recorded a total 210 nest attempts, of which 144 failed, and an additional 56 incidents of non-breeding. The overall rate of molt migration was 33.3% (n = 186 goose/season) for non-breeding and failed nesting Canada geese. Geese either moved relatively short distances from the nest to molt ($\bar{x}$ = 5.3 km ± 1.4 SE) or undertook long-distance molt migrations ($\bar{x}$ = 2,199.5 km ± 6.4). The primary factor associated with whether or not a goose molt migrated was the landscape in which they nested. Geese were more likely to molt migrate from areas of cropland and wetland and less likely from areas of open water, forest, and urban land uses. For geese that molt migrated, all went to the subarctic region near Hudson Bay, Canada. Geese that migrated to the subarctic spent more time foraging, less time in alert behaviors, and longer periods flightless compared to non-molt migrating geese. Overall survival of non-breeding, failed-nesting, and successful breeders exhibited variation across the season, with the lowest

survival in the month of September. Molt-migrating geese had greater survival until fall migration when harvest resulted in similar seasonal survival between groups. Our results provide useful insights into the costs and benefits of molt migration and the influence of urban habitat resources and harvest on the molt migration strategies of Canada geese.

INTRODUCTION

Long-distance migratory movements are energetically costly and dangerous, but allow avian species to access seasonally variable resources necessary for survival (Alerstam and Hedenström 1998). Migration is typically characterized by annual movements from cooler latitudes during the breeding period to warmer latitudes during winter, however some species undergo a distinct migration for the purpose of molting feathers (Jehl 1990, Alerstam et al. 2003). These movements, termed molt migrations, occur in a range of avian taxa (Leu and Thompson 2002, Tonra and Reudink 2018) and are well studied in waterfowl (Jehl 1990, Savard et al. 2007, Sheaffer et al. 2007).

Molt migration is a strategy by which non-breeding or failed breeding waterfowl, absent of parental obligations, migrate from areas of low-quality forage or greater predation risk to more optimal areas to undergo costly remigial molt (Gates et al. 1993, Reed et al. 2003, Fox et al. 2014). All waterfowl undergo simultaneous remigial molt, dropping all flight feathers to grow new ones at once, rather than replacing remiges sequentially (Guillemette et al. 2007). Simultaneous remigial molt is costly as waterfowl must meet the energetic costs of growing all remiges at once and become completely flightless for a period of weeks (Balham 1945, Gates et al. 1993, Fox et al. 2014). Despite the hazards of simultaneous molt, survival during the molting period is similar to other portions of the annual cycle (Fox et al. 2014). The cost of migration may be compensated for by reduced predation and greater forage resources at their molting location (Fox et al. 2014).

Molt migration is a common strategy among species and populations of geese, including temperate-breeding Canada geese breeding in the upper Midwest and southern Canada (Lawrence et al. 1998, Abraham et al. 1999, Luukkonen et al. 2008). Previous studies have reported molt migration rates from 27% of non-breeding and failed-nesting Canada geese from urban parks, to greater than 90% from areas in Illinois and Wisconsin (Zicus 1981, Lawrence et al. 1998, Luukkonen et al. 2008). This migratory behavior likely evolved in temperate-breeding Canada goose populations at a time when forage quality and quantity was limited in temperate regions and migration costs were low (Baldassarre and Bolen 2006, Sheaffer et al. 2007). However, urban greenspaces may have altered the costs and benefits of molt migration by providing additional food resources and reduced predation risk, while modern hunting seasons have likely increased the risk of mortality during their migration in autumn (Sheaffer et al. 2007, Luukkonen et al. 2008). Several species and populations of geese have demonstrated significant plasticity in migratory strategies, evidenced by large-scale and relative rapid shifts migratory behavior (Sheaffer et al. 2010, Clausen et al. 2018). Therefore, understanding selective pressures associated with molt migration may provide insights into the potential of future shifts in migratory behavior with important implications for harvest and management of geese associated with human-goose conflicts (Sheaffer et al. 2007).

We sought to quantify differences in survival and behavior of Canada geese to examine trade-offs between migrating to molt or molting in an individual’s breeding area. The overall goal of this study was to examine the influence of landscape factors on the propensity to molt migrate and costs and benefits of molt migration for temperate-breeding Canada geese. Our objectives were to: 1) examine effects landscape composition and breeding area on probability of molt migration, 2) compare foraging and alert behavior as a proxy for foraging environment quality and predation risk between temperate and subarctic areas, and 3) quantify differences in survival between geese that do and do not undertake molt migration. This research will improve our understanding of the factors geese use to determine whether to molt migrate and how recent changes to the landscape (urban development) and harvest (early-season goose season) may influence the costs and benefits of molt migration.

METHODS

Study Area

Our study area encompassed the cities of and areas surrounding the city of Chicago Illinois, USA and Toronto, Ontario, Canada. Both metropolitan areas have large breeding populations of Canada geese (Paine et al. 2003) and a gradient of highly developed to rural land uses. Breeding areas included large emergent cattail marshes in southwestern Wisconsin and small wetlands and islands along the shore of Lake Superior in Thunder Bay, Ontario. Temperate-breeding Canada geese are known to molt in the subarctic and arctic tundra, near the coast of Hudson Bay (Dieter and Anderson 2008, Luukonen et al. 2008). This region is dominated by lichen-heath tundra, wet-sedge meadows and numerous ponds, rivers, and wetlands (Abraham et al. 1999). The flora consists of short woody vegetation, lichens, and heath in more upland areas and mosses and sedges in low-lying areas (Abraham et al. 1999, Cotter et al. 2014).

Field Methods

We captured female Canada geese nesting in a range of urban areas from highly developed areas to less developed suburban/rural areas during March – May of 2018 – 2020 in both Toronto and northeastern Illinois. We used MagNet small animal net-guns (Wildlife

Capture Services, Flagstaff, Arizona, USA), landing nets, or hand-grabbing to capture female Canada geese during nesting. In addition, we captured both male and female Canada geese during fall and winter in northeastern Illinois using MagNet small animal net guns or rocket nets where conditions allowed. We used cloacal inversion to determine sex of non-nesting geese. We attached an aluminum leg band and fitted geese with solar-power Global Positioning System-Global System for Mobile transmitters (GPS-GSM) affixed to neck collars. We used GPS-GSM transmitter manufactured by Cellular Tracking Technologies (Rio Grande, New Jersey, USA) and Ornitela (Vilanius, Lithuania). Transmitters recorded and stored GPS fixes at one-hour intervals for geese marked in northeastern Illinois and fifteen-minute intervals for geese marked in Toronto, which we down-sampled to one-hour intervals. In addition, transmitters collected tri-axial acceleration data every 15 minutes using on-board accelerometers these data were then used to quantify behavior time budgets (see below). Transmitters were programmed to upload GPS and acceleration data every 3 days when in range of a cell tower.

