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**Ryan J. Askren**

ryanaskren@gmail.com

University of Illinois at Urbana-Champaign, Illinois Natural History Survey

**Mike W. Eichholz**

Southern Illinois University Carbondale

**Christopher M. Sharp**

Environment and Climate Change Canada

**Auriel M. V. Fournier**

Forbes Biological Station, Illinois Natural History Survey, University of Illinois Urbana- Champaign

**Jay A. VonBank**

Delta Waterfowl Foundation

**Mitch D. Weegman**

University of Saskatchewan

**Heath M. Hagy**

National Wildlife Refuge System

**Michael P. Ward**

University of Illinois at Urbana-Champaign, Illinois Natural History Survey

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# DRIVERS AND SURVIVAL CONSEQUENCES OF MOLT MIGRATION IN TEMPERATE-BREEDING CANADA GEESE

**Ryan J. Askren[1*], Mike W. Eichholz[2], Christopher M. Sharp[3], Auriel M. V. Fournier[4], Jay A. VonBank[5], Mitch D. Weegman[6], Heath M. Hagy[7], and Michael P. Ward[1,4]**

[1] University of Illinois at Urbana-Champaign, Department of Natural Resources and Environmental Sciences and Illinois Natural History Survey, Urbana, Illinois 61801, United States.
[2] Cooperative Wildlife Research Laboratory, Center for Ecology, Department of Zoology, Southern Illinois University Carbondale, Carbondale, Illinois 62901, United States.
[3] Environment and Climate Change Canada, Ottawa, Ontario K1A 0H3, Canada.
[4] Forbes Biological Station, Illinois Natural History Survey, Prairie Research Institute, University of Illinois Urbana-Champaign, Havana, Illinois 62644, United States.
[5] Delta Waterfowl Foundation, Bismarck, North Dakota 58504, United States.
[6] Department of Biology, University of Saskatchewan, Saskatoon, SK S7N 5E2, Canada.
[7] Habitat and Population Evaluation Team, National Wildlife Refuge System, U. S. Fish and Wildlife Service, Bismarck, ND 58501, United States.

Email addresses:
Ryan J. Askren: ryanaskren@gmail.com
Mike W. Eichholz: Eichholz@siu.edu
Christopher M. Sharp: Christopher.Sharp@ec.gc.ca
Auriel M. V. Fournier: Auriel@illinois.edu
Jay A. VonBank: Jvonbank@deltawaterfowl.org
Mitch D. Weegman: Mitch.weegman@usask.ca
Heath M. Hagy: Heath_hagy@fws.gov
Michael P. Ward: Mpward@illinois.edu

*Correspondence: Ryan J. Askren, ryanaskren@gmail.com. Present address: Five Oaks Ag Research and Education Center, Humphrey, Arkansas 72073, United States.

**Abstract**

**Background** Molt migration is a life history strategy in which birds move to areas with perceived higher-quality forage and/or reduced predation risk to undergo an energetically costly flight-feather molt. This strategy is well documented in non-breeding and failed-nesting Canada geese (*Branta canadensis*) across North America. We evaluated the propensity of temperate-breeding Canada geese to molt migrate and examined potential survival trade-offs between individuals that did and did not molt migrate.

**Methods** We fitted 157 Canada geese with Global Positioning System (GPS)-tri-axial acceleration transmitters mounted to neck collars in two temperate regions of North America (Chicago and Greater Toronto Area). We monitored movements, breeding status, nest attempts, nest success, and survival. GPS and acceleration data were used to compare movement behavior, habitat resource associations, and activity budgets between molt-migrating and non-molt-migrating geese.

**Results** Overall, 32.5% of non-breeding and failed-nesting geese (n = 243 goose-seasons) undertook molt migration. Geese either remained near nesting areas to molt ($\bar{x}$ = 5.3 km ± 1.4 SE) or undertook a long-distance migration to molt ($\bar{x}$ =2,304 km ± 242 SE). No successfully breeding geese engaged in a molt migration. Nesting landscape strongly influenced molt migration propensity: geese nesting in cropland-dominated landscapes were more likely to molt migrate, whereas geese in urban-dominated landscapes were less likely to do so. All molt migrants traveled to subarctic regions near Hudson Bay, Canada. Acceleration data indicated that molt migrants spent more time foraging, less time in alert behaviors, and experienced longer flightless periods than non-migrants. Molt migrants also exhibited greater survival until fall migration, when hunter harvest reduced differences in seasonal survival. Among geese

monitored across consecutive years that either failed to breed or failed nesting in both years (n = 67), 13.4% molt migrated in both years, 55.2% never molt migrated, and 31.3% switched strategies between years.

**Conclusions** Our findings demonstrate that molt migration in temperate-breeding Canada geese is a plastic trait strongly influenced by nest success and landscape composition, where individuals do not need to molt migrate, likely due to abundant forage and reduced predation risk in urban environments. Molt migrants appeared to perceive fewer threats and devoted more time to foraging but were also more susceptible to hunter harvest during fall migration. Molt migration thus joins the growing set of migratory behaviors in birds, ungulates, and cetaceans that are best understood as plastic traits rather than fixed strategies, with human-altered landscapes and the management actions applied within them acting as the proximate lever on their expression.

**Keywords** acceleration, Canada goose, life-history tradeoffs, molt migration, urban waterfowl

## Background

Long-distance migratory movements are energetically costly but allow avian species to access seasonally variable resources necessary for survival [1]. 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 flight feathers during or following the breeding season [2], [3]. These molt migrations occur across a range of avian taxa [4], [5] and are especially common in waterfowl [2], [6], [7].

Molt migration is a strategy by which non-breeding or failed-nesting waterfowl migrate

from greater predation risk, greater social competition with dominant family groups, and potentially lower quality forage to more optimal areas to undergo costly remigial molt [8], [9], [10]. All waterfowl undergo simultaneous remigial molt, dropping all flight feathers to grow new ones at once rather than replacing remiges sequentially [11]. 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 [12], [8], [10]. Despite the hazards of simultaneous molt, some evidence suggests that survival during the molting period is similar to other portions of the annual cycle [10]. The cost of migration may be compensated for by reduced predation risk, greater foraging resources, and other factors at their molting location [10].

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 [13], [14], [15]. 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 [16], [13], [15]. This migratory behavior likely evolved in temperate-breeding Canada goose populations at a time when predation risk was high, limited temperate forage was monopolized by socially dominant family flocks, and the costs of migration were low [7], [17]. 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 [7], [15]. Several species and populations of geese have demonstrated significant plasticity in migratory strategies, evidenced by large-scale and relatively rapid shifts in migratory behavior [7], [17]. 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 [7].

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 the effects of landscape composition around individual nesting location on the 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 hunting) 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 (hereafter, northeastern Illinois) and the Greater Toronto Area (GTA), Ontario, Canada. Both metropolitan areas have large breeding populations of Canada geese [18] and a gradient of highly developed to rural land use. In addition to northeastern Illinois and the GTA, breeding areas included large emergent cattail marshes in southeastern 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 [19], [15]. This region is dominated by lichen-heath tundra, wet-sedge meadows and numerous ponds, rivers, and wetlands [14]. The flora consists of short woody vegetation,

lichens, and heath in more upland areas and mosses and sedges in low lying areas [14], [20].

