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RESEARCH ARTICLE

Survival and habitat selection of Canada Geese during autumn and winter in metropolitan Chicago, USA

Brett E. Dorak,^{1,2} Michael P. Ward,^{1,2} Michael W. Eichholz,^{3#} Brian E. Washburn,^{4#} Timothy P. Lyons,^{1,2#} and Heath M. Hagy^{2,5*}

¹ Department of Natural Resources and Environmental Sciences, University of Illinois at Urbana–Champaign, Urbana, Illinois, USA

² Illinois Natural History Survey, Champaign, Illinois, USA

³ Department of Zoology, Southern Illinois University, Carbondale, Illinois, USA

⁴ USDA Wildlife Services, National Wildlife Research Center, Sandusky, Ohio, USA

⁵ Stephen A. Forbes Biological Station, Frank C. Bellrose Waterfowl Research Center, Havana, Illinois, USA

These authors contributed equally to the paper

* Corresponding author: heath_hagy@fws.gov

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ABSTRACT

Winter distribution and resource use of animals is driven by myriad interacting biotic and abiotic factors. Urban areas provide sanctuaries from hunting for game animals and may have thermal benefits during winter through reduced thermoregulatory costs. We deployed cellular GPS transmitters affixed to neck collars of 41 Canada Geese (*Branta canadensis*) in the Greater Chicago Metropolitan Area (GCMA) of northeastern Illinois, USA, to determine habitat selection and survival during autumn and winter. Canada Geese selected green spaces (59.8%) in greater proportion than available (14%), but they also regularly used industrial urban habitats such as rooftops and rail yards (11.3%), which has not been previously reported. Use of green spaces (–55.8%) decreased and use of industrial urban (+11.4%), riverine (+23.8%), and deep-water habitats (+140.7%) increased as temperatures dropped below the lower critical temperature for Canada Geese (i.e. the temperature at which increased thermoregulatory costs are incurred to maintain core body temperature). Most Canada Geese (85%) remained within the GCMA throughout winter, and none made foraging flights to agricultural fields within or outside of the urban area. Seasonal survival was considerably greater ($S = 1.0$) for geese that remained within the GCMA than those that left ($S = 0.48$) during winter. High survival, use of nontraditional habitats (e.g., green spaces, rooftops, and rail yards), and avoidance of agricultural fields suggests Canada Geese may be minimizing risk rather than maximizing energy intake by using urban areas during winter. Future research should focus on the thermoregulatory and movement strategies employed by geese to survive in urban areas where food resources may be limited. Further, researchers interested in discouraging geese should evaluate their response to harassment when temperatures are below the lower critical temperature.

Keywords: Canada Geese, habitat use and selection, home range, survival, transmitters, urban

Supervivencia y selección de hábitat de *Branta canadensis* durante otoño e invierno en el área metropolitana de Chicago, EEUU

RESUMEN

La distribución invernal y el uso de recursos de los animales están impulsados por un conjunto numeroso de factores bióticos y abióticos interactuantes. Las áreas urbanas brindan santuarios sin cacería para los animales de caza y pueden tener beneficios climáticos durante el invierno mediante la reducción de costos de termorregulación. Colocamos transmisores GPS de celular fijados en el cuello por medio de collares a 41 individuos de *Branta canadensis* en el Gran Área Metropolitana de Chicago (GAMC) del noroeste de Illinois, EEUU para determinar la selección de hábitat y la supervivencia durante otoño e invierno. La especie seleccionó espacios verdes (59.8%) en mayor proporción que los disponibles (14%), pero también usó regularmente hábitats urbanos industriales como techos y descampados del ferrocarril (11.3%), lo que no ha sido reportado con anterioridad. El uso de espacios verdes (–55.8%) disminuyó y el uso de hábitats industriales urbanos, (+11.4%), fluviales (+23.8%) y de aguas profundas (+140.7%) aumentó a medida que las temperaturas cayeron por debajo de la temperatura crítica inferior para *B. canadensis* (i.e. la temperatura a la cual se incurren en mayores costos de termorregulación para mantener la temperatura corporal central). La mayoría de los individuos de *B. canadensis* (85%) permaneció dentro del GAMC a lo largo del invierno y ninguno realizó vuelos de forrajeo a campos agrícolas dentro o fuera del área urbana. La supervivencia estacional fue considerablemente mayor ($S = 1.0$) para los individuos que permanecieron dentro del GAMC que para los que se fueron ($S = 0.48$) durante el invierno. La alta supervivencia, el uso de hábitats no tradicionales (e.g., espacios verdes, techos y descampados del ferrocarril) y la elusión de los campos agrícolas sugiere que *B. canadensis* puede estar minimizando los riesgos más que

maximizando el consumo de energía mediante el uso de áreas urbanas durante el invierno. Futuras investigaciones deberían enfocarse en las estrategias de termorregulación y de movimiento utilizadas por *B. canadensis* para sobrevivir en las áreas urbanas donde los recursos alimenticios pueden ser limitados. Más aún, los investigadores interesados en desalentar a los individuos de *B. canadensis* deberían evaluar sus respuestas al acoso cuando las temperaturas están por debajo de la temperatura crítica inferior.

Palabras clave: *B. canadensis*, rango de hogar, supervivencia, transmisores, urbano, uso y selección de hábitat

INTRODUCTION

The winter distribution of animals is driven by effects of multiple and interacting environmental factors (Brown 1984, Brown et al. 1995, Canterbury 2002), including average minimum temperature isotherms (Root 1988a,b). Decreasing temperatures may increase energy demands to boost metabolic rates concurrent with food resources becoming limited or unavailable for some migratory species during winter (Baldassarre and Bolen 2006). However, a number of adaptations may allow some species to overcome factors limiting their northern distributions and expand their wintering ranges. For example, nine-banded armadillos (*Dasypus novemcinctus*) expanded their range northward over the past several decades through selection of thermally beneficial den sites and behavioral adaptations to minimize heat loss (Bond et al. 2000, Eichler and Gaudin 2011). Gray-headed flying foxes (*Pteropus poliocephalus*) have expanded their winter range by utilizing urban areas that provide warmer winter conditions than rural areas (Parris and Hazell 2005). Exploitation of supplementary food resources related to human activities (e.g., bird feeders, agricultural waste grain) has allowed northward expansion of winter ranges of many bird species (Siriwardena et al. 2007, Zuckerberg et al. 2011). Further, an increasingly warming climate has shifted wintering ranges of many birds poleward, although variation among species and interacting factors affecting habitat suitability make predicting these shifts difficult (Princé and Zuckerberg 2015, Williams et al. 2015).