Nests

For geese captured at nests in Toronto and northeastern Illinois, we recorded nest location and estimated incubation based on embryo development using the float method or egg candling at time of nest check (Walter and Rusch 1997). In addition, we estimated nesting attempts, nest site, incubation length, and nest success by plotting daily movement distances and visually inspecting GPS locations for previously transmittered geese and those nesting outside of Illinois. Nesting attempts were evident from decreased movement and distances between mean locations of < 300 m in subsequent days. We estimated nesting success based on the length of incubation and movements after leaving the nest site. We defined a successful nesting individual as one whose incubation period was at least 25 days and the individual did not exhibit any rapid movements after leaving the nest site (~2.5 km/h) during March - May.

During 2018 – 2020, we removed 69 nests, by removing all eggs, of transmittered geese in northeastern Illinois and Toronto to artificially induce nest failure, remove parental obligations, and encourage molt migration. We removed eggs from nests at approximately 14 days of incubation in order to reduce the likelihood of renesting (Smith et al. 1999). We monitored locations to determine if renesting occurred and removed re-nesting individuals from subsequent analyses (n = 8). We tracked geese following nest failure, including nest depredation/abandonment from unmanaged goose nests, location of geese were monitored to determine incidence of molt migration (i.e., did or did not molt migrate), which we defined as large-scale movements (>100 km) in a northward direction following the breeding season. Our GPS-GSM transmitters relied on cellular network service to upload data and cellular coverage is limited in the subarctic, thus we did not have precise data on mortality in the Subarctic if birds did not return south during fall migration. However, we typically received data indicating northward migration from molt migrating Canada geese and had no instance of transmitters that were presumed to have died in the subarctic being reported in subsequent season. We included such cases of known molt migration in data on timing, landscape effects, and survival and assigned mortality to date of the last known location.

Propensity to Molt Migrate

We estimated the proportion of both non-breeding and failed nesting geese that undertook molt migrations. We quantified the mean linear distance from nests for each breeding individual by month to describe post-breeding movements. In order to quantify landscape composition for non-breeding geese not associated with a nest location, we used the mean location during the first two weeks of May, prior to the start of molt migration of temperate-breeding Canada geese

(Luukkonen et al. 2008). We used the mean distance of failed-nesting geese from nests during the month of July ($\bar{x} = 5.28$ km) to extract landscape composition (package *Raster*, Hijmans et al. 2015) from publicly available 2015 - North American Land Change Monitoring System data (NALCMS; MRLC.gov, *accessed* 15 May 2021). We used the NALCMS data layer as it provides uniform mapping of biologically relevant land uses for both the United States and Canada. We created a suite of candidate models representing the effects of land uses and breeding areas on the probability of molt migration of failed-nesting Canada geese using general linear mixed effects models (Bolker et al. 2009; Table 5.1). W then ranked models in an Aikaike's Information Criterion framework to choose the model that best describes the effects of landscape composition on the probability of molt migration (AIC_c; Burnham and Anderson 2002). We included additive and interactive combination of open water, wetland, cropland, forest, urban land uses (> 20% impervious surfaces), and breeding status (nonbreeding or failed breeding) with individual ID as a random effect (Table 5.1). We chose these land uses as predictors as previous work has suggested a relationship between propensity to molt migrate and surrounding land use (Luukkonen et al. 2008), the importance of wetlands and open water for nesting and molting geese (Jehl 1980), and agriculture is the dominate land use in northeastern Illinois and outside of Toronto.

Foraging and Duration of Molt

We used tri-axial accelerometer data to quantify differences in the proportion of time spent in foraging and alert behaviors as a proxy for foraging environment and predation risk (Weegman et al. 2017, VonBank et al. 2021). We built training datasets from which to train classification models by pairing observed behaviors, collected via video of transmittered geese in the field, to ACC packets that could be unambiguously classified as head-up (i.e., alert) and foraging behaviors. We quantified flight behavior in order to determine the duration of flightlessness. As flight was relatively rare during observation periods, we supplement training datasets with ACC packets that were recorded during periods of flight as indicated by GPS locations and patterns in acceleration data (Weegman et al. 2017). Alert behavior included any walking or stationary behaviors in which a goose's neck was erect, indicating vigilance, a behavior related to perceived predation risk (Atkins et al. 2017). Similarly, we defined foraging as active pecking or grazing, including walking with head outstretched while actively feeding.

We first calculated summary statistics for each ACC packet and translated these summarized ACC packets to instantaneous behaviors using a supervised machine learning approach and classification process (Shamoun-Baranes et al. 2012, Resheff et al. 2014, VonBank et al. 2021). Summary statistics include measures of overall acceleration among all axes, changes in acceleration in single axes, and relational measures between two axes following methods of Resheff et al. (2014). CTT transmitters recorded acceleration in g-force (range -4 – 4 g) while Ornitela transmitters recorded acceleration in millivolts (range -2049 – 2049 mV), therefore we analyzed the CTT and Ornitela accelerometry data separately (see below). We used a workflow with an extreme gradient boosting algorithm (package *XGboost*; Chen and Guestrin 2016) to build separate classification models for CTT and Ornitela transmitters (due to their different data outputs) to predict unknown ACC packets (Shamoun-Baranes et al. 2012, Kölzch et al. 2016, VonBank et al. 2021). We ran 100 iterations of a train-test split using 75% of the data to train and 25% of the training data to test accuracy. The accuracy of the trained, extreme gradient boosting algorithm was 89.1% for CTT and 93.8% for Ornitela transmitters (i.e., how often the observed behavior was the same as the predicted behavior). We then used the trained models to predict the probability of an unknown ACC packet belonging to each of the focal behaviors and assigned the predicted label to the behavior class that had the highest probability. We assigned predicted behaviors to the nearest GPS fix (i.e., 30 minutes before or after) via timestamps, resulting in ~ 4 behaviors per locations per GPS fix.

We tested for differences in the daily proportion in foraging and alert behaviors by month and molting region (subarctic and temperate) using general linear mixed effects models with individual ID as a random effect in package *lme4* (Bates et al. 2015). We considered differences significant at $P < 0.05$ and report means (±1 SE). In addition, we used incidence of flight derived from labeled accelerometer data as an index of flightlessness, or the duration without instances of in-flight behavior. In order to reduce false positive classification of fight, we selected classified data in the upper quartile range for each individual, leaving only ACC packets that had a high probability of being attributable to flight. We used linear mixed effect models to examine the effects of location (i.e. subarctic or temperate) and individual ID as a random effect on estimated length of flightlessness by molting geese.

Survival

We modeled monthly survival from May – October as a function of molt migration (did or did not), breeding success (failed, successful, nonbreeding), and nesting areas using known-fate models using package *RMark* (Laake and Rexstad 2008) to implement Program MARK using staggered entry encounter histories (Pollock et al. 1989,White and Burnham 1999). We evaluated the importance of predictor variables by investigating all possible variable combinations on survival (Table 5.1), including a null model, using AICc and cumulative weights (w_i) for each model (Rotella 2005). We identified mortalities based on repeated, stationary locations or reports of harvested transmitters. We located deceased transmittered birds whenever possible to determine if it was due to mortality or transmitter loss. We based mortality on the last date we received data from a given transmitter, so if transmitter movements indicated northward movement of a molt migration and no further data was received, due to lack of cell towers in the Subarctic molting areas, we assigned that mortality to the month we last received data. We calculated period survival and 95% CIs using the delta method and plotted cumulative survival function by taking the cumulative product of monthly survival estimates (Nur et al. 2004, Ryder et al. 2010). Lastly, we used a G-test for independence using 2 x 2 contingency tables to test differences between the ratio of molt migratory and non-molt migratory geese that were harvested and reported and considered results significant at $P < 0.05$ (Woolf 1957).