*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 2015 – 2020 in both the GTA and northeastern Illinois. We used MagNet small animal net-guns (Wildlife Capture Services, Flagstaff, Arizona, USA), landing nets, or hand-capture techniques 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-powered Global Positioning System-tri-axial acceleration transmitters (GPS-ACC) affixed to neck collars. GPS-ACC transmitters were manufactured by Cellular Tracking Technologies (Gen3 and ES400, 55 g, Rio Grande, New Jersey, USA) and Ornitela (OT-N44-3G, Vilnius, 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 the GTA, which we down-sampled to one-hour intervals. Transmitters collected ACC data every 15 minutes; these data were then used to quantify behavior time budgets (see below). GPS and ACC data were uploaded every three days via the Global System for Mobile Communication. When devices were not in GSM coverage, they stored data on board until back in GSM coverage.

*Nests*

For geese captured at nests in the GTA 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 [21]. 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 transmitter-marked geese and those nesting outside of the study area. Probable nesting attempts were evident from decreased movement and distances between mean locations of < 300 m in subsequent days. We interpreted apparent nesting success based on the length of incubation and movements after leaving the nest site. We defined a probable 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. We considered an individual non-breeding if GPS and ACC data revealed no period of restricted movement consistent with a nesting attempt and failed-nesting if a nesting attempt was evident but incubation lasted fewer than 25 days or the individual exhibited rapid movements after leaving the nest site.

During 2018 – 2020, we removed all eggs from 64 nests of transmitter-marked geese in northeastern Illinois to artificially induce nest failure, remove parental obligations, and encourage molt migration. These nests were also classified as failed-nesting. In Illinois, we collaborated with the USDA, Animal and Plant Health Inspection Service (APHIS) Wildlife Services program to remove eggs from nests at approximately 14 days of incubation as part of its nest management efforts. This timing was intended to reduce the likelihood of renesting [22]. In the GTA, we estimated non-breeding or failed-nesting individuals based on movement and ACC data. We monitored locations to determine if renesting occurred and removed re-nesting individuals from subsequent analyses. We tracked geese following nest failure, including nest depredation/abandonment from unmanaged goose nests, 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. We included 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 calculated 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 [15]. 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*, [23]) 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 in package lme4 [24] ([25]; Table 1). We then ranked models in an Akaike's Information Criterion framework to choose the model that best describes the effects of landscape composition on the probability of molt migration ($AIC_c$; [26]). We considered models within 6 ΔAICc units of the top-ranked model to be plausible, because simulation studies indicate that the conventional 2 ΔAICc threshold frequently excludes parsimonious models and can lead to incorrect inference [27,28]. From that set we then removed any more-complex model whose AICc was not lower than that of every simpler model in which it was nested, because the additional parameters in such models are uninformative and should not be interpreted as

ecological effects[27,29]. We based inference on Akaike weights (wi) and report effect sizes from the model carrying the greatest weight. We included additive and interactive combinations of open water, wetland, cropland, forest, urban land uses (> 20% impervious surfaces), and breeding status (non-breeding or failed-nesting) with individual ID as a random effect (Table 1). We chose these land uses as predictors because previous work has suggested a relationship between propensity to molt migrate and surrounding land use [15], the importance of wetlands and open water for nesting and molting geese [2], and agriculture is the dominant land use in northeastern Illinois (i.e., corn, soybeans) and outside of Toronto.

*Foraging and duration of molt*

We used ACC data to quantify differences in the proportion of time spent in foraging and alert behaviors as a proxy for foraging environment and predation risk [30], [31], [32]. We built datasets to train classification models by pairing observed behaviors, collected via video of transmitter-marked geese in the field, to ACC bursts that could be unambiguously classified as head-up (i.e., alert) and foraging behaviors [33]. We quantified flight behavior to determine the duration of flightlessness, by visually identifying ACC bursts linked with successive GPS data that indicated movement possible only by flight [30]. 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 [34]. 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 burst and translated these summarized ACC bursts to instantaneous behaviors using a supervised machine learning approach and classification process [35], [36], [31]. 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 [36]. Cellular Tracking Technologies (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 acceleration data separately (see below). We used a workflow with an extreme gradient boosting algorithm in package *XGboost* [37] to build separate classification models for CTT and Ornitela transmitters (due to their different data outputs) to predict unknown ACC bursts [35], [38], [31]. 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 88.5% (SD 4.9) for CTT and 91.3% (SD 4.9) for Ornitela transmitters (i.e., how often the observed behavior was the same as the predicted behavior). Per-class precision and recall from the same iterations were 0.83 and 0.98 (alert), 0.91 and 0.69 (foraging), 0.95 and 0.98 (flight), and 0.96 and 0.86 (resting) for CTT transmitters, and 0.88 and 0.92 (alert), 0.94 and 0.88 (foraging), 0.90 and 0.99 (flight), and 1.00 and 0.79 (resting) for Ornitela transmitters. Because labelled bursts were obtained during a small number of observation sessions, and most behaviors were observed on only a few days, random train-test splits may assign bursts from the same session to both the training and test sets; when whole sessions were withheld instead, accuracy was 71.9% for CTT and 78.2% for Ornitela transmitters, with the largest reductions in the behaviors observed on the fewest days. We then used the trained models to predict the probability of an unknown ACC burst 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 assigned per GPS fix.

We modeled the daily number of ACC bursts classified as foraging, and separately as

alert, out of all classified bursts for each goose during June – August using beta-binomial generalized linear mixed models (logit link) in package glmmTMB [39], with a random intercept for goose-year and a first-order autoregressive term across days within goose-year to account for temporal dependence in daily behavior. Transmitter type was included in every behavior model, including the null, because CTT and Ornitela transmitters were classified with separate models and CTT transmitters were deployed only in Illinois. Candidate models represented competing explanations for differences in behavior: molting region (subarctic or temperate, assigned daily from each goose's location, with locations ≥50°N classed as subarctic), month, their additive and interactive combinations, astronomical day length at each goose's daily location [40], day length with month, and molting region with day length (Additional file 1). Molting region and day length were correlated ($r = 0.78$), but their coefficients retained their signs and their standard errors increased by only ~15% when both were included. Behavior analyses included all temperate-breeding geese with ACC data (CTT and Ornitela transmitters in northeastern Illinois and Ornitela transmitters in the GTA); six goose-years of subarctic-breeding geese captured in winter in Illinois were excluded. We ranked models with AICc, using the number of goose-years as the sample size, applied the same 6 ΔAICc threshold and uninformative-parameter criteria described above, and report model-predicted means with 95% confidence intervals. To describe seasonal patterns from March to October (Fig. 4), we fitted the same model structure separately for each month, with transmitter type and molt strategy (molted in the subarctic or remained in temperate regions, assigned per goose-year) as fixed effects. We used an information-theoretic framework where our inference depended on comparing competing, non-nested hypotheses represented by a candidate model set (i.e., landscape and breeding-status effects on the probability of molt migration, predictors of monthly survival, daily foraging and alert behavior,

and the duration and timing of flightlessness), and null-hypothesis tests where our inference depended on a single a priori contrast for which no competing model set existed (i.e., the proportions of molt-migrating and non-migrating geese that were harvested); we did not use model selection and null-hypothesis testing within the same analysis [41]. In addition, we used incidence of flight derived from labeled ACC data as an index of flightlessness, or the duration without instances of in-flight behavior. To reduce false-positive classification of flight, we selected classified data in the upper quartile range for each individual, leaving only ACC bursts that had a high probability of being attributable to flight. We modeled the duration (gamma distribution, log link) and the start and end dates (Gaussian) of flightlessness of failed-nesting and non-breeding geese, one value per goose-year, with a random intercept for individual, comparing a null model and models containing molting region, transmitter type, mean day length during the flightless period, and their additive combinations by AICc (Additional file 1). Because molting region and day length were strongly correlated during the flightless period ($r = 0.92$), we did not include both in the same model.

