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Avian Behavior, Ecology, and Evolution

In the clear: weather drives the northward movement of American Tree Sparrows (*Spizelloides arborea*) as spring progresses

En claro: el clima impulsa el movimiento hacia el norte de los Gorriones Arbóreos Americanos (*Spizelloides arborea*) a medida que la primavera avanza

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ABSTRACT. The American Tree Sparrow (*Spizelloides arborea*) is a sub-Arctic breeding species that spends the nonbreeding season in temperate regions of North America and is a high priority candidate for conservation status assessment. To provide new information about their movement ecology and migratory connectivity, we used automated radio telemetry to track their movements and stable-isotope analysis of feathers to infer breeding or natal origin. Following capture on their nonbreeding grounds in southern Ontario, Canada, from January to mid-April, birds interspersed periods of residency with punctuated regional-scale movements biased northwards from early February to mid-May. These movements predominantly occurred during dusk or night, increased in frequency with day of year, and were positively associated with higher temperature, higher atmospheric pressure, less cloud cover, and winds with less of a westerly component. These characteristics indicate that late nonbreeding to pre-breeding migratory movements may serve to track the advancement of spring in our region. All birds had left the southern Ontario study region (< 45.8°N) by late April, and two birds were detected en route to breeding areas north of 45.8°N in May. A few birds (nine of 71) retained their tags, returned to the study region, and were detected in the subsequent fall, with one individual being detected at their initial capture site. Stable-isotope analysis of feathers suggested that wintering American Tree Sparrows in Ontario originated across a broad area of the breeding range from eastern Alaska to Nunavut. Results from our study provide the first data linking breeding and nonbreeding locations and provide a mechanistic basis for the timing of pre-breeding migration for this northern breeding species.

RESUMEN. El Gorrión Arbóreo Americano (*Spizelloides arborea*) es una especie que se reproduce en el sub-Ártico, y que pasa la época no-reproductiva en regiones templadas de Norte América, y es una candidata de alta prioridad para la evaluación de su estado de conservación. Para proporcionar información nueva sobre su ecología de movimientos y conectividad migratoria, usamos radio telemetría automatizada para rastrear sus movimientos y análisis de isótopos estables de plumas para inferir su origen natal o reproductivo. Después de la captura en sus áreas no reproductivas del sur de Ontario, Canadá, desde Enero hasta mediados de Abril, las aves intercalaron periodos de residencia con movimientos puntuales a escala regional hacia el norte desde principios de Febrero hasta mediados de Mayo. Estos movimientos predominantemente ocurrieron durante el atardecer o la noche, incrementaron en frecuencia con el día del año, y estuvieron positivamente asociados con temperaturas mayores, presiones atmosféricas mayores, menor cobertura de nubes, y vientos con menor componente occidental. Estas características indican que los movimientos migratorios no-reproductivos a pre-reproductivos pueden servir para rastrear el avance de la primavera en nuestra región. Todas las aves se fueron de nuestra región de estudio en el sur de Ontario (< 45.8°N) para finales de April, y dos aves fueron detectadas en ruta hacia áreas reproductivas al norte de 45.8°N en Mayo. Pocas aves (nueve de 71) conservaron sus etiquetas, retornaron a la región de estudio, y fueron detectadas en el otoño subsiguiente, con un individuo siendo detectado en su sitio de captura inicial. El análisis de isótopos estables de plumas sugirió que los Gorriones Arbóreos Americanos en Ontario se originaron en una amplia zona del rango reproductivo desde el este de Alaska hasta Nunavut. Los resultados de nuestro estudio proporcionan los primeros datos que enlazan sitios reproductivos con no-reproductivos y proporcionan una base mecanicista para el momento de la migración pre-reproductiva para esta especie reproductora del norte.