RESULTS

We captured 157 Canada geese in Toronto (n = 58 geese) and northeastern Illinois (n = 99 geese). Of the 99 geese captured in northeast Illinois, 37 were captured during nesting and 62 during winter. Of the geese captured in winter in Illionis20 nested in southeastern Wisconsin (n = 20 nests), 10 in Thunder Bay, Ontario (n = 20 nests), and 21 in Illinois (n = 27 nests). Geese transmittered in Toronto were captured during nesting (n = 56) or during molt (n = 2) and all nested locally. We monitored 206 nests, of which 69 were managed (33.5%) and 8 of which resulted in second nest attempts (11.6%). Of 137 unmanaged nests in this study, 63.5% failed due to predation or abandonment (n = 87 nests), 30.7% were successful (n = 42 nests), and nest success could not be determined for 5.8% (n = 8 nests). Mean estimated incubation length was 15.5 and 13.8 days for failed and managed nests, respectively, and 28.6 days for successful, first nest attempts (Table 5.3). Mean start date of first nest attempts was the first week of April, while second nest attempts occurred in the first two weeks of May (Table 5.3). We recorded 41 molt migrations (29.9% of failed nesters) originating from 137 managed and unmanaged failed nests, excluding renesting geese. In addition, we recorded 49 instances of geese not breeding or attempting to breed for a season (n = 37 geese) of which molt migration occurred in 22 instances

(42.9%). The overall rate of molt migration was 33.3% (*n* = 186 goose/seasons) for non-breeding and failed nesting Canada geese. Of non-breeding and failed-nesting geese that were alive in consecutive seasons (*n* = 67), 14% molt migrated in both years (*n* = 9), 61% did not molt migrate in either year (*n* = 37), 25% switched behaviors from one year to the next (*n* = 21).

Distribution and Timing of Molt Migration

Transmittered geese either molted near nest sites (mean distance = 5.3 km ± 1.4 SE) or undertook a long-distance molt migration to the Subarctic (mean distance = 2,199.5 km ± 6.4) with few exceptions (Fig. 5.1). Geese departed breeding areas at the end of May and early June (x̄ = 6-Jun (± 1.3 days SE) and arrived in the Hudson Bay region on average 3 days after departure (x̄ =9-Jun ± 0.9 days; Table 5.4). Geese that molt migrated from breeding areas in Illinois, Wisconsin, and Thunder Bay, Ontario molted along western Hudson Bay, north of Churchill, Manitoba (58.8°N, -94.2°W) and as far north as Baffin Island, Nunavut (70.0°N, -82.7°W, Fig. 5.2). Toronto breeding geese that molt migrated went to areas along southeastern Hudson Bay near Umiujaq, Quebec (70.0°N, -82.7°W) to south of Ivujivik, Quebec (62.4.0°N, -77.9°W). Geese remained in northern portions of the Hudson Bay region for ~3 months (x̄ = 83.7 days ± 2.5) until approximately the last week of September (Table 5.4). Geese marked in northeastern Illinois often took more westerly routes south (during autumn migration) and several staged for greater than 5 days in parts of Manitoba, Minnesota, and Wisconsin (Fig. 5.2), before returning to temperate-breeding latitudes in September and October.

Effects of Landscape Composition on Molt Migration

The top ranked model of probability of molt migration was the global model including the effects of all land uses and region (w_i = 0.67; Table 5.2) followed by the model including all land uses (w_i = 0.31; Table 5.1). The probability of molt migration increased by 0.7% for every percent increase in crop and 1.8% for wetland, and decreased by 0.4% for every percent increase in forest, 0.1% for urban, and 0.8% for open water (Figure 5.3). In addition, the propensity to molt migrate was greatest for geese breeding in southeastern Wisconsin (76.4%, CI_{95} = 59.8 – 94.0%), followed by northeastern Illinois (42.0%, CI_{95} = 32.2 – 51.8%), Toronto (13.7.0%, CI_{95} = 3.3 – 24.1%), and Thunder Bay (3.8%, CI_{95} = -18.8 – 26.3%; Fig. 5.3)

Foraging Behavior and Duration of Molt

Geese molting in the Subarctic spent 3.8 hours more time foraging each day ($\bar{x}$ = 50.5% ± 0.8 SE) than those molting in temperate regions ($\bar{x}$ = 34.4% ± 1.2, $F_{1,8867}$ = 118.65, $P < 0.01$) during June – August. Conversely, geese molting in the Subarctic spent 4.3 hours less in alert behaviors ($\bar{x}$ = 34.4% ± 1.2) than those molting in temperate regions ($\bar{x}$ = 34.4% ± 1.2, $F_{1,8867}$ = 319.4, $P < 0.01$). Subarctic molting geese received an average of 20.2 hours (± 4.4) of daylight during June and July compared to 15.0 hours (± 3.1) for temperate molting geese. However, the daily proportion of time spent foraging was greater in the Subarctic during June – August than temperate regions (Fig. 5.4). Conversely, daily proportion of time spent in alert behavior was less in the Subarctic during June – August than temperate regions (Fig. 5.4). The flightless period of failed-nesting Canada geese molting in the subarctic was longer ($\bar{x}$ = 56.6 days ± 3 SE) than those in molting temperate regions ($\bar{x}$ = 30.1 days ± 4, $F_{1,70}$ = 17.8, $P < 0.01$). There were no differences in the estimated start date of flightlessness between failed-nesting geese molting in the subarctic and temperate regions ($\bar{x}$ = 16-June ± 2 SE, $F_{1,70}$ = 1.3, P = 0.26), but end date of flightlessness was 27 days later in the Subarctic ($\bar{x}$ = 11-Aug ± 4) than temperate regions ($\bar{x}$ = 15-July ± 3, $F_{1,70}$ = 59, $P < 0.01$).

Survival

For all non-breeding, failed-nesting, and successful breeding Canada geese, the top-ranked model of monthly survival was the time-specific (i.e., effect of month) model (w_i = 0.74%). Monthly survival varied with highest survival during June – August and lowest in September. The next supported model included the interaction of molt migration (did or did not) by time (w_i = 0.26; Table 5.5). Overall cumulative survival of all Canada geese was 83.2% (CI_{95} = 77.6 – 87.6%). Plots of cumulative survival by month revealed greater survival of molt migrants during May – August compared to temperate nesting geese but an 8.7% decrease during the month of September, resulting in similar end of period survival for those individuals that molt migrated and those that did not (Fig. 5.5).