Some bird species have shifted their wintering range northward by taking advantage of conditions in urban areas (Zuckerberg et al. 2011). Urban areas at the northern edge of a migratory species' wintering range can provide habitat resources (e.g., food, living space, and water), sanctuary from predators, and reduced energy expenditure associated with reduced migration distance (Conover and Chasko 1985, Anderies et al. 2007, Zuckerberg et al. 2011). Urban areas may provide sanctuary from hunting for game species and may be warmer than the surrounding rural landscape (Oke 1973, Grimmond 2007). Such northward shifts in wintering ranges and adaptation to urban areas have been documented for several species of waterfowl, including Canada Geese (*Branta canadensis*; Gates et al. 2001, Baldassarre and Bolen 2006).

Use of urban areas by Canada Geese during the breeding period can be advantageous (e.g., increased clutch size, nest success, and annual survival compared to use of rural areas; Raveling 1981, Paine et al. 2003, Balkcom 2010), but few benefits have been documented outside of the breeding season. Waterfowl select habitats during non-breeding periods that provide the resources required to maintain a favorable energy balance and maximize survival (Gates et al. 2001, Baldassarre and Bolen 2006). Waste grain in agricultural fields can increase food availability during late autumn and winter, and urban areas may provide thermal benefits allowing birds to maintain positive energy balances in more northerly areas (Jokimäki et al. 1996, La Sorte and Thompson 2007). Urban areas also attract migrating Canada Geese from subarctic-breeding populations (*B. c. interior*), which sometimes aggregate during autumn and winter with temperate-breeding geese (*B. c. maxima*) in urban areas, creating large concentrations and potential conflicts with humans (Conover and Chasko 1985, Smith et al. 1999). For Canada Geese, mixing of populations with different population management objectives is one of several challenges for managers in urban areas (Coluccy et al. 2001, Scribner et al. 2003, United States Fish and Wildlife Service 2015). Hunting is an important population management tool that can be used to reduce overabundant populations and wildlife–human conflicts (Conover 2001). However, regulations preventing hunting in urban areas can create sanctuaries, increasing potential wildlife–human conflicts and limiting management options.

We studied Canada Geese wintering in or migrating through a large urban area in the midwestern USA during late autumn and winter to better understand habitat use and selection, survival within and outside of the urban areas, and movements to agricultural fields where there was potential for mortality due to hunting. Specifically, our objectives were to (1) determine core use areas and overall home ranges during winter, (2) identify habitat use and selection, (3) estimate survival within and outside of urban areas and identify cause of mortality, and (4) describe migration phenology in relation to hunting. We predicted that Canada Geese would use large green spaces and deep-water areas for roosting and conduct daily flights to agricultural fields to obtain food and maintain energy reserves (Conover and Chasko 1985, Smith et al. 1999). We predicted that reduced risk of

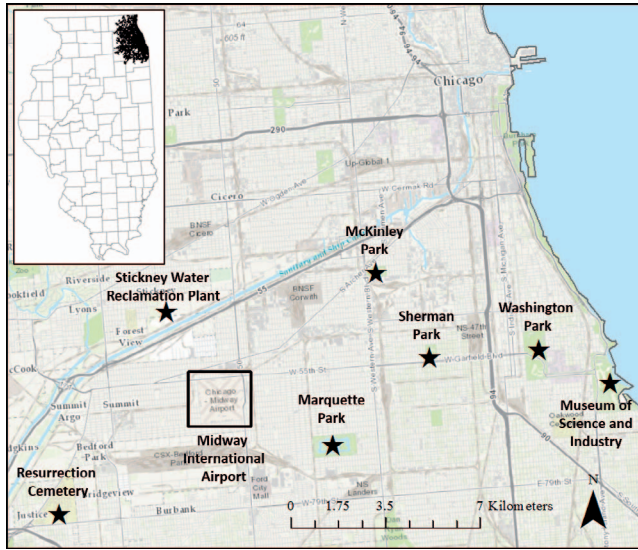


FIGURE 1. Main capture locations ($n = 7$) of Canada Geese (*Branta canadensis*) in relation to Midway International Airport within the Greater Chicago Metropolitan Area, Illinois, USA (inset).

mortality from hunting would increase survival of Canada Geese in urban areas compared to those that used rural areas (Balkcom 2010).

METHODS

Study Area

Canada Geese (hereafter, geese) were captured in the Greater Chicago Metropolitan Area (GCMA; $\sim 915 \text{ km}^2$) in northeastern Illinois, USA, during late autumn and winter (Figure 1). The GCMA included portions of Cook, Du Page, and Will counties and was heavily urbanized with some agricultural fields present within and near city limits (United States Department of Agriculture 2015). Agricultural fields of primarily corn and soybeans were located within 10–30 km of capture and marking locations of geese. The GCMA averages 43 days annually with temperatures dropping below 0°C and 7 days below -18°C . November has an average high of 9°C and a low of 0°C , December has an average high temperature of 2°C with a low of -6°C , January has an average high of 0°C and a low of -9°C , and February has an average high of 2°C and low of -7°C (National Oceanic and Atmospheric Administration 2015a). Chicago averages 93 cm of snowfall annually (National Oceanic and Atmospheric Administration 2015a). The GCMA has an estimated temperate-breeding Canada Goose population exceeding 30,000 individuals (Paine et al. 2003) and a human population of 9.4 million in Chicago and surrounding suburbs (United States Census Bureau 2013; Figure 1).