Key Words: *automated radio telemetry; migration; movement; sparrow; stable-isotope analysis; weather*

INTRODUCTION

Avian populations are currently facing a suite of environmental stressors because of rapid global climate change. For example, at northern latitudes, excess heat in the atmosphere is expected to change the dominant patterns of climate variability, resulting in earlier spring warming and more extreme weather at finer temporal and spatial scales (Horton et al. 2015, Bush and Lemmen 2019). Within this dynamic context, individuals of latitudinally migrating species shift their home ranges across the annual cycle, thereby linking breeding and nonbreeding periods (sensu Albert and Siegel 2024). These landscape to continental scale migratory movements, which are generally thought to track favorable conditions for flying and refueling (Alerstam 1990), are underpinned by complex regulatory mechanisms involving the integration of endogenous programs, external environmental cues, and individual state (Åkesson and Helm 2020). The precise mechanisms used to track seasonality in abiotic and biotic conditions are likely to be species and season specific, depending on life history, trophic guild, latitude, and migration strategy. For example, analyses of long-term data sets on the phenology of

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species—spanning primary producers, primary consumers and secondary consumers—show seasonal associations with climate variables that vary in direction and magnitude depending on the taxonomic group and trophic level (Thackeray et al. 2016). Comparative analyses of distributional shifts based on eBird data show that species with different migration strategies differ in their response to the seasonal timing of vegetation green-up (La Sorte and Graham 2021, Youngflesh et al. 2021) and extreme weather events (La Sorte et al. 2016). Despite the documented prevalence of species-level variation in phenological responses to climate, less is known about the underlying movement processes at the individual level, especially during the transition from nonbreeding to pre-breeding migration (but see Cooper et al. 2023).

In birds, the onset of migration is generally thought to be a distinct switch to a movement mode characterized by directional and long-range flights interspersed with predeparture and stopover periods for resting and refueling. In species that undertake their migratory flights at night, another hallmark seen in captive-held individuals is a change in diel activity pattern toward nocturnal activity or restlessness (reviewed in Winkler et al. 2016). In addition to migratory flights, after alighting at stopover sites, birds may engage in shorter distance relocation flights. Such movements are less directed and typically happen later in the evening and closer to dawn (Taylor et al. 2011, Schmaljohann and Eikenaar 2017). Although the onset of migration may be triggered by an endogenous circannual program entrained by photoperiod cues (Åkesson and Helm 2020), a large suite of abiotic and biotic cues can modulate stopover departure and flight decisions and therefore migration rate (Schmaljohann and Eikenaar 2017, Shamoun-Baranes et al. 2017, Sjöberg et al. 2017). In the Great Lakes region of North America, seasonal cues (e.g., calendar date or daylength, temperatures, and greenness) and localized weather conditions (e.g., wind and atmospheric pressure) appear to be dominant factors influencing migratory movements at the macro scale, as determined from eBird citizen-science data (La Sorte et al. 2014a, La Sorte et al. 2014b), and at the individual scale, as determined by tracking studies (e.g., Dossman et al. 2016, Morbey et al. 2018, Beauchamp et al. 2020, Cooper et al. 2023).

Tracking studies of migratory species during presumably stationary periods are revealing complex movement patterns, often involving the use of multiple sites with movements driven by climate and resource-related factors (Teitelbaum et al. 2023). Movement patterns during nonbreeding periods also can be inferred from distributional differences. In eastern North America, for example, extreme weather events during winter have been associated with changes in occurrence and abundance to varying degrees depending on the species (Cohen et al. 2021). More generally, in northeastern North America we might expect species to show sensitivity to sudden variation in snow conditions (Casson et al. 2019). In temperate regions of the United States, for example, snow cover is an important predictor of species occurrence and/or abundance, with some species associating with snow and others avoiding snow (Zuckerberg et al. 2011, Keyser et al. 2023). Movement strategies in response to local conditions can also vary among species that experience cold and snowy winters during nonbreeding periods. For example, nonbreeding Snow Buntings (*Plectrophenax nivalis*) have a nomadic lifestyle during winter and engage in diurnal landscape-level relocations that are driven by local snow conditions (McKinnon et al. 2019). Flexible extension of postbreeding migration has been shown in Yellow-rumped Warblers (*Setophaga coronata*; Terrill and Ohmart 1984), and facultative expression of nocturnal restlessness during nonbreeding periods has been shown in captive studies of Dark-eyed Juncos (*Junco hyemalis*; Terrill 1987) and stonechats (*Saxicola* spp.; Van Doren et al. 2017). In American Tree Sparrows (*Spizelloides arborea*), birds engaged in a multi-night nocturnal movement event in response to a midwinter storm with heavy snow and frigid temperatures (Niles et al. 1969). These studies highlight that nocturnal movements are not restricted to discrete migratory periods and may be a common component of movement repertoires in temperate environments (Terrill 1987).