We recorded 39 mortalities during May – October, including 30 geese marked in northeastern Illinois and 9 marked in Toronto. Of 39 mortalities, 13 were attributed to hunter harvest, 10 non-harvest causes (i.e., depredation, vehicle strike, etc.), 7 that left on molt migration but did not return (i.e., natural mortality, transmitter failure, etc.), and 8 for which cause could not be determined. The proportion of molt-migrating geese that were harvested was greater ($\bar{x}$ = 13.4%, n = 67 molt migrations) compared to geese that remained in temperate regions ($\bar{x}$ = 3.0%, n = 133 geese/years; G_{adj}=7.11, P <0.01). Molt migrating geese were harvested in Minnesota (n = 4), Wisconsin (n = 3), Ontario (n = 1), and New York (n = 1; Fig. 5.6).

DISCUSSION

Molt migration in Canada geese is a strategy that likely evolved when the Subarctic provided a better foraging environment than temperate regions and migration was relatively safe (pre-early goose hunting season). However, we found that survival of transmittered geese that undertook molt migrations was higher than those molting in temperate regions, but decreased greatly during the months of September and October, when autumnal migration occurred.

Modern hunting seasons have likely increased mortality during autumn migrations, making molt migration less adaptive, while urbanization has simultaneously created suitable and safer molting habitats (turf grass areas with ponds) in temperate regions. Furthermore, year-to-year variation within individuals suggests this strategy is plastic and that the effects of hunting and urbanization are providing selective pressure against the undertaking of molt migration by temperate-breeding Canada geese. Our use of GPS telemetry and accelerometry revealed the timing and distribution of molt migration, influence of landscape composition of the propensity to molt migrate, and distinct trade-offs between both strategies in temperate-breeding Canada geese.

The propensity to molt migrate was negatively correlated with urbanization (Sheaffer et al. 2007, Luukkonen et al. 2008), but indicated strong effects of open water near nest sites on decreased incidence of molt migration (Fox et al. 2014). Open water likely confer reduced predation risk due to increased visibility and escape from predators and likely played a strong role in the evolution of simultaneous, remigial molt as only waterbirds exhibit this behavior (Jehl 1990, Fox et al. 2014). Well-maintained and fertilized turf lawns are common along the shores of most urban open water habitats, providing the resources necessary for molt adjacent to safe areas away from most predators (Gates et al. 1993, Fox et al. 2014). The availability of open water adjacent to turf lawns is likely driving observed decreases in propensity to molt migrate in urban areas (Luukkonen et al. 2008). In our study, geese that nested in areas with the lowest propensity to molt migrate (individuals in Thunder Bay and Toronto) used near shore areas of Lake Superior and Lake Ontario, respectively, more extensively than geese in northeastern Illinois use Lake Michigan.

Likewise, emergent marshes provide important molting and nesting areas for many species of waterfowl as they offer safety from predators and food abundance (Ringelman 1990, Fleskes et al. 2010). However, our results demonstrated a greater proportion of non-breeding and failed geese departing from areas of wetlands, primarily in Wisconsin, on molt migration. Our transmittered geese nested in and around Horicon Marsh, a large emergent cattail marsh, which is a major breeding and fall staging area for Canada geese (Kennedy and Arthur 1974, Heinrich and Craven 1992). We suggest the effects of landscape composition and potential social dynamics of the Horicon Marsh area are most similar to the historic conditions under which molt migration evolved. The high rates of molt migration from this and other wetland areas across the upper Midwest are likely driven by limited foraging areas in the marsh and surrounding agricultural landscape as well as higher densities of geese including socially dominate, family flocks (Raveling 1970, Bêty et al. 2004).

While the single effect of breeding region was not supported, breeding region was included in our top model (Table 5.1) and there appears to be regional variation in the propensity to molt migrate. Previous studies have proposed genetic or social dynamics as a potential reason for low rates of molt migration from some areas (Sheaffer et al. 2007). Temperate-breeding Canada goose populations are partially the result of re-introduction and introduction efforts following near extinction of giant Canada geese (*Branta canadensis maxima*) in the first half of the 20th century (Hanson 1965). While the origins and genetic makeup of geese in our breeding areas is unknown, it is likely young geese learn molt locations and migratory routes from adult geese due to complex social dynamics (Oudman et al. 2020). Temperate-breeding Canada geese were re-introduced to Midwest stern states by state and federal agencies starting in the 1960s. However, reintroduction efforts were limited in geographic extent and may have led to spatial variation in molt migratory behavior of geese (Butler 1987). The fact that individuals changed strategies yearly regarding whether to molt migrate may suggest the behavior is mediated by social factors as opposed to innate behaviors. Further investigation into whether recently introduced populations of Canada geese in Europe and New Zealand molt migrate would provide further support or disprove molt migration as an innate behavior.

Despite subarctic-molting geese spending more time foraging and less time alert indicating in a presumably high-quality foraging environment, our estimates of flightless duration were nearly twice as long as geese in temperate molting areas. Flight is an important predator avoidance behavior (Blumstein 2010, Eichholz et al. 2012) and reducing the length of time flightless should be adaptive under the threat of predation (Fox et al. 2014). The flightless period in arctic-nesting. Previous studies have suggested molting quickly is adaptive to reduce predation risk and demonstrated relationships between mass loss and food. However, our data demonstrated longer flightless periods in the subarctic were we expected lower predation risk. We suggest that a longer flightless period might reflect decreased, perceived predation risk, either due to differences in predator communities, densities, or availability of escape habitat. We note that our measurement of the flightless period relied on actual incidences of flight rather that the growth of remiges adequate for flight. It is possible that geese in the Subarctic were capable of flight earlier than our estimate but chose not to move, possibly due to a combination of the habitat they use, the predators in the area, and the perceive disturbances might have resulted in the differences in flightlessness.

Previous studies have suggested nest removal may serve as an important tool for indirectly affecting adult survival rates as molt migrants return through hunted areas in the fall (Sheaffer et al. 2007, Dieter and Anderson 2009). However, geese nesting in more urban areas, were geese are more often associated with conflicts, were less likely to molt migrate. Therefore, harvest during autumn migration is unlikely to reduce goose abundances associated with conflicts and may select against geese nesting in rural areas. This suggests hunting pressure, coupled with the use of urban areas for molting, has likely increased the cost of molt migration and provided increased selection pressure for nesting and molting in urban areas. While early hunting seasons offer increased opportunities for hunters, they may have unintended consequences on molt migratory behavior and greater abundances of geese using urban areas. Further research is needed to assess the effects of early hunting seasons on rural- versus urban-nesting temperate Canada geese.

TABLES AND FIGURES

Table 5.1. Candidate generalized linear mixed effects models representing the effects surrounding landscape composition of non-breeding and failed nesting Canada goose (*Branta canadensis*) on molt migration from temperate breeding areas during 2019 – 2020. We report model parameters, number of parameters (K), Akaike's Information Criterion for small sample sizes (AICc), difference in AICc from the top model (▲AICc), AICc weight (W_i), and log-likelihood [*Log (L)*].