*Survival*

We modeled monthly survival from May to October as a function of molt migration (did or did not), breeding success (failed-nesting, successful, non-breeding), and nesting areas using known-fate models using package *RMark* [42] to implement Program MARK using staggered entry encounter histories [43], [44]. We evaluated the importance of predictor variables by investigating all possible variable combinations on survival (Table 2), including a null model, using AICc and Akaike weights ($w_i$) for each model [26]. We applied the same 6 ΔAICc threshold and uninformative-parameter criteria described above. We identified mortalities based on repeated, stationary locations or reports of harvested transmitters. We located deceased transmitter-marked 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 GSM coverage in 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 [45]. 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 $P < 0.05$ [46].

**Results**

We captured 157 Canada geese in the GTA ($n$ = 58 geese) and northeastern Illinois ($n$ = 99 geese) and tagged them with GPS-ACC transmitters. Of the 99 geese captured in northeastern Illinois, 37 were captured during nesting and 62 during winter. Of the geese captured in winter in Illinois, 20 nested in southeastern Wisconsin ($n$ = 20 nests), 10 in Thunder Bay, Ontario ($n$ = 20 nests), and 21 in Illinois ($n$ = 27 nests). Geese transmitter-marked in the GTA were captured during nesting ($n$ = 56) or molt ($n$ = 2) and all nested locally. We monitored 203 nests, of which 64 were removed (31.5%); eight resulted in second nest attempts (12.5%). Of 139 unmanaged (not removed) nests in this study, 64.0% failed due to predation or abandonment ($n$ = 89 nests), 30.2% 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 3). Mean start date of first nest attempts was early-to-mid April, while second nest attempts occurred in the first two weeks of May (Table 3). We recorded 41 molt migrations (27.7% of failed-nesting geese) originating

from 148 removed 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 (44.9%). The overall rate of molt migration was 32.5% ($n$ = 243 goose-seasons) for non-breeding and failed-nesting Canada geese. Molt migration occurred in 26 of 53 non-breeding goose-seasons (49.1%) and 53 of 167 failed-nesting goose-seasons (31.7%); no successfully breeding geese (0 of 52) molt migrated. Of the geese that were alive in consecutive years and who either did not breed or whose nest failed or was removed in consecutive years ($n$ = 67), 13.4% molt migrated in both years ($n$ = 9), 55.2% did not molt migrate in either year ($n$ = 37), 31.3% switched molt migration behavior from one year to the next ($n$ = 21).

*Distribution and timing of molt migration*

Transmitter-marked 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 = 2,304 km ± 242 SE) with few exceptions (Fig. 1). Molt-migrating geese departed breeding areas at the end of May and early June ($\bar{x}$ = 6 Jun ± 1.3 days SE) and arrived in the Hudson Bay region on average 3 days after departure ($\bar{x}$ = 9 Jun ± 0.9 days; Table 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. 2). GTA-breeding geese that molt migrated went to areas along southeastern Hudson Bay near Umiujaq, Quebec (56.5°N, -76.6°W) to south of Ivujivik, Quebec (62.4°N, -77.9°W). Geese remained in northern portions of the Hudson Bay region for ~3 months ($\bar{x}$ = 83.7 days ± 2.5) until approximately the last week of September (Table 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. 2), before returning to temperate-breeding latitudes in September and October. Molt migration occurred predominantly during daylight (~79% of migratory-step distance) but geese also moved at night (~21%). Migratory steps (> 20 km between successive locations) averaged 44 km in spring (northward) and 57 km in fall (southward); the longest single flight leg exceeded 1,200 km.

*Effects of landscape composition on molt migration*

The top ranked model of probability of molt migration included the effects of all land uses and region ($w_i$ = 0.57; Table 1) followed by the model including all land uses ($w_i$ = 0.27; Table 1). Four models fell within 6 ΔAICc units of the top-ranked model and together carried 98% of the total Akaike weight; all four were retained, because each added term lowered AICc relative to the simpler model in which it was nested and none therefore contained uninformative parameters (Table 1). The two remaining plausible models carried considerably less support (wi = 0.09 and 0.06; Table 1). We therefore report effect sizes from the top-ranked model. The probability of molt migration increased by 0.7% for every percent increase in cropland 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 (Fig. 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%, $CI_{95}$ = 3.3 – 24.1%), and Thunder Bay (3.8%, $CI_{95}$ = 0 – 26.3%; Fig. 3). The model did not support difference in molt migration between sexes.

*Foraging behavior and duration of molt*

During June – August, the best-supported model of daily foraging included molting

region and day length ($w_i$ = 0.99), as did the best-supported model of alert behavior ($w_i$ = 0.83); the only other alert model within 6 ΔAICc units included the interaction of molting region and month (ΔAICc = 3.2, $w_i$ = 0.17; Additional file 1). Geese in the subarctic spent 4.8 more hours foraging each day (predicted proportion of time foraging = 51.6%, 95% CI = 49.2 – 54.0%) than geese in temperate regions (31.7%, 30.1 – 33.3%), and 5.7 fewer hours in alert behaviors (28.8%, 25.9 – 32.0% vs. 52.6%, 49.3 – 55.9%). Geese in the subarctic experienced an average of 20.1 hours (± 1.9 SD) of daylight during June and July compared to 15.3 hours (± 0.4) for geese in temperate regions. With day length held constant, the regional difference in foraging was reduced to 2.1 hours (43.5% vs. 34.9%), whereas the difference in alert behavior was largely unchanged (4.8 hours; 31.2% vs. 51.4%). Daily proportions of foraging and alert behavior were similar between geese that molted in the subarctic and those that remained in temperate regions during March – May and September – October (differences ≤ 6 percentage points), and diverged only during June – August (Fig. 4). The best-supported model of flightless duration of failed-nesting and non-breeding geese included molting region ($w_i$ = 0.72; n = 61 goose-years): geese molting in the subarctic were flightless longer (predicted 54.2 days, 95% CI = 43.7 – 67.2) than those molting in temperate regions (32.1 days, 27.0 – 38.0). The null model was best supported for the start date of flightlessness ($\bar{x}$ = 22 June, 95% CI = 16 – 28 June), whereas the best-supported model of the end date included molting region ($w_i$ = 0.61): flightlessness ended 14 days later in the subarctic (13 August, 7 – 18 August) than in temperate regions (30 July, 26 July – 3 August).

*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 ($w_i$ =0.70;

Table 2). Monthly survival varied with highest survival during June – August and lowest in September. The only other model within 6 ΔAICc units of the top-ranked model included the interaction of molt migration by time (ΔAICc = 1.75, $w_i$ = 0.29; Table 2). That model, however, added six parameters to the time-only model within which it is nested without a commensurate reduction in deviance (a reduction of 10.44 for six additional parameters), and its AICc was consequently higher; these parameters were therefore uninformative [27,29] and we did not interpret them as evidence that molt migration influenced monthly survival. Overall cumulative seasonal survival (May – October) of all Canada geese was 81.8% ($CI_{95}$ = 77.2 – 86.6%). Plots of cumulative survival by month suggested that molt migrants tended to have higher cumulative survival during May – August than geese that molted in temperate areas, followed by an 8.7% decrease during the month of September (the period of several state and provincial hunting seasons for molt-migrating Canada geese), resulting in similar end of period survival for those individuals that molt migrated and those that did not (Fig. 5).