The American Tree Sparrow is included on the list of common birds in steep decline by Partners in Flight (Rosenberg et al. 2016), based on precipitous declines in recent decades. Given documented declines of ~87% in Canada from Breeding Bird Survey data (Smith et al. 2023), it is currently a high priority candidate for conservation status assessment by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2024). American Tree Sparrows breed near the treeline and spend the nonbreeding period in temperate North America, where they inhabit open and early successional habitat and frequently visit backyard bird feeders (Naugler et al. 2020). Suitable breeding habitat for this species is expected to decline with climate change, with predicted reductions in breeding range distribution and abundance in future decades (Raymundo et al. 2023). Stressors occurring across the nonbreeding range pose additional threats and include agricultural intensification, forest maturation, and predation by cats (*Felis catus*; Naugler et al. 2020). Based on range-wide distributional shifts in relative abundance, pre-breeding migration occurs from 22 February–17 May, and postbreeding migration occurs from 20 September–6 December (Fink et al. 2023); thus, migration can overlap with meteorological winter (December–February) in temperate environments. Migration of American Tree Sparrows is thought to occur primarily at night (Baumgartner 1968), which is supported by acoustic monitoring of their night flight calls during postbreeding migration (Van Doren et al. 2023). In general, little is known about the scale of individual movements by American Tree Sparrows during nonbreeding and migration or their migratory connectivity apart from inferences made from limited recaptures of marked birds and observational data (Naugler et al. 2020).

Understanding connectivity in populations of migratory birds, especially those experiencing steep population declines, is an important precursor to conservation (Webster et al. 2002, Webster and Marra 2005). Further, quantifying the timing and routes of migration and where birds reside during the breeding and nonbreeding periods is important for identifying the potential drivers of population declines and developing species management plans to ameliorate them (Macdonald et al. 2012, Allen and Singh 2016, Rushing et al. 2016, Knight et al. 2018, Will et al. 2024). These efforts have gained traction because of recent advances in the development and novel use of extrinsic markers to track bird movements (e.g., light-level geolocators, passive radiotelemetry, etc.; Stutchbury et al. 2009, Taylor et al. 2017). However, these technologies have limitations for northern breeding birds (Hannah et al. 2020a). Specifically, if birds require recapture to recover logged data or if birds must pass within proximity of receiver antennas (e.g., coded VHF tags), then species with remote breeding locations and poorly understood winter site fidelity are especially problematic. For these species, combining extrinsic approaches with intrinsic markers, such as the measurement of stable-hydrogen isotope ratios in bird feathers (δ^2H_f) to infer molt or natal origins, may improve understanding of migratory linkages (Hobson et al. 2015, Hobson and Wassenaar 2019).