Models	K	AICc	▲AICc	W_i	Log (*L*)
Crop + forest + urban + open water + wetland + region	11	202.18	0.00	0.67	-89.45
Crop + forest + urban + open water + wetland	8	203.70	1.52	0.31	-93.51
Region	6	209.88	7.69	0.01	-98.74
Region*open water	7	213.39	11.21	0.00	-99.43
Region*wetland	7	214.86	12.67	0.00	-100.16
Wetland	4	219.86	17.68	0.00	-105.84
Region*urban	7	221.38	19.20	0.00	-103.42
Cropland	4	224.34	22.16	0.00	-108.08
Open Water	4	227.92	25.73	0.00	-109.86
Forest	4	241.20	39.02	0.00	-116.51
Null	3	241.71	39.53	0.00	-117.80
Urban	4	243.14	40.96	0.00	-117.48
Sex	5	243.75	41.57	0.00	-116.74

Table 5.2. AICc model selection table of monthly survival of Canada geese (*Branta canadensis*) associated with naturally failed nests or artificially managed nests. We report model parameters, number of parameters (K), Akaike's Information Criterion for small sample sizes (AICc), difference in AICc from the top model (▲AICc), AICc weight (W_i), and log-likelihood [*Log (L)*].

Models	# Parameters	AICc	▲AICc	Weight	Deviance
S(~Time)	6	314.30	0.00	0.70	201.64
S(~Molt migrated*time)	12	316.05	1.75	0.29	191.20
S(~NULL)	1	325.26	10.96	0.00	222.67
S(~Molt migrated)	2	327.18	12.88	0.00	222.58
S(~region)	7	330.27	15.97	0.00	215.59
S(~Year)	6	330.56	16.26	0.00	217.90
S(~Molt migrated*region)	13	335.02	20.72	0.00	208.13
S(~Breeding success)	8	335.93	21.63	0.00	219.22
S(~Region*time)	42	359.53	45.23	0.00	171.82
S(~Breeding success*time)	48	374.01	59.71	0.00	173.33

Table 5.3. Count of nest fate (n = 207 nests) with mean start and end date of incubation (± SE) for temperate-breeding Canada geese (*Branta canadensis*) during 2015 – 2020.

		Incubation		
Nest fate	# of nests	Start	End	Duration
Failed	84 (n = 53 geese)	15-Apr (± 1.3)	28-Apr (± 1.4)	15.5 (± 1.1)
Removed	64 (n = 51 geese)	6-Apr (± 1.1)	21-Apr (± .8)	13.8 (± 0.9)
Successful	39 (n = 28 geese)	10-Apr (± 2.2)	9-May (± 2.2)	28.6 (± 0.5)
Unknown	8 (n = 7 geese)	23-Apr (± 2.3)	10-May (± 4.0)	14.9 (± 4.2)
2nd nest -failed	5 (n = 5 geese)	11-May (± 2.6)	20-May (± 2.4)	9.2 (± 1.5)
2nd nest -successful	3 (n = 3 geese)	7-May (± 2.7)	5-Jun (± 2.3)	29.0 (± 0.6)

Table 5.4. Calendar dates (±SE) of departure from and return to the temperate-breeding region of failed- and non-nesting Canada geese (*Branta canadensis*) transmittered in Chicago and Toronto during 2015 – 2020.

Nest state	n	Spring departure	Spring arrival	Fall departure	Fall Arrival
IL	39	9-Jun (± 1.5)	9-Jun (± 1.2)	12-Sep (± 3.1)	18-Sep (± 2.6)
ON	13	10-Jun (± 2.2)	11-Jun (± 2.2)	17-Sep (± 4.7)	9-Sep (± 4.1)
WI	20	30-May (± 2.5)	7-Jun (± 1.5)	24-Sep (± 3.2)	1-Oct (± 4.1)

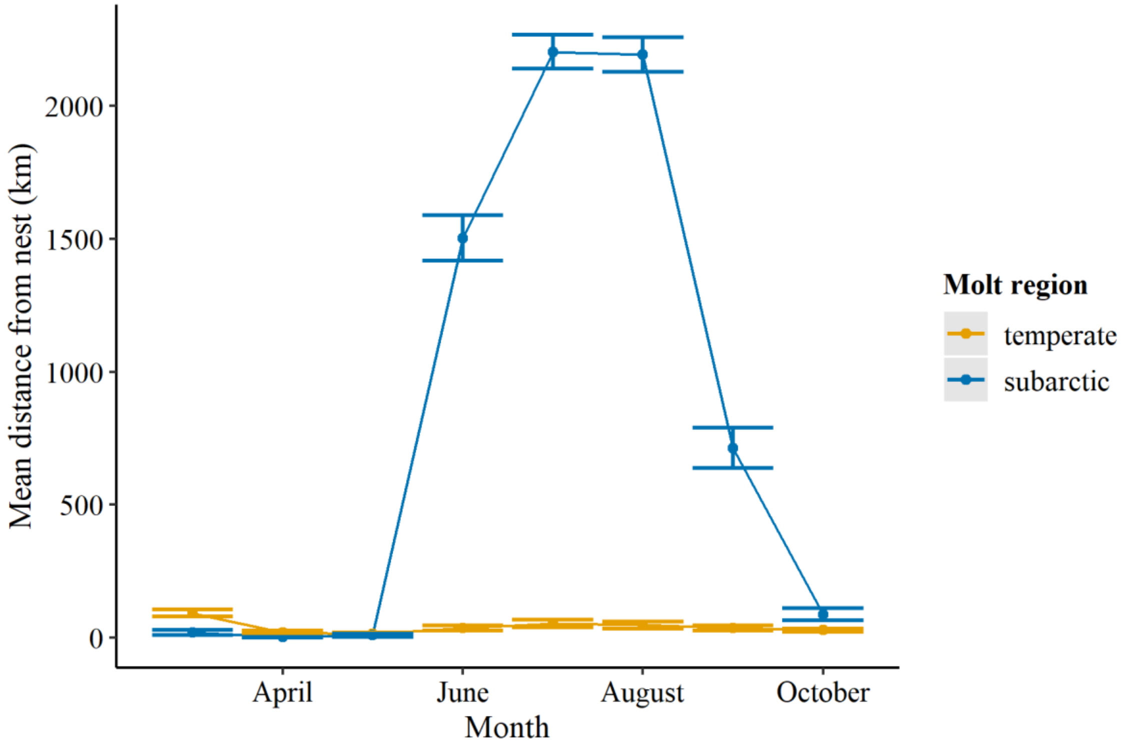

Figure 5.1. Mean monthly movement distances of failed-nesting Canada geese (*Branta canadensis*) of molting in temperate and subarctic regions from nest sites during March – April of 2015 – 2020.