We recorded 39 mortalities during May to October, including 30 geese transmitter-marked in northeastern Illinois and 9 in Toronto. Of these, 12 were attributed to hunter harvest and 9 to non-harvest causes (i.e., depredation, vehicle strike); the remaining 18 were of undetermined cause, including 3 geese that departed on molt migration and were never relocated. The proportion of molt-migrating geese that were harvested was greater ($\bar{x}$ = 10.7%, $n$ = 84 molt-migration goose-seasons) compared to geese that remained in temperate regions ($\bar{x}$ = 3.0%, $n$ = 133 goose-seasons; $G_{adj}$=5.07, $P$ = 0.02). Molt migrating geese were harvested in Minnesota ($n$ = 4), Wisconsin ($n$ = 3), Ontario ($n$ = 1), and New York ($n$ = 1), whereas non-molt migrating geese were harvested in Illinois ($n$ =1), Wisconsin ($n$ = 1), and Ontario ($n$ = 1; Fig. 6).

**Discussion**

For subarctic-molting Canada geese, we found that the proportion of time dedicated to foraging was greater, time spent vigilant was reduced, and survival was higher pre-fall migration than temperate molting geese. 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, prior to early September goose seasons [10]. We found that survival of transmitter-marked geese that undertook molt migrations was higher than those molting in temperate regions early in the year, survival decreased greatly during the months of September and October, when autumnal migration coincides with the early goose hunting season. Modern hunting seasons have likely increased mortality during autumn migrations, making molt migration less adaptive [47], while urbanization has simultaneously created suitable and safer molting habitats (turf grass areas with ponds) in temperate regions compared to evolutionary history [48]. Furthermore, year-to-year variation within individuals suggests this strategy is plastic and that the effects of hunting and urbanization may be providing selective pressure against the undertaking of molt migration by temperate-breeding Canada geese. The drivers of this within-individual switching, however, remain unresolved. Determining whether individuals alternate strategies in response to body condition, the outcome of the previous breeding attempt, spring phenology, or local disturbance would clarify whether molt migration is a facultative response to annual conditions or a fixed strategy expressed inconsistently and would improve our capacity to anticipate how temperate-breeding populations respond to continued urbanization and harvest pressure. Our use of GPS and acceleration data 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 [7], [15] and

indicated strong effects of open water near nest sites on decreased incidence of molt migration [10]. Open water likely confers 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 [2], [10]. Well-maintained and fertilized turf lawns are common along the shores of most urban open water areas providing the resources necessary for molt adjacent to safe areas away from most predators [8], [10], [48]. The availability of open water adjacent to turf lawns is likely driving observed decreases in propensity to molt migrate in urban areas [15]. Similarly, we saw a relationship with forest composition, likely related to the presence of wooded areas in the urban matrix. In our study, geese that nested in areas with the lowest propensity to molt migrate (individuals in Thunder Bay and GTA) 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 [49], [50]. However, our results demonstrated a greater proportion of non-breeding and failed-nesting geese departing from areas of greater wetland density, primarily in Wisconsin, on molt migration. Our transmitter-marked geese nested in and around Horicon Marsh, Wisconsin a large emergent wetland complex, which is a major breeding and fall staging area for Canada geese [51], [52]. We suggest the effects of landscape composition and potential social dynamics of the Horicon Marsh area are 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 dominant, family flocks [53], [54].

While the single effect of breeding region was not supported, breeding region was included in our top model (Table 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 [7] and there is a genetic basis for different molt migration patterns in painted buntings (*Passerina ciris*; [55]). 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 [56]. 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 [57]. Temperate-breeding Canada geese were re-introduced to Midwestern 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 [58]. The fact that individuals changed strategies yearly regarding whether to molt migrate may suggest the behavior is mediated by social factors or individual condition as opposed to innate behaviors, however more research is needed. Molt migration has been documented in introduced populations of Canada geese in the United Kingdom [59] and New Zealand [60]. Further investigation into whether recently introduced populations of Canada geese in Europe and New Zealand molt migrate would further our understanding of molt migration as an innate or adaptive behavior [61], [60].

The reallocation of time toward foraging and away from vigilance in the subarctic provides insights into how predation risk shapes life history characteristics. Subarctic molt migrants devoted a substantially greater proportion of the day to foraging, and less to alert behaviors, than temperate-molting geese. Longer days in the subarctic accounted for roughly half

of the additional time spent foraging but little of the reduction in alert behavior. Greater foraging effort need not indicate richer forage, however; under otherwise similar conditions it can equally reflect a more time-constrained environment in which geese must forage longer to meet the energetic costs of molt [62], [63]. Indeed, the assumption that geese molt-migrate to reach higher-quality forage is not well supported by available nutritional data. The fertilized, frequently mown cool-season turfgrasses that dominate the urban landscapes these geese depart are exceptionally nitrogen-rich, commonly exceeding 20% crude protein, are preferentially selected by foraging geese, and elicit higher feeding rates as their nitrogen and protein content increases [64]. By contrast, the subarctic salt-marsh graminoids characteristic of Hudson Bay molting areas are strongly nitrogen-limited [65]; their forage value derives less from high absolute nutrient content than from a grazing-lawn dynamic in which intense grazing and fecal-nitrogen deposition sustain a continuously regrowing sward of young, digestible tissue synchronized to the flightless and brood-rearing period [66], [67]. On raw nitrogen and protein, then, urban turf is at least comparable to, and frequently exceeds, subarctic forage, the same quality that allows resident geese to thrive in temperate urban settings. We therefore interpret the elevated foraging effort of subarctic molt migrants cautiously: that this does not represent poorer forage quality in subarctic areas as much as it does the near-absence of disturbance and predators during the vulnerable flightless period. On balance, our findings give greater weight to reduced predation and disturbance risk, alongside a predictable, if not intrinsically richer, food supplyas drivers of molt migration than to forage quality alone.

Despite subarctic-molting geese spending more time foraging and less time in alert behaviors, their estimated flightless periods were about 22 days (70%) longer than those of geese molting in temperate areas. Flight is an important predator-avoidance behavior [68], [69], and

selection should favor minimizing the duration of flightlessness when predation risk is high [10]. Previous studies have similarly suggested that rapid molt may reduce vulnerability to predation and have demonstrated links between molt duration, food availability, and body condition [70]. Our findings suggest that geese molting in the subarctic remained flightless for longer periods, where we expected lower predation risk. One explanation is that longer flightless periods reflect reduced perceived predation risk associated with differences in predator dynamics, access to foraging habitat, or the availability of escape habitat in the subarctic. Importantly, our estimate of flightlessness was based on observed flight activity rather than feather growth sufficient for powered flight. Thus, geese in the subarctic may have regained the physical capability for flight earlier than indicated by our estimates but simply chose not to fly. Differences in habitat structure, disturbance regimes, or predator communities may have reduced the need for frequent escape flights. Alternatively, molt migrants may prolong the flightless period to maximize resource acquisition, allowing simultaneous feather regrowth and replenishment of body reserves prior to autumn migration.

Canada geese whose nests fail or that forgo breeding face a complex set of trade-offs between remaining within highly urbanized landscapes, such as Chicago and Toronto, or migrating thousands of kilometers to remote subarctic habitats of Hudson Bay. Framing this decision solely in terms of the survival costs and benefits of molt migration likely oversimplifies the process. Our findings instead highlight the remarkable behavioral plasticity of Canada geese. Individuals nesting in densely urban environments must contend with regular anthropogenic disturbance, including traffic, human activity, and altered predator communities, yet some subsequently undertake long-distance migrations to vastly different ecological conditions in the subarctic. Within only a few days, geese can transition from navigating highly urbanized

landscapes such as Chicago's Lake Shore Drive to remote tundra environments characterized by different predators, climates, and disturbance regimes. This flexibility in movement behavior and habitat use is likely one of the primary factors underlying the species' success in colonizing and thriving in urban environments across North America and elsewhere.