Our main study objective was to characterize the movements of American Tree Sparrows from capture through to and during pre-breeding migration. To do so, we used the Motus Wildlife Tracking System (https://motus.org) to track the movements of individuals among an array of coordinated automated radiotelemetry receivers concentrated in southern Ontario, Canada. Stable hydrogen isotope analysis of feathers was used to assign likely breeding and/or natal origins. Our second objective was to test whether movement events have migratory qualities in terms of their directional intensity and timing. Under this hypothesis, American Tree Sparrow movement events should occur predominantly at night, be directed northwards toward breeding areas, and increase in frequency with day of year, mild weather, and favorable tailwinds for northward progression.

METHODS

Field work

We captured American Tree Sparrows (n = 77) at two locations in southern Ontario (Long Point Bird Observatory, Old Cut Research Station, 42.583°N, 80.398°W; Guelph Lake Nature Centre, 43.598°N, 80.267°W; Fig. 1) using mist nets or baited ground traps from 13–28 February 2019 (median = 18 February) and 17 January–24 April 2020 (median = 6 February). Old Cut is a lower elevation site (~180 m above sea level) on the shoreline of the Great Lakes, whereas Guelph Lake is a higher elevation (~360 m above sea level) inland site. Capture dates overlapped with the nonbreeding and pre-breeding migration periods as defined by eBird Status and Trends (Fink et al. 2023). Birds were aged based on plumage (e.g., Pyle 1997). We grouped hatch year (HY, before 31 December) and second year (SY, after 31 December), and after hatch year (AHY, before 31 December) and after second year (ASY, after 31 December) age classes into HY and AHY, respectively (Macdonald et al. 2016; Table 1). The prebasic molt occurs on or near the breeding grounds, beginning with primary feathers, which are replaced distally, from P1–P9 (Baumgartner 1968). Therefore, we plucked the single innermost primary feather (P1) from a subset of birds (n = 45) for feather δ^2H analysis because this feather would best represent breeding or natal origins. We sent a subset of feathers for genetic sexing, but sample sizes were too small for further analysis.

We radio-tagged birds with coded nanotags (Lotek NTQB2-3-2, 0.68 g, 19.9 s burst rate, battery life = 294 days) and released them to be detected by Motus stations at the trapping locations and elsewhere (Hannah et al. 2020b). Additional measurements made on birds but not analyzed in the current study were body mass, unflattened wing chord, and fat score on a seven-point scale (Ralph et al. 1993). All procedures were approved by the Eastern Wildlife Animal Care Committee of Environment and Climate Change Canada (Permits: 18KH01, 19KH01) and the Canadian Bird Banding Office (Permits: 10169, 10685M, 10847G, 10865, 10909).

Fig. 1. Map of southern Ontario showing the two tagging locations for American Tree Sparrows (*Spizelloides arborea*; squares) and the locations for acquiring NCEP and Tillsonburg weather data. The inset shows North America, the region shown in the main map (red square), and American Tree Sparrow breeding (reddish) and nonbreeding (blue) regions based on eBird Status and Trends. GLNC = Guelph Lake Nature Centre; NCEP = National Centers for Environmental Prediction. © Stadia Maps © Stamen Design © OpenMapTiles © OpenStreetMap contributors.