Field Methods

During mid-November through late February 2014–2016, we captured and attached transmitters to 41 geese within the GCMA. Our research also involved goose–aircraft collision risk, so we focused capture efforts where geese concentrated in fall and winter near Midway International Airport ($41^\circ 47' 6.5'' \text{N}$, $87^\circ 45' 6'' \text{W}$), including large parks, cemeteries, and the Stickney Water Reclamation Plant (Figure 1). We used rocket nets, cast nets, and small animal net guns (Wildlife Capture Services, Flagstaff, Arizona, USA) to capture geese. We determined sex and age using cloacal inversion and feather characteristics. We took standard morphological measurements (mass, skull length, culmen length, tarsus length) using a caliper (nearest 0.1 mm) and a digital scale (nearest 0.01 kg). To each goose, we attached an aluminum tarsal band and a GPS transmitter affixed to a white plastic waterfowl neck collar with black alphanumeric codes.

Transmitters ($n = 10$ in 2014–2015 and $n = 31$ in 2015–2016) were deployed during 4 time periods each year (mid-November, early December, mid-December, and early January) and at 7 different capture locations to account for temporal spatial variation in migration chronologies of geese. Transmitters recovered from hunters ($n = 3$) were redeployed during late February. Transmitters included solar-powered GPS units (Cellular Tracking Technologies, Somerset, Pennsylvania, USA), which operated on the global system for mobile communications network and were configured to acquire a GPS location once per hour. Generation 2 models were used during 2014–2015 ($\bar{x} = 69.7$ grams, $\text{SE} = 0.2$) and Generation 3 models were used during 2015–2016 ($\bar{x} = 62.2$ grams, $\text{SE} = 0.2$). Transmitters were $< 2\%$ of the body mass of captured geese ($\bar{x} = 4,713$ grams, $\text{SE} = 10.6$).

Data Analysis

We removed locations from the day of capture from analysis, except for survival analysis, to minimize potential influences of capture on movements and habitat use. Transmitters required a once-weekly cellular connection to program their duty cycle to the standardized rate of 1 location hr^{-1} for the entire day and upload locations to an accessible database. Data from transmitters with less than 10 days of data collection were removed from analysis ($n = 1$ in 2014–2015 and $n = 4$ in 2015–2016). Locations with only one satellite fix or with a horizontal dilution of precision value above 5 were removed because GPS coordinates were either not obtained or they had extremely low accuracy (Cellular Tracking Technologies 2015). All analyses were performed using R Version 3.1.3 (R Core Team 2015).

Core use areas and overall home range analysis. To characterize spatial use of the GCMA, we estimated core use areas (50% utilization distribution [UD; km^2]) and

overall home ranges (95% UD) using a dynamic Brownian bridge movement model (dBBMM) and the `adehabitatHR`, `rgdall`, and `move` packages in R (Calenge 2006, Bivand et al. 2015, Kranstauber and Smolla 2015). We estimated core use areas to target specific areas used by geese during winter where management actions may need to focus and overall home ranges to represent the majority of spatial use of geese during winter. A dBBMM is a more appropriate method to estimate spatial use than kernel density estimates because it incorporates the temporal structure of the locations to estimate potential trajectories of the segments between those locations using a maximum likelihood function (Horne et al. 2007, Kranstauber et al. 2012) and accounts for nonindependence of systematically collected data (Worton 1989, Fieberg et al. 2010). If a goose emigrated from the GCMA, all locations from migration date forward were removed from core use area and overall home range analysis. All locations obtained from November 15 through February 28 of both years were used to calculate core use areas and overall home range. We also divided autumn and winter into 3 distinct periods: early winter (November 15–December 31), mid-winter (January 1–January 31), and late winter (February 1–February 28; Raveling et al. 1972). We used mean imputation to fill in missing data for time period analysis due to temporal spacing of transmitter deployment and migration, which simultaneously retained important core use area and overall home range information (Zar 2010). Transmitters ($n = 6$) from 2014–2015 that were present in the GCMA during 2015–2016 were not used for analysis during the second year because of limited locations with poor temporal spacing (i.e. weeks between locations) and low accuracy. In separate linear mixed models (R; `lme` function in the `nlme` package; Pinheiro et al. 2016), we modeled the response variables of core use area size and overall home range size as functions of time period (i.e. early, mid-, and late winter) with location of capture and year as random effects. We inspected residuals to ensure a normal distribution and designated $\alpha = 0.05$.

Resource selection. To identify habitat use and selection, we plotted all locations of geese on Google Earth Pro using the `rgdal` and `adehabitatLT` packages in R (Calenge 2006, Bivand et al. 2015). We defined habitat as the resources and other conditions present at a transmitter location where geese were present that could influence occupancy and established 5 categories of habitat which we assumed were independent (Hall et al. 1997). Habitats were classified manually by visually assigning green space, riverine, deep-water, industrial urban, or residential identifiers to each use location or random point using available aerial imagery and ancillary information. Green spaces were typically parks, cemeteries, small grass lawns and areas between buildings, and other areas primarily in grass cover that contained a

mixture of ponds, trees and shrubs, large sports fields, and golf courses within their boundaries (Dorak 2016). Riverine areas consisted of the open water, sand bars, mud flats, and other various vegetation and cover types within and immediately adjacent to the main river channel of the Des Plaines River and Calumet River systems. Deep-water areas included the Chicago Sanitary and Ship Canal, which had steep concrete walls and warm-water discharges along the canal corridor, and the Stickney Water Reclamation Plant. We classified the entire Stickney Water Reclamation Plant as deep-water because most anecdotal observations of geese there were in or immediately adjacent to settling ponds; however, this area contained developed areas, green spaces, and deep-water areas in a highly interspersed arrangement. Industrial urban habitat included flat rooftops, which were typically large flat industrial buildings and retail stores, and adjacent rail yards composed of large complex series of railroad tracks where railcars were loaded, unloaded, and stored. Residential areas were typically houses and developments, parking lots, and miscellaneous other land uses occurring in residential areas.