In our study areas, Canada geese are among the most rapidly increasing bird species and are also associated with substantial human-wildlife conflicts [71]. Previous studies have suggested that nest removal may indirectly influence adult survival because failed-nesting geese that molt migrate must later pass through hunted areas during autumn migration [7], [19]. However, geese nesting in more urbanized areas, where conflicts with humans are often greatest, were less likely to molt migrate. Consequently, harvest mortality during autumn migration may have limited effects on reducing urban goose populations and could disproportionately affect geese breeding in more rural landscapes [47].

Nest management mitigates conflicts associated with geese aggressively defending nests or broods and prevents hatching, thereby reducing recruitment [72], [73]. Consistent with previous experimental work [15], [72], nest removal also increased the probability of molt migration relative to successful nesters, mitigating conflicts during the molting period, and any additional mortality experienced by molt migrants could further contribute to population reduction [15], [74]. Nevertheless, nest management is labor intensive, and even a small number of successful nests can produce substantial recruitment. Whether molt migration ultimately contributes to population reduction depends on its fitness consequences, which we could not fully evaluate here. Future work with larger samples of marked individuals that links molt strategy to reproductive performance, from breeding propensity through recruitment, and to seasonal and annual survival would clarify the population-level effects of nest management and

help refine strategies for reducing urban goose conflicts.

**Conclusions**

Molt migration in temperate-breeding Canada geese is a facultative, plastic strategy rather than a fixed trait. It was undertaken only by non-breeding and failed-nesting individuals, its probability was strongly structured by the landscape surrounding the nest, increasing with cropland and wetland and decreasing with urban land use and open water and roughly a third of individuals monitored in consecutive non-breeding or failed-nesting years switched strategies between years. Molt migrants traded higher survival through the flightless period, together with more time foraging and less time in alert behavior in the subarctic, for elevated exposure to hunter harvest during autumn migration, so that end-of-season survival converged with that of geese that remained in temperate areas. Because geese nesting in the most urbanized landscapes, where human–goose conflicts are greatest, were the least likely to depart, harvest during autumn migration is unlikely to be an effective lever on urban goose abundance and may fall disproportionately on geese breeding in more rural landscapes. These results suggest that the decision to molt migrate or remain in breeding regions is governed less by a fixed migratory tendency than by trade-offs based on individual and local conditions. Therefore, breeding outcome determines whether migration is an option, the surrounding landscape shapes the cost-benefit of remaining versus leaving. If these tradeoffs are closely balanced then modest changes in local conditions, such as continued urbanization or shifts in harvest pressure, may be enough to alter the proportion of individuals that migrate, offering a mechanism by which migratory behavior can erode rapidly in human-modified landscapes.

**Abbreviations**

ACC: acceleration; AICc: Akaike's Information Criterion corrected for small sample size;

APHIS: Animal and Plant Health Inspection Service; CI: confidence interval; GTA: Greater Toronto Area; GPS: Global Positioning System; GPS-ACC: Global Positioning System – tri-axial acceleration; GSM: Global System for Mobile communications; NALCMS: North American Land Change Monitoring System; SE: standard error; USDA: United States Department of Agriculture; USFWS: United States Fish and Wildlife Service.

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**Authors' contributions**

RJA, MPW, MWE, HMH, and CMS conceived and designed the study. RJA, MPW, HMH, CMS, and AMVF secured funding, handled project administration, and coordinated field logistics, and RJA led capture, transmitter deployment, and data collection. RJA processed and analyzed the GPS and accelerometer data and conducted the survival, movement, and behavioral analyses, with analytical input from JAV and MDW. MDW advised on accelerometer-based behavioral classification. CMS oversaw all capture, transmitter deployment, and data collection

in the GTA. RJA wrote the original draft. All authors contributed critically to revisions and interpretation. All authors read and approved the final manuscript.

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**Availability of data and materials**

The data and R code supporting this study are openly available in the Dryad Digital Repository [Note: DOI and web address will be added when assigned]. The archive contains the GPS locations, nest records, known-fate encounter histories, daily accelerometer-derived behavior summaries and labelled accelerometer training data needed to reproduce every analysis, and the R code is also archived on Zenodo [Note: to be added when assigned]. Raw GPS and accelerometer data are also stored in the Movebank Data Repository (https://www.movebank.org) under Project #3062609550 and Project #329155299.

**Declarations**

**Ethics approval and consent to participate**

Work was conducted with all necessary permits, including institutional (University of Illinois IACUC No. 20039; ECCC-CWS Animal Care Protocols 15CSh01, CSH01_2016, CSh-1_2017,

SH01-2018, 19CS01, 20SC02), Illinois state scientific (No. 6079), Chicago Parks District Scientific Research (No. 1839), ECCC Scientific Permit (SC-OR-2020-00333), Chicago Water Reclamation District (No. P-557; 17-NE 014), and federal banding permit (USGS BBL No. 23923; ECCC 10847). Nest removal was conducted by USDA – APHIS – Wildlife Services personnel as part of their concerted efforts across the Chicago Metropolitan Area and under the authority of a Damage or Danger permit to the Toronto Region Conservation Authority in the GTA.

**Consent for publication**

Not applicable.

**Competing interests**

The authors declare that they have no competing interests.

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**Tables and figures**

**Table 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 2015 – 2020 (n = 188 goose/years). We report model parameters, number of parameters (K), Akaike's Information Criterion for small sample sizes (AICc), difference in AICc from the top model (ΔAICc), AICc weight (wi), and log-likelihood [*Log (L)*]. Region denotes breeding region (northeastern Illinois, Greater Toronto Area, Thunder Bay, or Wisconsin). Crop, forest, urban, open water, and wetland indicate the proportion of each landcover type within a 5.26 km buffer. Models within 6 ΔAICc units of the top-ranked model were considered plausible [27]; the four such models retained 98% of the total Akaike weight, and none contained uninformative parameters [29].

| Models | K | AICc | ΔAICc | *wi* | Log (*L*) |
|---|---|---|---|---|---|
| Cropland+ forest + urban + open water + wetland + region | 11 | 202.18 | 0.00 | 0.57 | -89.45 |
| Cropland + forest + urban + open water + wetland | 8 | 203.70 | 1.52 | 0.27 | -93.51 |
| Cropland + forest + open water + wetland | 7 | 205.78 | 3.59 | 0.09 | -95.62 |
| Cropland + open water + wetland | 6 | 206.75 | 4.56 | 0.06 | -97.17 |
| Region | 6 | 209.88 | 7.69 | 0.01 | -98.74 |
| Region*open water | 7 | 213.39 | 11.21 | 0.00 | -99.43 |
| Cropland + wetland | 5 | 214.47 | 12.28 | 0.00 | -102.09 |
| 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 |

**Table 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 (ΔAICc), AICc weight (wi), and deviance. Time represents month (May–October); Region denotes breeding region (northeastern Illinois, Greater Toronto Area, Thunder Bay, or Wisconsin); and Breeding success indicates whether geese failed nesting, nested successfully, or did not breed. Two models fell within 6 ΔAICc units of the top-ranked model, but S(~Molt migrated*Time) added six parameters to S(~Time) without a commensurate reduction in deviance and is therefore an uninformative-parameter model[29]; inference is based on S(~Time) alone.

| Models | # Parameters | AICc | ΔAICc | wi | 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 3**. Count of nest fate (n = 203 nests) with mean start and end date of incubation (± SE) for temperate-breeding Canada geese (*Branta canadensis*) in northeastern Illinois and the Greater Toronto Area 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 4.** Calendar dates (±SE) of departure from and return to the temperate-breeding region of failed- and non-breeding Canada geese (*Branta canadensis*) transmitter-marked in northeastern Illinois and the Grater Toronto Area during 2015 – 2020.