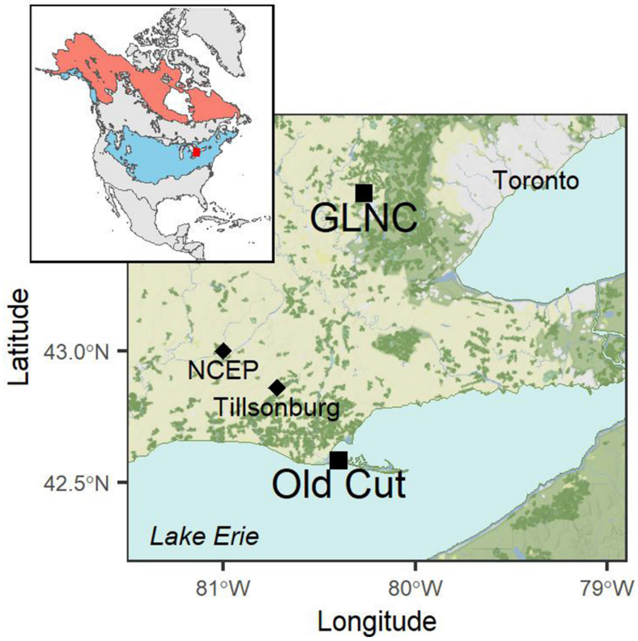


Table 1. Distribution of radio-tagged American Tree Sparrows (*Spizelloides arborea*) by year, capture site (GLNC = Guelph Lake Nature Centre), and age class (HY = hatch year; AHY = after hatch year; U = unknown).

Year	Site	HY	AHY	U	Row total
2019	GLNC	1	8	0	9
	Old Cut	9	20	0	29
2020	GLNC	6	5	0	11
	Old Cut	13	14	1	28
Column total		29	47	1	77

Motus data acquisition, tidying, and preprocessing

All Motus data acquisition, preprocessing, and visualization were done in R 4.3.2 (R Core Team 2025) following recommended protocols (Crewe et al. 2018, Birds Canada 2024). Briefly, we identified and removed probable false detections, which can occur because of environmental noise or interference among overlapping signals from multiple tags. Detections likely to be false were flagged in the Motus data—by the variable motusFilter—primarily based on having short runs of fewer than four detections, where a run is a sequence of consecutive detections of a tag at a unique receiver and antenna. By this definition, probable false detections also include birds near the edge of an antenna's detection range, which is up to 15 km with a clear line of sight (Taylor et al. 2017) but much lower (< 1 km) in cluttered environments (Crewe et al. 2019). We also used contextual information and run length to identify other probable false detections at unrealistic locations or times. In addition, we identified eight birds that likely dropped their tags or died based on a rapid change to very low variability in signal strength. Two of these birds were recaptured and re-tagged and thus had lost their tags; in the other six cases, it was not possible to distinguish tag loss from mortality. Out of an initial 13,059,457 detections, we removed 293,712 detections flagged with motusFilter = 0 (2.2%), 170 other probable false detections (0.001%), and 3,378,829 detections for the eight stationary tags (25.9%). After filtering, most detections were contained within the spatial extent of 41.5–45.8°N and 78.7–82.4°W; exceptions were one bird with 29 nocturnal detections at Moosonee, Ontario (51.3°N, 80.6°W) and one bird with six nocturnal detections near York Factory, Manitoba (57.1°N, 91.7°W).

After filtering, we split the data into spring (17 January–26 May) and fall (17 October–1 January) datasets; there were no detections outside of these periods. We note that these periods are not synonymous with standard meteorological definitions (i.e., spring: March–May; fall: September–November) or astronomical definitions (i.e., spring: ~21 March–~21 June; fall: ~21 September–~21 December) of the seasons in our region. Moreover, they do not coincide exactly with the pre- and post-breeding seasons as defined by Fink et al. (2023). Seventy-one birds had spring data totalling 9,382,217 detections. Nine birds had fall data totalling 4529 detections. Spring detections were plentiful because birds were tagged and released near Motus stations; fall detections were few because they required that birds survive, retain their tags, return to be detected, and occupy habitat in the detection range of Motus stations.

We considered the hierarchical nature of movement behavior to inform our analyses (Getz 2022). In this framework, birds have a canonical activity mode nested within a daily activity routine, and daily activity routines can change seasonally. During exploration of signal strength variation, we identified three major activity modes: routine diurnal activity, nocturnal roosting, and nocturnal flights comprised of fly-bys. A fly-by is characterized by an isolated and short sequence of detections at a single Motus station and antenna, often with increasing then decreasing signal strength (Taylor et al. 2017). Figures A1.1 and A1.2 in Appendix 1 show exemplars of these activity modes, provide more extensive descriptions, and highlight the discontinuous nature of automated radiotelemetry data. While birds were detected near their capture locations, their activity routine was comprised of diurnal activity and nocturnal roosting. Data coverage during this period of residency was highly variable (Fig. A1.3). After birds departed their capture locations, some were detected at other Motus stations during one or more nocturnal flights, but daytime detections were extremely sparse and insufficient for further analysis.