To determine habitat availability for comparison with use locations, we used a random number generator to create 500 locations within the study area and assigned each point to a habitat as described previously. We compared habitat use and availability across the entire autumn and winter period for both years and when the temperature dropped below the theoretical lower critical temperature (LCT) for Canada Geese (-6°C ; Calder and King 1974, Alisauskas and Ankney 1992). The LCT is the ambient temperature below which an animal must increase its metabolic rate and potentially increase its metabolization of endogenous resources to maintain body temperature; it is estimated using ratios of body mass to body temperature, and surface area and plumage (Alisauskas and Ankney 1992, Dawson and O'Connor 1996). We acknowledge that the LCT likely varies by individual and over time through a complex interplay of physiological, morphological, and behavioral characteristics that may also be related to individual habitats or physical characteristics of sites (McKinney and McWilliams 2005, Livolsi et al. 2015). Although we acknowledge the inherent variability among individuals, habitats, and conditions, we believe the selected LCT represented an approximate temperature threshold, which likely influenced thermoregulatory costs of geese in the GCMA during winter (Alisauskas and Ankney 1992, Gates et al. 2001). Additionally, we compared habitat use across the 3 time periods (early, mid-, and late winter). We determined the phenology of spring and autumn migration by noting when a marked individual emigrated from the GCMA and did not return for >30 days and when an individual

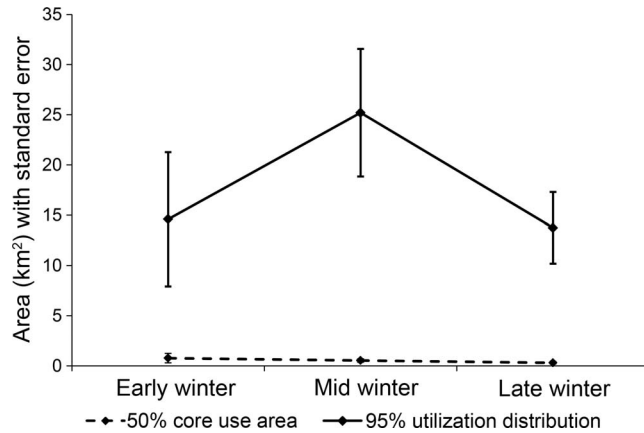


FIGURE 2. Change in 50% core use areas and 95% utilization distribution estimates with standard error bars across 3 time periods for Canada Geese (*Branta canadensis*) during autumn and winter 2014–2016 in the Greater Chicago Metropolitan Area, Illinois, USA.

immigrated into the GCMA after being gone for a period >30 days.

We used a resource selection function (RSF) with an exponential link to describe habitat selection ($w(x)$; McDonald 2013). A $w(x) > 1$ represented selection, $w(x) = 1$ represented habitat use in proportion to availability, and $w(x) < 1$ represented habitat avoidance. We analyzed the RSF as a function of habitat (i.e. green space, riverine, deep-water, industrial urban, and residential), time of day (i.e. diurnal or nocturnal), an interaction of habitat and time of day, and snow depth (cm). In a separate analysis, we analyzed RSF as a function of habitat, time of day, an interaction of habitat and time of day, and minimum daily temperature ($^{\circ}\text{C}$; Manly et al. 2007, McDonald 2013). We set the diurnal time period to 0500–1900 to include crepuscular movements and the nocturnal time period 1901–0459 to exclude crepuscular movements. We used a quadratic term because we expected that there would be a threshold in both snow depth and minimum daily temperature where habitat use would cease. Weather data were obtained from the weather station at Midway International Airport (Weather Underground 2016). We plotted the parameter estimates to make predictions of RSF within the range of minimum daily temperatures and snow depth data (Neter et al. 1996) and used a smoothing factor to interpolate the predicted RSF between large gaps in snow depth data.

Survival. Winter survival (S) with 95% confidence intervals (CI) was calculated for the time period November 15 through February 28, 2014–2016, using the Known-Fate model in Program MARK because transmitters provided fine-scale data and status (i.e. alive or dead) of all geese was known (Cooch and White 2006). We assumed that all transmitted geese were independent and because of spatial variation in transmitter deployment, we used a staggered

entry design. We divided time intervals into 3 periods (i.e. early, mid-, late winter) and calculated a body condition index (BCI) following Arsnö et al. (2011; Devries et al. 2008). We conducted an ordinary least-squares regression of adjusted mass and an index of body size (principal component 1 of skull, culmen, and tarsus length) and then divided the residuals from the predicted mass to create a condition score for each bird. We created 6 models to evaluate the effects of BCI, group (remained in GCMA or emigrated from GCMA), and time period on survival and ranked models using Akaike's information criterion adjusted for a small sample size (AIC_c ; Burnham and Anderson 2002). We summed model weights (w_i) of top models in which a variable appeared to determine relative variable importance.

RESULTS

Data collected from winter 2014–2015 were limited due to battery recharging issues with Generation 2 transmitters ($n = 9$ transmitters, $\bar{x} = 10.5$ locations per transmitter per day, $\text{SE} = 2.9$, range 2.0–26.4). Generation 3 transmitters deployed in winter 2015–2016 provided increased battery life and efficiency ($n = 27$ transmitters, $\bar{x} = 20.8$ locations per transmitter per day, $\text{SE} = 0.4$, range 15.4–23.3). Time between locations was greater for Generation 2 transmitters in 2014–2015 ($\bar{x} = 274.1$ min, $\text{SE} = 75.2$) than Generation 3 transmitters in 2015–2016 ($\bar{x} = 70.1$ min, $\text{SE} = 1.3$). We obtained 3,496 usable locations in 2014–2015 and 35,896 usable locations in 2015–2016.