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

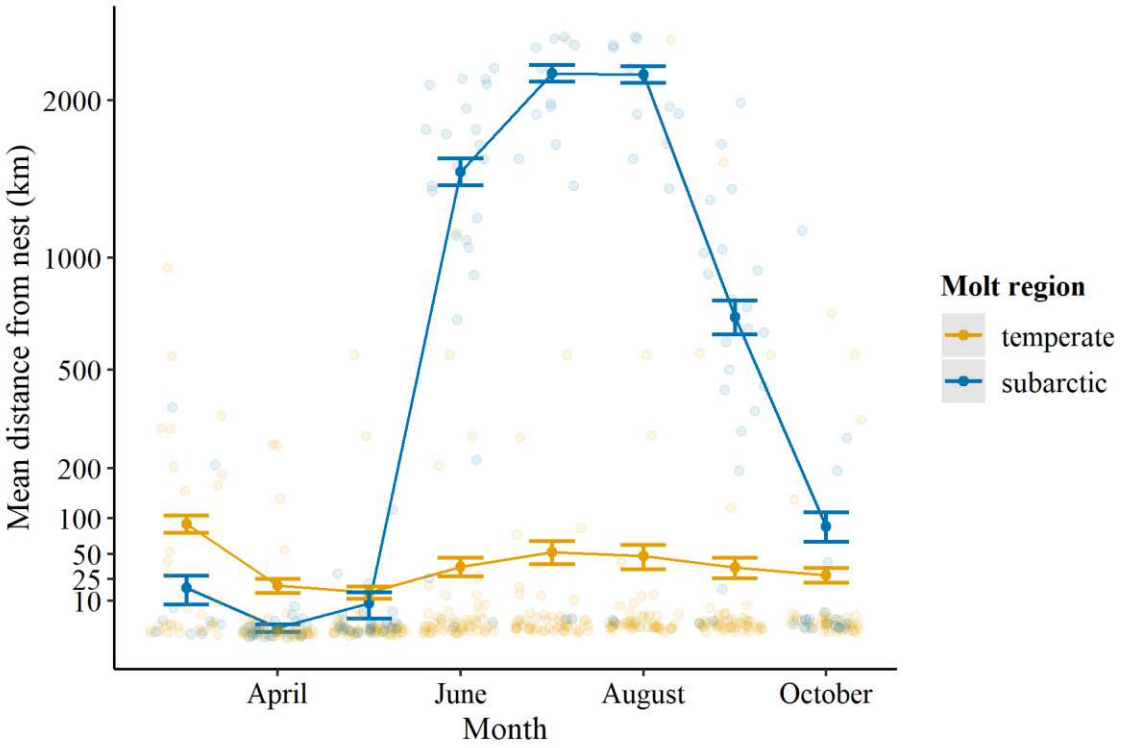


**Figure 1**. Mean monthly distance (± 1 SE) of failed-nesting Canada geese (*Branta canadensis) molting in temperate* and subarctic regions from nest sites during March – October of 2015 – 2020. Note scale is square root transformed.

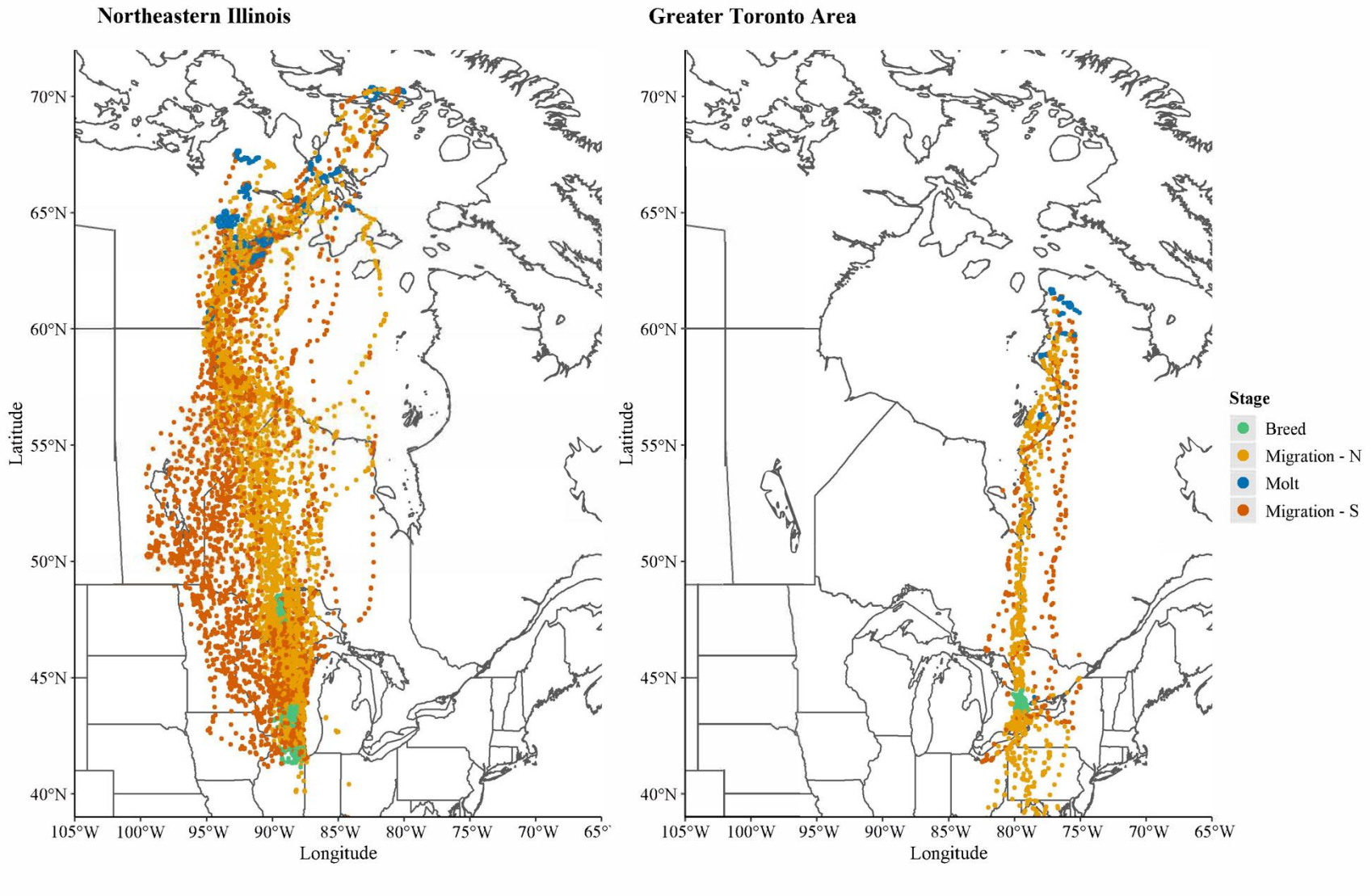


**Figure 2**. Map depicting breeding areas and molt migratory routes (n =79 goose/years) of Canada geese (*Branta canadensis*) marked in the northeastern Illinois (n = 63 goose/years) and Greater Toronto Area (n = 16 goose/years), during March – October 2015 – 2020.