We specified criteria a priori to aid in the assignment of biological transitions or events. We considered birds to be present at their capture site on a given day if supported by > 20 detections at the closest Motus station, and present during a five-minute period if supported by > 4 detections. We defined the day of departure from the capture site as the last diurnal period with detections. We assigned departure time as the last detection time during the last five-minute period of presence on their departure day. One bird appeared to have false departures from Old Cut on 13 April; this individual was detected at nearby stations at 22:30 and 23:30, but diurnal detections continued at Old Cut the following day. Departure times showed a distinct mode near sunset. To capture this diel pattern of variation, we classified departures from 1 h before sunset to 0.5 h before sunrise as nocturnal; we classified all others as diurnal. Previous studies show that a period of inactivity often typifies migratory departures (Zúñiga et al. 2016, Schofield et al. 2018), but quiescence—which is not distinguishable from roosting based on radiotelemetry data—may not always be detectable by automated radiotelemetry (Morbey et al. 2020). We found that nocturnal departures that were detected much later than sunset usually were preceded by quiescence and likely marked the initiation of a relocation flight (i.e., a movement beyond the detection range of the Motus station). Nocturnal departures near sunset were not preceded by quiescence and likely signalled the end of diurnal activity (onset of quiescence and out of detection range), with a later relocation flight also going undetected.

We defined a regional passage event as a night with at least one fly-by. In some cases, a regional passage event could include fly-bys past several stations on the same night. In the spring dataset, three birds had brief periods of daytime detections away from the capture site, but later fly-bys at nearby stations suggest that these birds were engaged in routine diurnal activities. In the fall, one bird had daytime detections at Old Cut. Diurnal detections were not considered to be part of a regional passage event. We defined a nocturnal relocation event as a night with a nocturnal capture-site departure or a regional passage event and associated it with the date of the most recent daytime period. Movement paths were visualized on maps with maptype=stamen_terrain using functions in package ggmap (Kahle and Wickham 2013).

Acquisition of weather data

Daily weather data were obtained from the NCEP/NCAR reanalysis project (http://www.esrl.noaa.gov/psd/; Kalnay et al. 1996) and interpolated at a regional location (43°N, 81°W) and time (12:00 EST) using NCEP.interp in the R package RNCEP (Kemp et al. 2012). Weather variables included near surface temperature (converted to °C), atmospheric pressure (kPa), total cloud cover (%), precipitable water at surface (rain or snow in $kg \cdot m^{-2}$), and the u and v components of wind ($m \cdot s^{-1}$) at 1000 mb pressure level (equal to standard altitude of 111 m). Daily snow on ground (cm) was obtained from Environment and Climate Change Canada using package weathercan (LaZerte and Albers 2018). These data were obtained for Tillsonburg WWTP (42.86° N, 80.72°W; Fig. 1), a station between the tagging locations with good data coverage. At this location, average monthly temperatures range from about -5 °C in January to 22 °C in July. We associated nocturnal relocation events to the regional weather variables by date. Local weather could not be ascertained for all nocturnal relocation events because we could not know where birds had spent the previous daytime once they had left the capture site.

Time-to-event models

Using the spring data, we compared departure day of year between years, capture sites, age classes, and departure type (nocturnal vs. diurnal) using Cox proportional hazard models and Weibull accelerated failure time models (Allison 1995) using functions from package survival (Therneau and Grambsch 2000, Therneau 2023). These models make different assumptions about how covariates affect event timing and thus provide complementary information. Departure timing was visualized with Kaplan-Meier survival curves.