Neither core use areas ($\bar{x} = 0.7 \text{ km}^2$, $\text{SE} = 0.3$; $F_{1,95} = 1.3$, $P = 0.26$) nor overall home ranges ($\bar{x} = 24.5 \text{ km}^2$, $\text{SE} = 5.2$; $F_{1,95} = 0.37$, $P = 0.54$) of geese ($n = 36$) varied by time period (Figure 2). Geese selected green space (59.8%), deep-water (15.2%), industrial urban (11.3%), and riverine (8.1%) habitats in greater proportion than their availability ($P \leq 0.05$; Table 1). When temperatures dropped below LCT, geese increased use of deep-water (+140.7%) and riverine habitats (+23.8%) and decreased use of green space (–55.8%; Table 1). Green space was used more than any other habitat and selected across time periods, but proportional use declined from early winter (80.4%) to mid-winter (52.2%) and late winter time periods (52.8%; Table 2). Geese increased use of deep-water habitat from 1.9% in early winter to 21.8% during mid-winter and 18.2% in late winter (Table 2). Similarly, geese increased use of industrial urban habitats from early winter (6.8%) to mid-winter (11.3%) and late winter (14.2%; Table 2).

Snow depth ($F_{1, 78,728} = 119.2$, $P < 0.01$), minimum daily temperature ($F_{1, 78,728} = 183.6$, $P < 0.01$), time of day ($F_{1, 78,728} = 9.2$, $P < 0.01$), and all interactions ($P < 0.01$) affected habitat use. The resource selection function (RSF) was above 1 for every habitat except residential, indicating that geese selected green space, industrial urban, riverine, and deep-water habitats but avoided residential habitats

TABLE 1. Percentage of available habitat (Available), percentage of locations occurring in each habitat across all temperatures (All Locations), and percentage of locations occurring in each habitat use when temperature was above (Above LCT) and below (Below LCT) the lower critical temperature (LCT; -6°C) for Canada Geese in the Greater Chicago Metropolitan Area, Illinois, USA, during autumn and winter 2014–2016.

Habitat	Available	2014–2015			2015–2016			Total		
		All locations	Above LCT	Below LCT	All locations	Above LCT	Below LCT	All locations	Above LCT	Below LCT
Green space	14.0%	30.1%	41.6%	18.4%	62.7%	67.4%	40.8%	59.8%	66.0%	36.0%
Riverine	2.2%	14.1%	12.6%	15.6%	7.6%	6.6%	12.0%	8.1%	6.9%	12.8%
Deep water	1.0%	20.9%	12.3%	29.6%	14.6%	9.1%	40.1%	15.2%	9.3%	37.8%
Industrial urban	8.0%	30.6%	29.0%	32.3%	9.4%	10.5%	4.4%	11.3%	11.5%	10.4%
Residential	74.8%	4.3%	4.5%	4.1%	5.7%	6.4%	2.7%	5.6%	6.3%	3.0%

(Figures 3 and 4). As snow depth increased, selection increased for industrial urban, riverine, and deep-water habitats, while selection for green space decreased (Figure 4). Geese tended to avoid residential habitat across almost all snow depths and minimum daily temperature ranges (Figures 3 and 4). Geese selected riverine and deep-water habitats more often during nocturnal than diurnal periods (Figures 3 and 4). As minimum daily temperature decreased, selection of riverine and deep-water habitats increased. Selection of industrial urban habitats increased as temperature decreased until approximately -5°C (Figure 3). Use of green space declined as temperature decreased until -20°C (Figure 3). Notably, we recorded no use of agricultural fields within or outside of the GCMA by geese that remained within the GCMA during winter.

Winter survival was 100% for geese using the GCMA ($n = 35$) and 48% (95% CI range = 16–82%; $n = 6$) for geese that emigrated from the GCMA. Although BCI was related negatively to survival, confidence intervals overlapped zero indicating a weak effect. Weekly survival for emigrating geese was 95% (95% CI range = 86–98%) across the entire winter period. The top two models explaining survival ($\sum w_i = 0.9$) included time period (Table 3). Weekly survival was 100% during early winter, 85% (95% CI range = 62–95%) during mid-winter, and 100% during late winter. We documented 3 direct mortalities from hunting during the mid-winter time period. Mortalities occurred an average of 8 days (range 2–

16) after the geese left the GCMA. Hunting mortalities occurred in northwest Indiana, southwest Illinois, and northwest Tennessee. The majority of geese (85%) fitted with transmitters never migrated south from the GCMA. During 2014–2015, 3 of 10 geese left the GCMA. One goose left on November 30, 2014, and 2 left on January 4, 2015. During 2015–2016, 3 of the 31 geese emigrated south from the GCMA between December 30, 2015, and January 13, 2016.

In 2015, most geese ($n = 7$) initiated spring migration during March 11–16 while 2 geese remained in the GCMA for the breeding season. During 2016, most geese ($n = 15$) initiated spring migration during February 20 through April 1, although a larger percentage (48%; $n = 14$) remained within the GCMA during spring and summer 2016 than in 2015. Geese showed high fidelity to the GCMA across seasons and years. All geese with active transmitters from winter 2014–2015 ($n = 7$) returned to or remained within the GCMA during the autumn of 2015 and 17 of 21 geese with active transmitters from winter 2015–2016 remained in or returned to the GCMA during the autumn of 2016. Return flights to the GCMA ranged from August through November in 2015 and from August through October in 2016. All 6 geese with active transmitters that were marked during winter 2014–2015 returned to or stayed within the GCMA during the autumn of 2016. We were unable to assign breeding locations to geese that left the GCMA.

TABLE 2. Percentage of available habitat (Available), percentage of locations occurring in each habitat across all temperatures (All Locations), and percentage of locations occurring in each habitat use when temperature was below the lower critical temperature (Below LCT; -6°C) for Canada Geese in the Greater Chicago Metropolitan Area, Illinois, USA, during 3 periods of the autumn and winter 2014–2016.