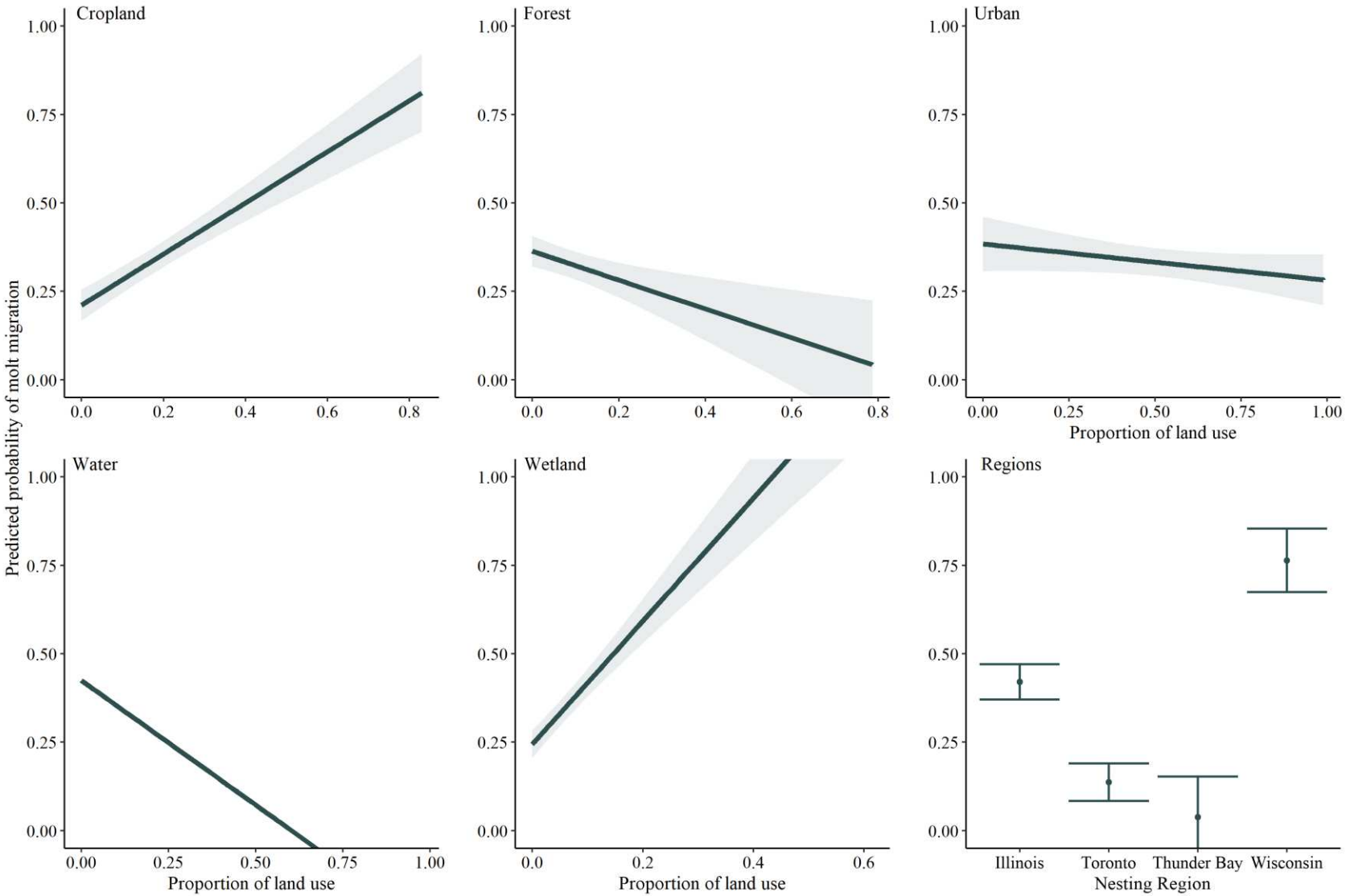


**Figure 3**. Effects (± 1 SE) of cropland, forest, urban land uses, open water, wetlands, and breeding region on the probability of molt migration of Canada geese (*Branta canadensis*) from breeding areas in the upper Midwest during 2015 – 2020.

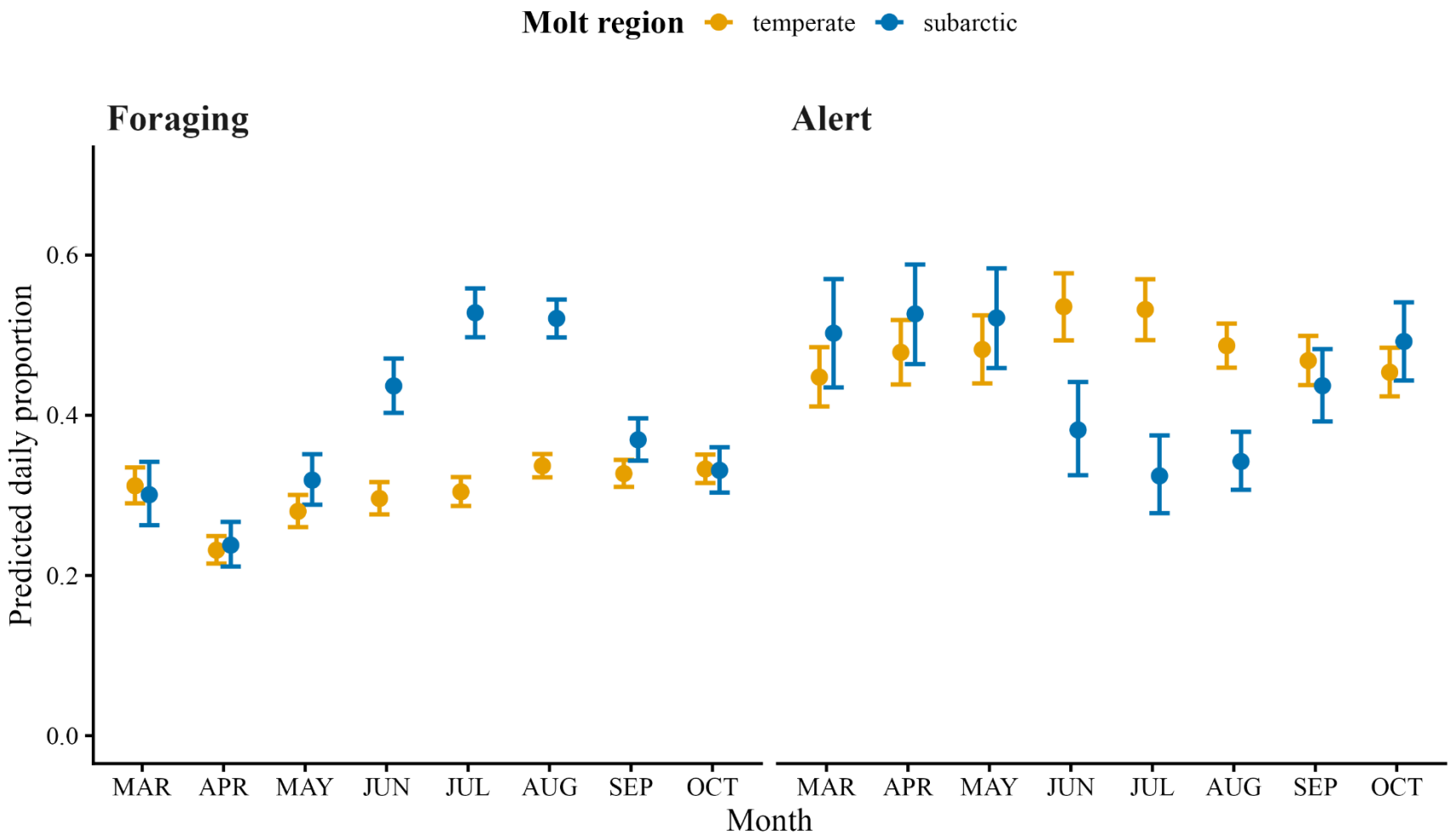


**Figure 4.** Model-predicted daily proportion (95% CI) of time spent foraging and in alert behavior by Canada geese (*Branta canadensis*) that molted in temperate regions (n = 110 goose-years) or in the subarctic (n = 36 goose-years), by month, 2015 – 2020. Predictions are from monthly beta-binomial mixed models adjusted for transmitter type (see Methods).