We analyzed the seasonal timing of nocturnal relocation events with recurrent (or repeated) event analysis in a Cox proportional hazard modeling framework (Allison 1995) using coxph in package survival. This approach accommodated variable start dates, a variable number of relocation events per individual, different types of censoring, and time-varying covariates. For this analysis, five relocation events north of 45°N were excluded, because Motus station coverage becomes quite sparse (Fig. A1.4). Events at 44°N–45°N were considered terminal (i.e., the final flight north out of the study region). Events were right censored at day of year = 124 (4 May 2019 or 3 May 2020) to ensure a common end date in the two years. Recurrent events (i.e., multiple events per individual) were accommodated by specifying the cluster argument as individual. In effect, this treated individual as a random effect. Initial models included all time-varying weather covariates and the individual level covariates age class, capture site, and year. The top model was selected through a backwards stepwise process whereby the variable with the highest p value was removed until the lowest AIC was achieved. Likelihood ratio tests confirmed that no nested model outperformed the top model.

Stable-isotope analysis

Prior to isotope analysis, feathers were cleaned of surface oils and other contaminants using a 2:1 chloroform: methanol solvent rinse. Vane samples from feather tips were then weighed in silver capsules (350 µg; Wassenaar and Hobson 2006) and loaded into a Eurovector Uni-Prep carousel (60 °C) interfaced with a Eurovector elemental analyzer. Following pyrolytic combustion on glassy carbon at 1350 ° C, H_2 gas was introduced into a Thermo (Bremen, Germany) Delta V Plus isotope-ratio mass spectrometer under continuous flow. Analysis of δ^2H was conducted using the comparative equilibration method of Wassenaar and Hobson (2003) with three calibrated keratin reference materials (CBS = -197‰, KHS = -54.1‰, and SPK = -121.6‰) and corrected for linear instrumental drift. Based on within-run analyses (n = 5 each) of the keratin standards, measurement error was approximately ± 2‰ for hydrogen isotopes in feathers (δ^2H_f). Values of δ^2H_f are reported relative to the Vienna Standard Mean Ocean Water-Standard Light Antarctic Precipitation (VSMOW-SLAP) scale. We compared feather δ^2H values between year-age combinations with a linear model that also included capture location. HY birds sampled in 2019 (n = 2) were excluded because of low sample size.

We assigned birds to geographic origin of feather growth using likelihood methods. To do so, we calibrated an amount-weighted growing-season δ^2H precipitation (δ^2H_p) isoscape (Bowen et al. 2005) obtained from G. Bowen (11 August 2021; https://www.waterisotopes.org; *unpublished data*) using known-origin δ^2H_f data available in AssignR (v. 2.4.0; Ma et al. 2020). Specifically, we incorporated any ground-foraging songbirds (Hobson and Wassenaar 1997, Hobson et al. 2004, Hobson et al. 2012, Hobson and Koehler 2015, Magozzi et al. 2021), including any short distance and long-distance migrants and residents. All data were transformed to the same scale as the unknown origin birds (OldEC.1_H_1; Magozzi et al. 2021). We used a reduced major axis regression to determine the calibration relationship (n = 395; $\delta^2H_f = \delta^2H_p \times 0.89 - 19.58‰$) and derived the calibration error (i.e., standard deviation of calibration residuals, 15.4‰) using an OLS regression. After applying the calibration equation, predicted δ^2H_f isoscapes were then clipped and masked to the American Tree Sparrow breeding range sourced from eBird (Fink et al. 2023).

We determined likely natal (HY) or molt (AHY) origins following likelihood-based assignment methods within the isocat package (v. 0.2.6; Campbell et al. 2020). Likelihood of origin was estimated on a cell-by-cell basis, applying a normal probability density function, which utilized the predicted mean δ^2H_f at that cell and is the predicted error at that cell. Cell-specific error was calculated by taking into account the isoscape error and calibration error. Probability of origin surfaces were normalized to sum to 1 and converted into binary regions of origin using a 2:1 odds ratio (i.e., upper 66% of probability density).