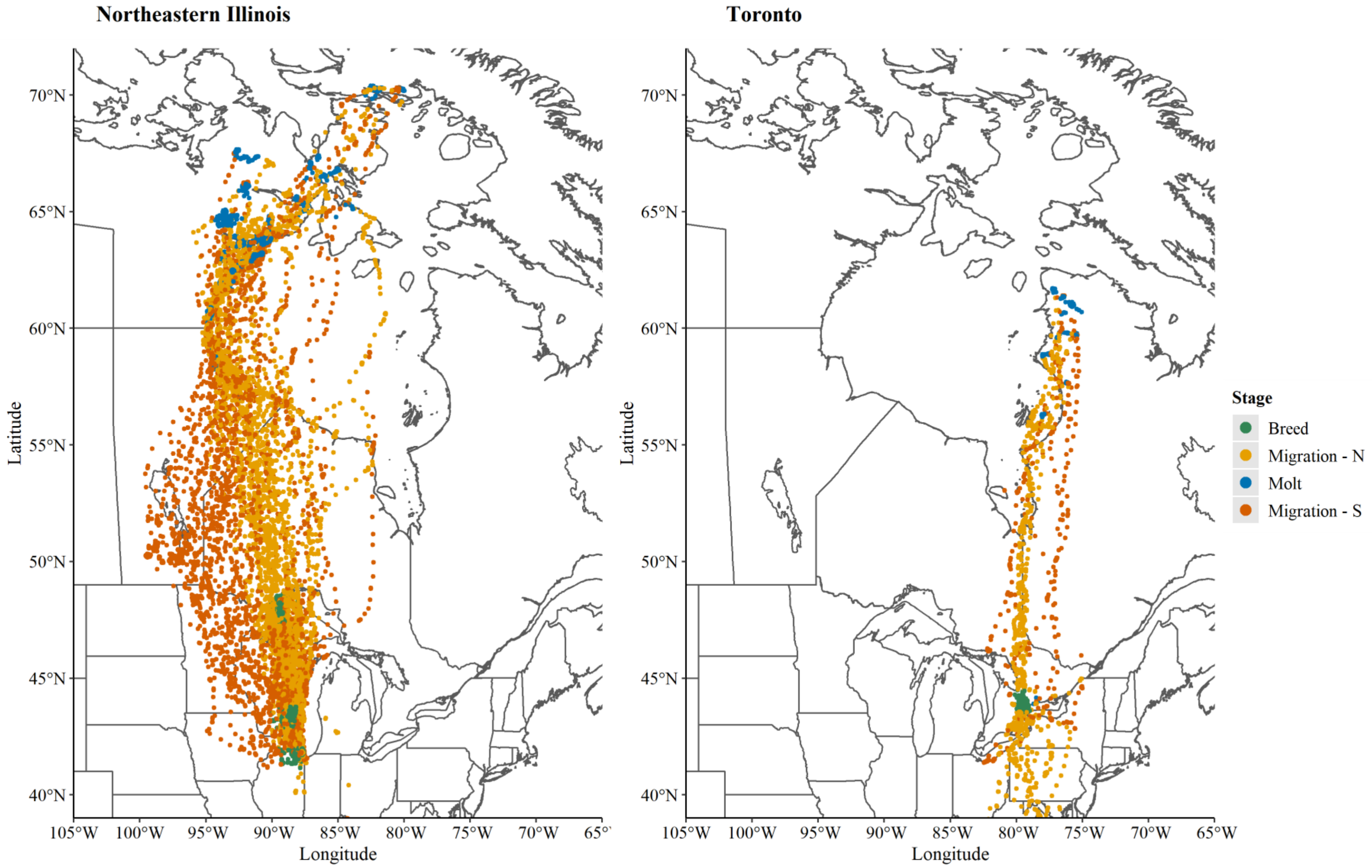

Figure 5.2. Map depicting breeding areas and molt migratory routes of all Canada geese (*Branta* canadensis), during March – October 2015 – 2020, transmittered in northeastern Illinois and Toronto.

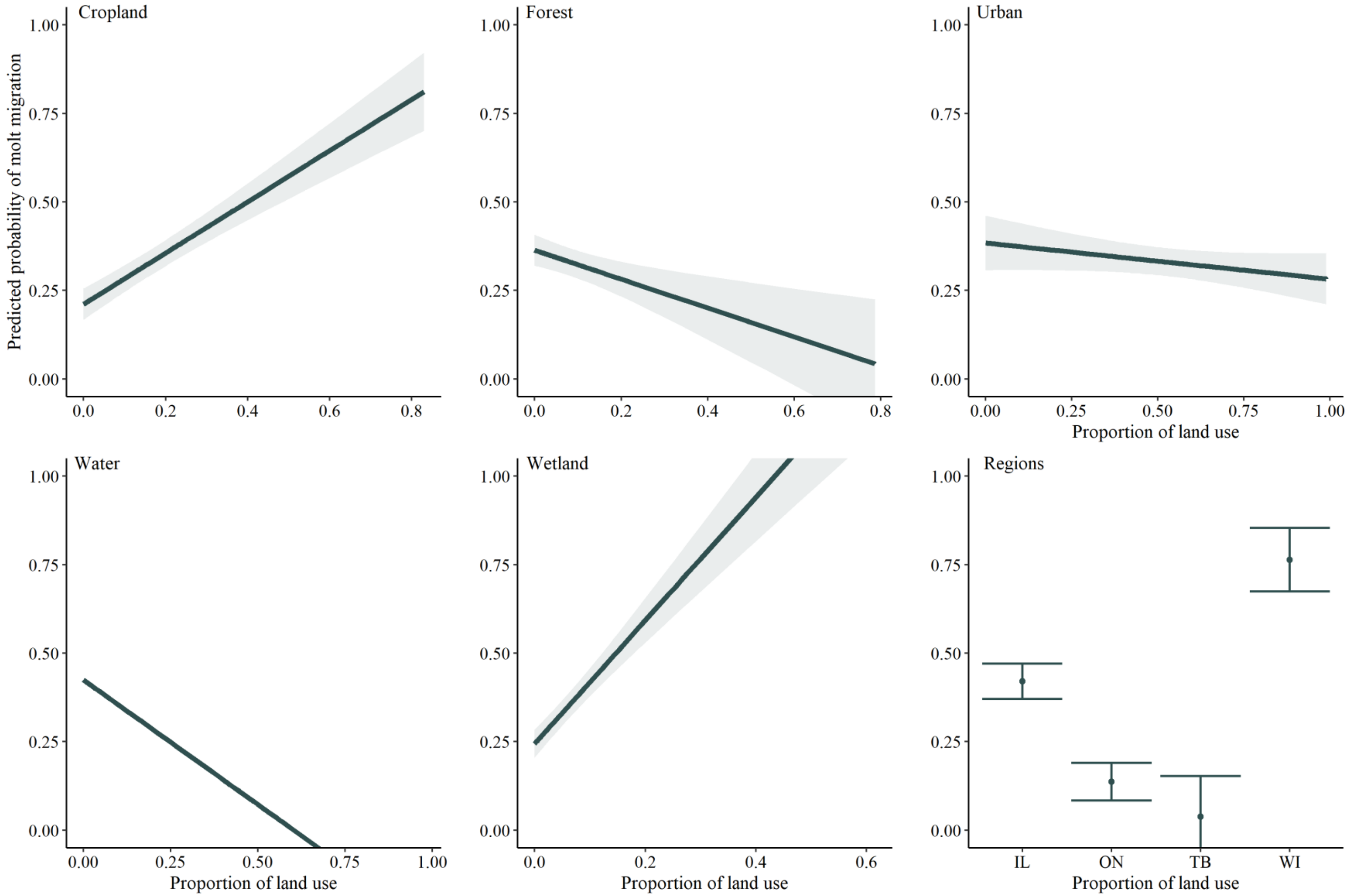

Figure 5.3. Effects of cropland, forest, urban land uses, open water, wetlands, and breeding region on the probability of molt migration of Canada geese (*Branta canadensis*) from breeding areas in the upper Midwest during 2015 – 2020.