Habitat	Available	Early winter		Mid-winter		Late winter	
		All locations	Below LCT	All locations	Below LCT	All locations	Below LCT
Green space	14.0%	80.4%	84.7%	52.2%	38.7%	52.8%	30.6%
Riverine	2.2%	3.5%	7.3%	11.4%	11.8%	8.4%	14.0%
Deep water	1.0%	1.9%	0.7%	21.8%	41.7%	18.2%	37.5%
Industrial urban	8.0%	6.8%	0.3%	11.3%	6.2%	14.2%	14.2%
Residential	74.8%	7.4%	7.0%	3.3%	1.6%	6.4%	3.7%

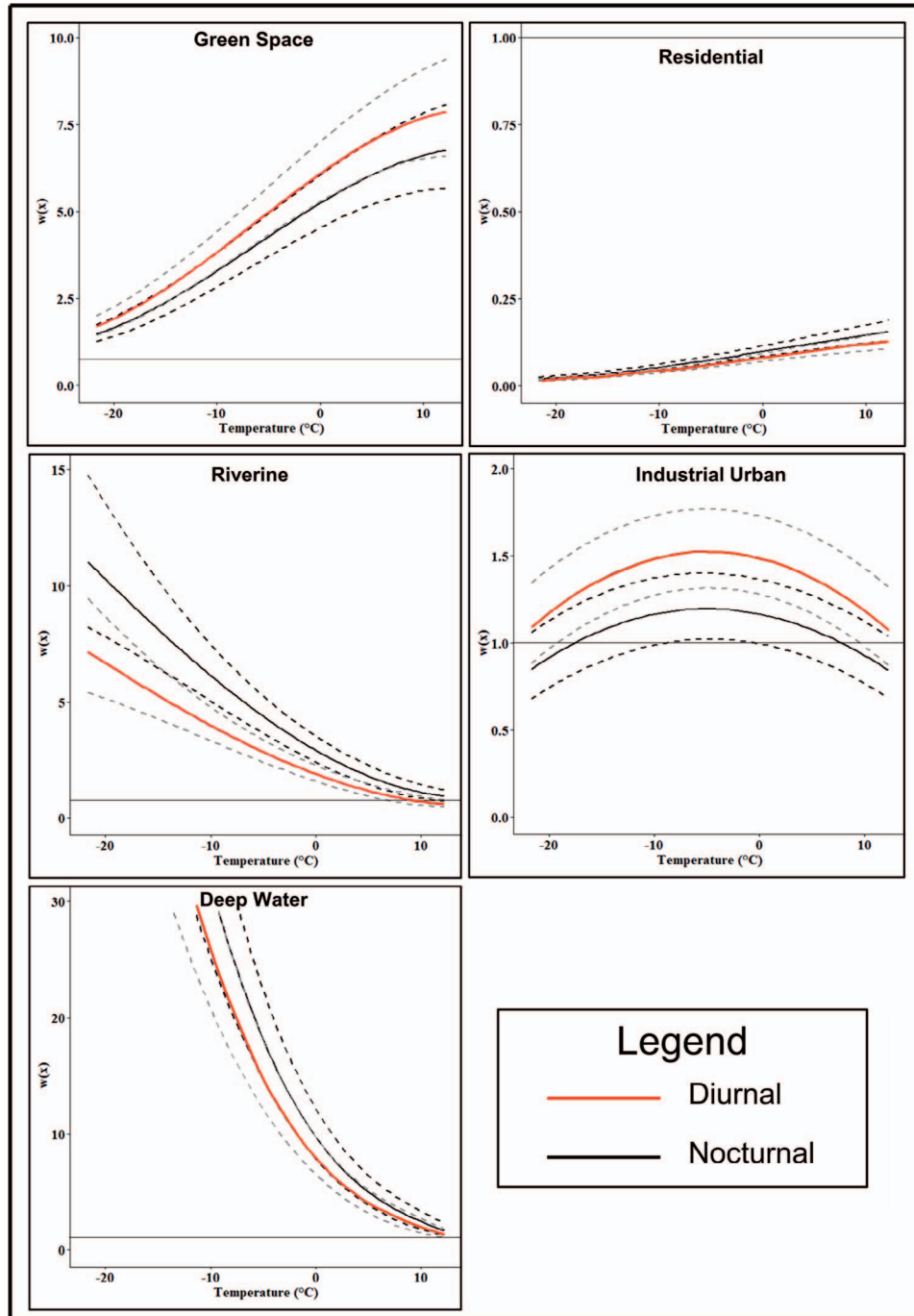


FIGURE 3. Resource selection function $w(x)$ with 95% confidence intervals (broken lines) for habitats used by Canada Geese (*Branta canadensis*) relative to minimum daily temperatures (°C) from November 2015 through February 2016 in the Greater Chicago Metropolitan Area, Illinois, USA. A value of 1 (designated by horizontal line) indicates no selection or avoidance.

DISCUSSION

Our results suggest that the GCMA has become a large sanctuary for Canada Geese, but the expansion of agriculture and availability of open water may not be the most important environmental factors behind the north-

erly shift in wintering ranges of geese (Baldassarre 2014, Dorak 2016). Canada Geese within the GCMA had relatively small core use areas and most did not leave the urban area during winter. Although agricultural fields were present within and near the GCMA (~10 km from core study area), within reasonable daily flight distances, geese