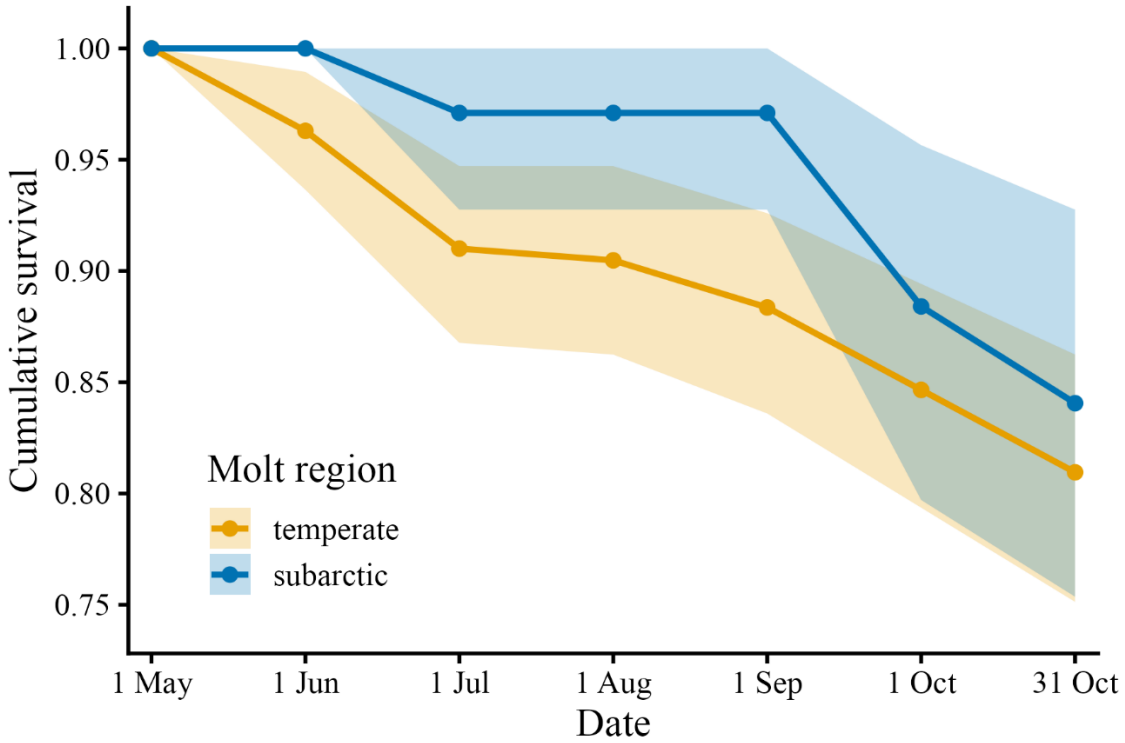


**Figure 5**. Cumulative survival (shaded bands = 95% bootstrap confidence intervals) by month from known-fate models of the effects of molt migration*time on all (failed-nesting, non-breeding, successful breeder) Canada goose (*Branta canadensis*). Non-molt migrate birds includes non-breeding and failed-nesting geese that did not molt migrate and successful breeders, whereas, molt migrating birds includes non-breeding and failed-nesting geese that molt migrated.

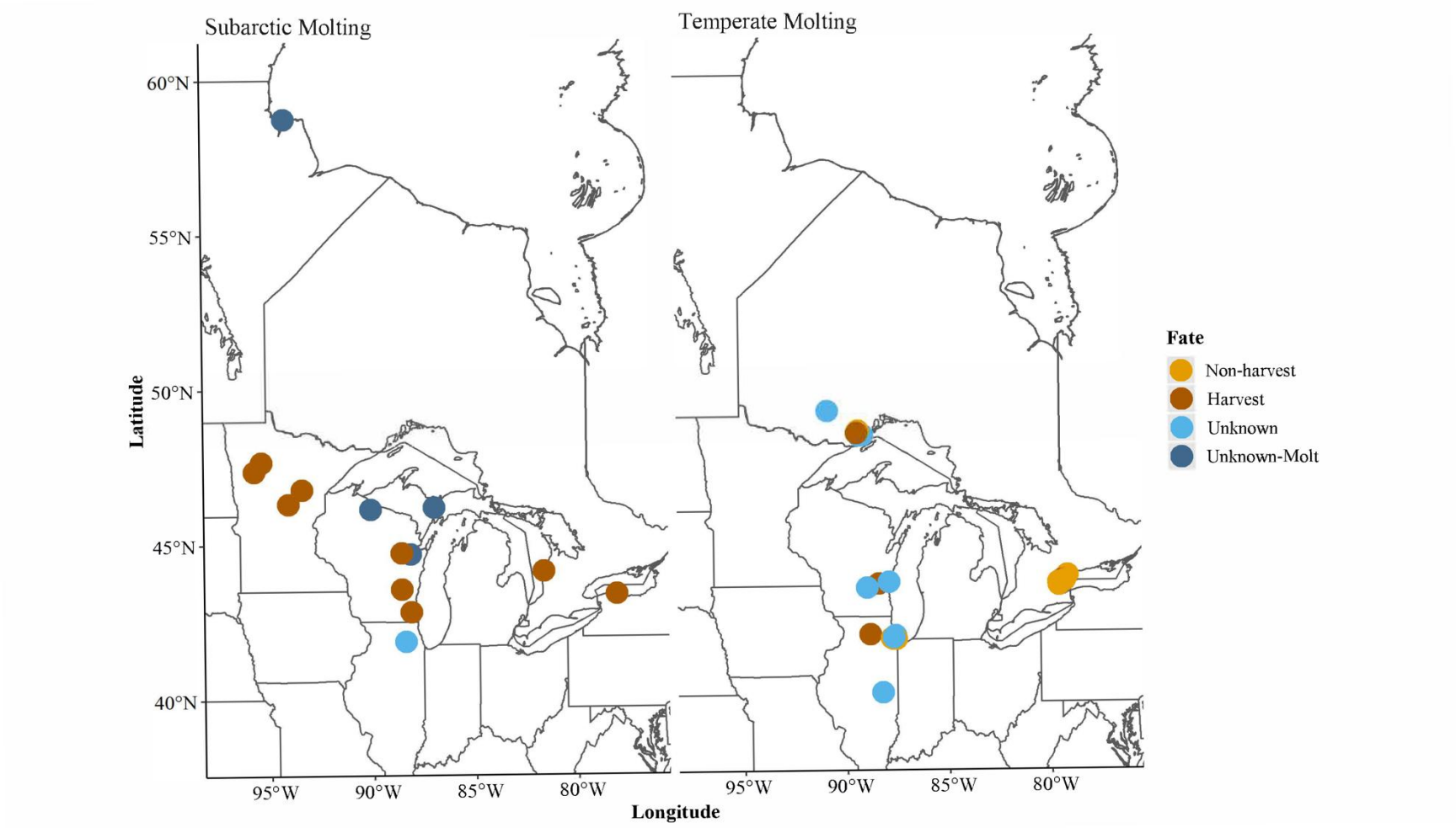


**Figure 6.** Distribution of mortalities of Canada geese (*Branta canadensis*) by molting region, with mortality locations of those that undertook a molt migration to the subarctic (left) and those that molted in temperate breeding areas (right). We classified a mortality as non-harvest when movements indicated a stationary carcass and as harvest when the transmitter or leg band was reported by a hunter. Geese were transmitter-marked in northeastern Illinois and the Greater Toronto Area during 2015 – 2020.