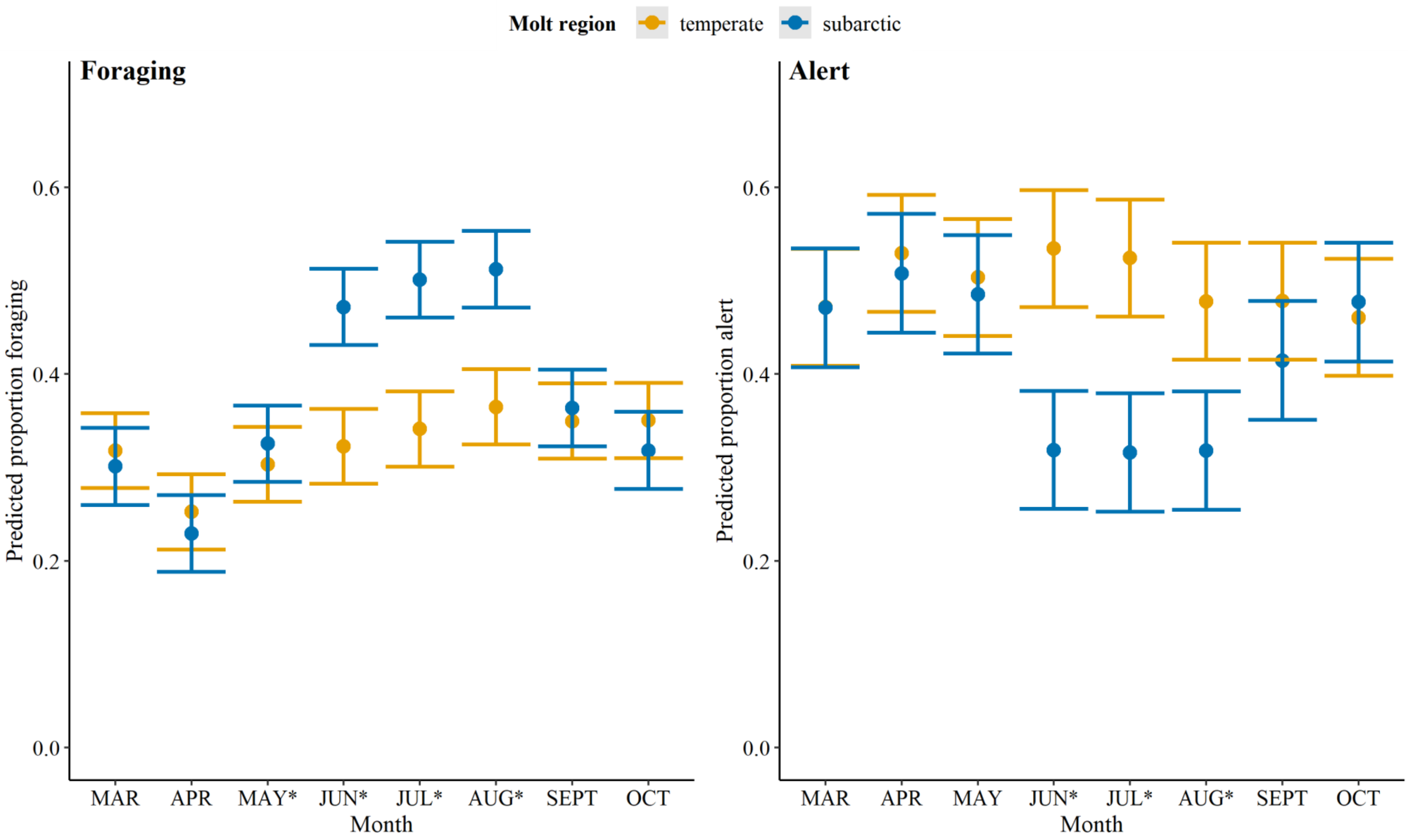

Figure 5.4. Estimates of daily proportion of time spent foraging between Canada geese (*Branta canadensis*) molting in temperate regions (n = 106 geese) compared to those in the Subarctic (n = 37 geese) by month during 2015 – 2020, weighted by daylight hours to account for differences in day length. Significance ($P < 0.05$) denoted by (*) next to each month.

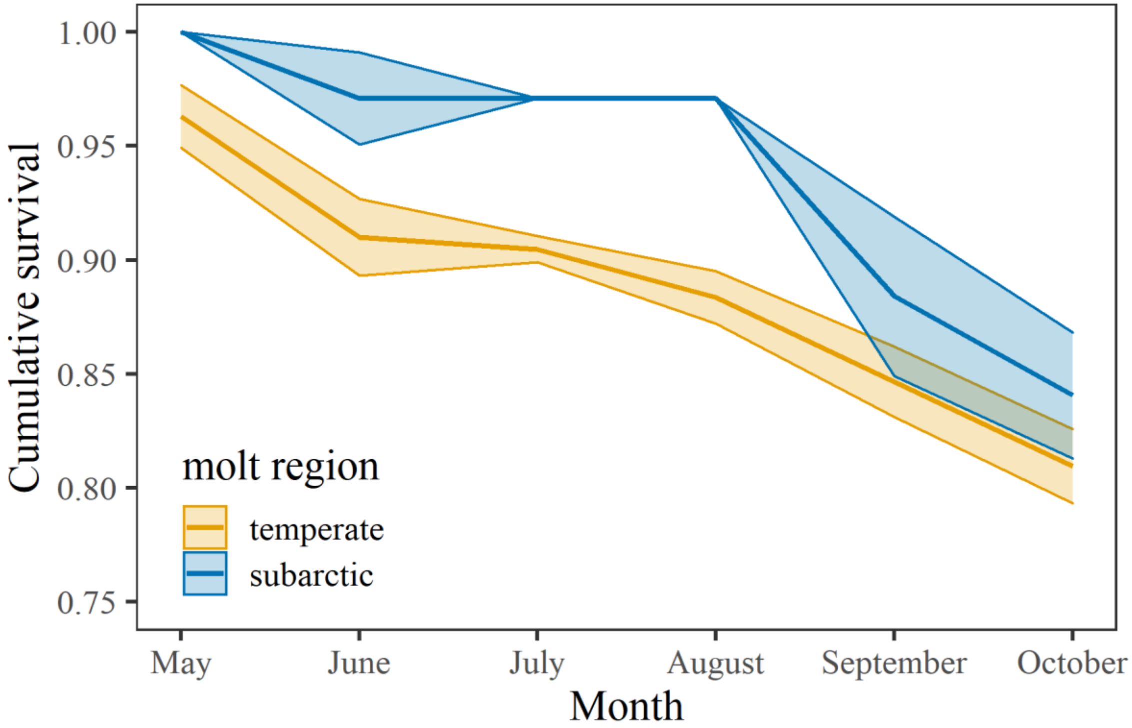

Figure 5.5. Cumulative survival by month from Known-Fate models of the effects of molt migration*time on all (failed, non-breeders, successful breeder) Canada goose (*Branta canadensis*). Non-molt migrate birds includes non-breeders and failed breeders that did not molt migrate and successful breeders, whereas, molt migrating birds includes non-breeders and failed breeders that molt migrated. The shaded areas are standard errors.