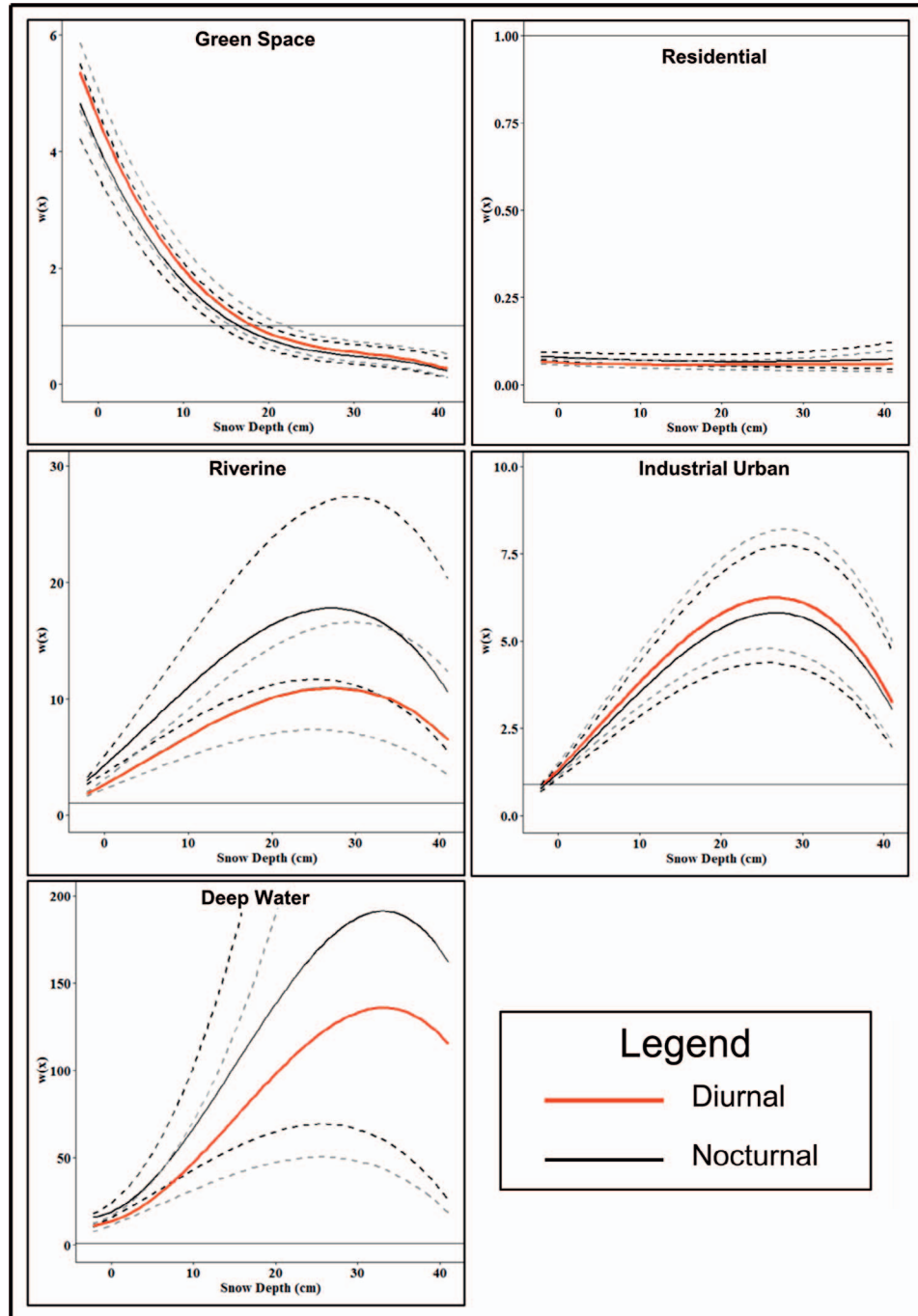


FIGURE 4. Estimated resource selection function $w(x)$ with 95% confidence intervals (broken lines) for habitats used by Canada Geese (*Branta canadensis*) relative to snow depth (cm) from November 2015 through February 2016 in the Greater Chicago Metropolitan Area, Illinois, USA. A value of 1 (designated by horizontal line) indicates no selection or avoidance.

did not make foraging flights to agricultural fields during winter. Accordingly, geese that remained within the GCMA during winter had high survival, but those that left the GCMA had high mortality. Survival rates were greater for geese that remained within the GCMA and much lower for geese that left the urban area than

previously reported during open hunting seasons (Hestbeck and Malecki 1989, Groepper et al. 2008, Rutledge et al. 2015). Sanctuary may have been a more important selective pressure than high-quality forage during winter for geese in our study area (Luukkonen et al. 2008, Balkcom 2010, Pilotte et al. 2014).

TABLE 3. Results of linear models evaluating the effects of period (early winter, mid-winter, late winter), group (stayed or emigrated from the Greater Chicago Metropolitan Area), and body condition index (BCI) on survival (S) of Canada Geese (*Branta canadensis*) captured and transmittered during autumn and winter 2014–2016 in the Greater Chicago Metropolitan Area, Illinois, USA, with Akaike's Information Criterion adjusted for sample size AIC_c , number of parameters (k), difference in AIC_c with top model (ΔAIC_c), model weight (w_i), and deviance. Lowest AIC_c value was 22.5.

Model	k	ΔAIC_c	w_i	Deviance
S(Period)+(Group)+(BCI)	4	0.0	0.5	14.4
S(Period)	3	0.5	0.4	16.9
S(Group)	2	5.7	0.0	24.1
S(Constant)	1	14.5	0.0	35.0
S(BCI)	2	15.3	0.0	33.7

Geese used a mix of habitats in the GCMA, including many that were nontraditional (e.g., water treatment facilities, deep-water areas within shipping canals) and had not been previously documented (e.g., rooftops, rail yards). Geese selected green space, riverine, and deep-water habitats and avoided residential habitats across both years of our study. Despite extensive use of these novel industrial urban habitats, use was nearly equivocal with availability across years. Large green spaces were selected across all time periods and years, had the greatest proportional use among habitats, and likely provided necessary food, water, and sanctuary needed by geese across most temperature ranges. However, when snow depth increased and temperatures decreased, geese reduced their use of green spaces and increased use of industrial urban, deep-water, and riverine habitats. This change may have been in response to the reduced availability of interspersed open water and/or forage within green spaces when covered by ice and snow. There were likely physiological benefits of geese using industrial urban and deep-water habitats during cold weather associated with energy conservation strategies (Gates et al. 2001).

Industrial urban, deep-water, and riverine habitats perhaps provided thermal benefits, reduced disturbance, and even food resources needed during harsh weather conditions. Rooftops may have provided thermoregulatory benefits associated with warmer ambient temperatures or sanctuary from disturbances and predators, which may have reduced energy expenditures. Although most anecdotal observations of geese foraging occurred in green spaces, we observed geese foraging in rail yards and speculate that spilled grain from rail cars or other foods may have been available. Deep-water and riverine habitat may have provided open water for safe roosting locations, which enhanced energy conservation. The ability of Canada Geese to use these novel habitats in urban areas

illustrates a remarkable behavioral adaptability to improve survival during winter (Gates et al. 2001).