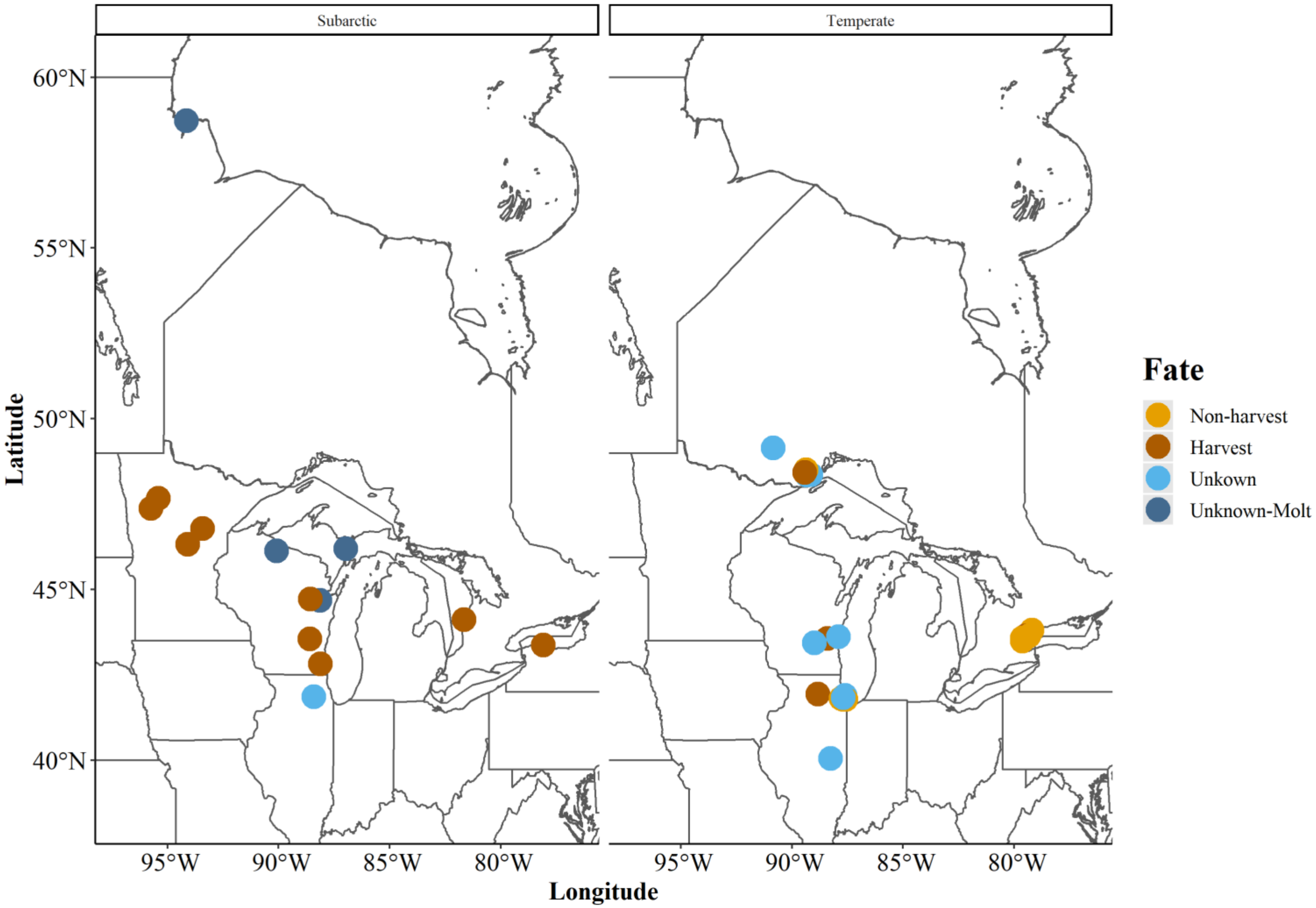

Figure 5.6. Distribution of mortalities of Canada geese (*Branta canadensis*) associated with geese undertaking molt migration (left) and temperate-molting geese (right) by fate. We classified mortalities as non-harvest if movements indicated a stationary carcass, harvest.

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CHAPTER 6: SUMMARY

This project was initiated with the goal of disentangling the complex life histories and behaviors of Canada geese (*Branta canadensis*) with the goal informing management of both goose abundances associated with conflicts and those that provide hunting opportunities around human population centers. While Canada geese are well studied, the behavioral adaptations that have allowed them to thrive across the human-altered landscape are poorly understand. I used data from 201 transmittered Canada geese to quantify trade-offs associated with unique life history strategies during winter and the post-breeding season. In chapter 2, I examined differences in how movements, behaviors, and survival differ related to trade-offs in predation risk and resource availability. I found that rural-wintering geese chose areas that provided access to high-energy waste grain, but increased risk from hunting while geese in urban areas used areas that were safe from hunting, but less access to high-quality forage and increased risk of starvation/exposure during extreme cold periods. These results provide insights into urban-adaptation and how varying selection pressures may influence future distributions in and around urban areas. In Chapter 3, I quantified how the land uses and weather conditions influence the potential risk of goose movements to air traffic. Results demonstrated week effects of temperature, snow, or wind on risk of movements, but rather the juxtaposition of foraging habitats (i.e. railyard, parks) with roosting habitats (i.e. rooftops, waterbodies) had the strongest influence. In Chapter 4, I worked with USDA – Wildlife Services to quantify behavioral responses to targeted, winter harassment. The goal of harassment was to alter the behavioral time budgets by increasing the perceived risk of the site, leading to decreased fitness and emigration from the areas. While harassment did increase the amount of time in alert and flight behaviors, overall site use did not differ from controls and harassed geese returned quickly. Results did demonstrate potential for harassment to incur greater costs at waterbodies and rooftops during extreme cold periods. Lastly, I shifted seasons to study trade-offs associated with molt migration in Chapter 5. Molt migration is a unique phenomenon of failed and non-breeding geese migrating several thousand kilometers to undergo simultaneous, flight feather molt in the subarctic rather than remaining in breeding areas. I examined landscape effects on the propensity of molt migration, trade-offs in foraging environments between the two regions, and survival during the entire period to gauge if urbanization and modern hunting season had altered the selective pressures influencing molt migration. I found decreased probability to molt migrate was associated with waterbodies and that the proportion of failed-breeders migrating varied among breeding areas. Geese molting in the subarctic spent more time foraging and less time in alert behavior compared to geese in temperate regions, even when accounting for increased day lengths. Despite a better-quality foraging environment, molt migrants resumed flight much later. While there is potential for biases in these estimations, we suggest this represents a much lower predation risk rather than insufficient energetic resources to regrow flight feathers. In addition, individual variation from year to year suggests the trait is plastic rather than innate, and that urbanization has made molting areas more available while early hunting season have increased the cost of migration. Overall, Canada geese are an urban adapted species and the various studies I conducted suggest that urban areas provide relatively safe and high-quality areas for geese, and it is likely that urban geese populations will continue to increase in urban areas throughout their range.