Patterns of habitat use differed across years of our study in response to different weather conditions. The winter of 2014–2015 was 2 °C colder and had 32 cm more snow accumulation than an average winter, compared to 2015–2016, which was 3 °C warmer with 30 cm less snow than average (National Oceanic and Atmospheric Administration 2015b, 2016). Harsh winter conditions during 2014–2015 appear to have resulted in geese reducing their use of green spaces and increasing the use of industrial urban habitats relative to the milder winter of 2015–2016. Use of deep-water and riverine habitat had a larger proportional increase when temperatures were below the LCT in the milder winter of 2015–2016 than in the colder winter of 2014–2015. Use of industrial urban habitats was substantially greater during the colder winter of 2014–2015, regardless of the LCT. Changing patterns of habitat use in urban areas in response to winter severity may indicate that energetic strategies were influenced by behavioral adaptations to maximize survival rather than driven solely by endogenous physiological rhythms (Gates et al. 2001).

We found further evidence of plasticity in the life-history strategies employed by geese in our study (Ankney 1996). During spring and summer following transmitter attachment, a portion of marked geese remained within the GCMA and other temperate areas, but others migrated to subarctic areas during breeding or molting periods (Dorak 2016). Migration timing and wintering locations of subarctic-breeding Canada Geese have changed concurrent with land use patterns, hunting regimes, and abundance of temperate-breeding geese (Gates et al. 2001, Scribner et al. 2003). For example, the Mississippi Valley population of subarctic-breeding Canada Geese (*B. c. interior*) shifted their wintering range northward from Mississippi and Arkansas to southern Illinois and north-west Kentucky in the mid-twentieth century. During 1980–2000, this population further shifted its wintering range northward to northern Illinois and southern Wisconsin (Craven et al. 1986, Gates et al. 2001, Arctic Goose Joint Venture 2013). Wintering at more northerly latitudes minimizes spring migration distances, allowing geese to arrive at breeding grounds earlier but has energetic tradeoffs (Alerstam and Lindstrom 1990).

Geese wintering in northern areas with cold temperatures must forage daily or arrive with sufficiently large energy reserves to ensure adequate body condition is maintained. Geese captured in the GCMA were 11–13% heavier than geese captured near Rochester, Minnesota (McLandress and Raveling 1981), and 18–20% larger than those wintering in southern Illinois and east-central Wisconsin (Gates et al. 2001). While diet information for geese in the GCMA is not available, we observed geese primarily foraging on dead grass during winter, which was

likely a low-quality forage compared to agricultural grains (Kaminski et al. 2003), and we suspect that geese arrive in the GCMA during fall with large energy reserves to offset poor foraging conditions during winter. Geese that left the GCMA during winter may have been nutritionally stressed and the risk from hunting may have been outweighed by the risk of staying within the GCMA and facing continued declines in body condition. Additionally, geese may have exploited different types of food resources to offset reduced availability of waste grain within urban areas, similar to the behavioral plasticity exhibited by Atlantic Brant (*Branta bernicla hrota*) on the Atlantic Coast (Ladin et al. 2011). Historically, geese have met increased energy requirements by feeding on waste grain in agricultural areas, but hunting pressure and increasing urbanization have created vast sanctuaries where both temperate- and subarctic-breeding geese congregate in winter to maximize survival (Gates et al. 2001).

Interestingly, migration phenology of subarctic-breeding Canada Geese in our study also appears to be timed so that geese reach the GCMA before most hunting seasons open in the fall. Autumn migration of geese returning to the GCMA occurred earlier than other studies in the Midwest (Wege and Raveling 1983, Luukkonen et al. 2008). Approximately 70% of our transmittered geese returned to the GCMA prior to open hunting seasons. Moreover, 85% of the individuals marked in this study never left the GCMA during winter when hunting seasons were open. Increased hunting pressure outside of urban areas likely created a strong selection pressure for geese to remain in urban areas (Lima and Dill 1990). Given small home ranges and high survival rates in urban areas closed to hunting, management of goose populations in the GCMA using hunting may be challenging, as has been noted in other northern temperate areas (Luukkonen et al. 2008, Beaumont et al. 2013, Pilotte et al. 2014).

Dense concentrations of geese in urban areas can pose threats to humans, including contamination of water sources (Allan et al. 1995), aggressive behavior toward humans (Smith et al. 1999), disease transmission (Smith et al. 1999, Kullas et al. 2002), and strikes with aircraft (Dolbeer et al. 2000). Geese are the largest bird commonly struck by aircraft in North America and were responsible for 1,403 recorded bird strikes to civil aircraft from 1990 to 2012 (Dolbeer and Eschenfelder 2003, Dolbeer et al. 2014). Noteworthy goose-aircraft strikes include the destruction of a \$190 million U.S. Air Force aircraft, which resulted in 24 human deaths (Dolbeer et al. 2000, Richardson and West 2000) and U.S. Airways Flight 1549 that crash-landed in the Hudson River in New York after striking multiple subarctic-breeding Canada Geese (Marra et al. 2009). Thus, geese can pose risks to human health and safety in urban areas, especially during winter when large flocks congregate around limited resources and there is a strong

disincentive (i.e. lower survival probability) for emigration outside of the city.

Given the strategy possibly employed by geese in the GCMA to maximize energy conservation and minimize foraging in risky areas, we suggest that managers consider harassment during cold winter weather conditions when geese are below their LCT and energetic costs of moving following disturbances could affect survival. Harassment of geese during cold periods may “push” geese to the point where they have to choose to either move out of the area to find additional food or potentially risk death due to increased energy demands. However, we acknowledge the logistical and social challenges related to harassment of geese in urban areas; population management outside of winter may be necessary to reduce human-wildlife conflicts. Future research should focus on the thermoregulatory and movement strategies employed by geese in urban areas where food resources are likely limited.

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