To identify groups of individuals with similar origins, we used the clustering approach based on spatial similarity assessed via Schoener's D-metric (Schoener 1970). Hierarchical clustering was performed in pvclust (v. 2.2-0; Suzuki et al. 2019), using the same odds ratio as the cutoff (compared against the approximately unbiased, AU, p value). Using a lower cutoff here allows for broad clustering while ignoring small groups of similar individuals with very high AU values. All surfaces for a given cluster were summed to produce a final map showing the number of individuals assigned to each cell.

RESULTS

Movement patterns

American Tree Sparrows departed their capture site over a protracted period from 13 February 2019–28 April 2019 (median = 13 April 2019) and 4 February 2020–28 April 2020 (median = 3 April 2020; Fig. 2). Of the 71 departures, 50 were nocturnal, with most occurring soon after sunset. Twenty-one were diurnal, and of these, two occurred within the 30 minutes prior to sunrise (Fig. 3). Based on Cox proportional hazard models of departure day of year, there was no evidence that birds departed from their capture locations according to different seasonal schedules between years (z = -0.027, p = 0.978; Fig. 2), age classes (z = -1.037, p = 0.300), or capture sites (z = 0.144, p = 0.886). There was some indication that nocturnal departures occurred later than diurnal departures based on the former's lower hazard of departure (β = -0.514, SE = 0.263, z = -1.957, p = 0.050). The accelerated failure time models produced similar results for year (z = -0.56, p = 0.575), age class (z = 0.63, p = 0.529), capture site (z = -0.13, p = 0.897), and departure type (β = 0.087, SE = 0.047, z = 1.85, p = 0.064). The Weibull accelerated failure time models had regression scale parameters of ~0.18, indicating that the hazard for departure increased from 0 at an accelerating rate with day of year.

Following departure from the capture sites, 58 birds were detected at other Motus stations for a total of 202 nocturnal fly-bys during the spring period. These fly-bys began 0.7–10.4 hours after sunset (median = 3.3 h after sunset; all were before sunrise). Including the nocturnal departure events and regional passage events, there

Fig. 2. Kaplan-Meier curves showing the day of departure from the capture site in American Tree Sparrows (*Spizelloides arborea*) in 2019 and 2020. Shading indicates the 95% confidence intervals and the dotted lines show the medians in 2019 (day 101) and 2020 (day 91.5).

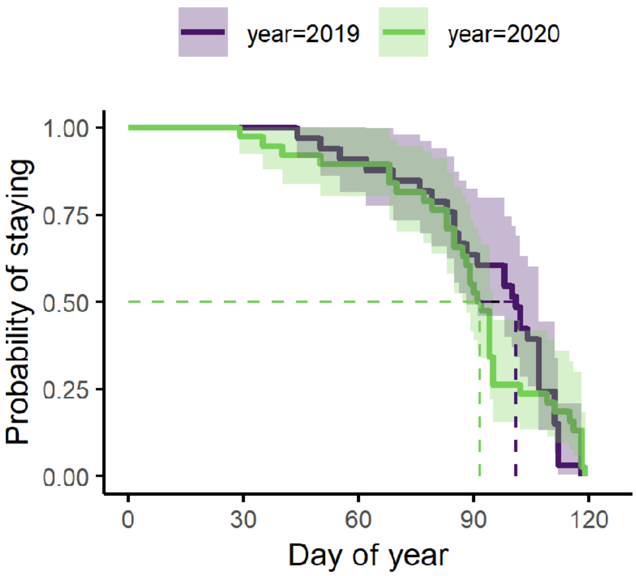


Fig. 3. Time of departure (hours since sunset) from capture locations in American Tree Sparrows (*Spizelloides arborea*). Diurnal (open bars) and nocturnal (hatched bars) are shown for after hatch year (AHY) and hatch year (HY) birds.

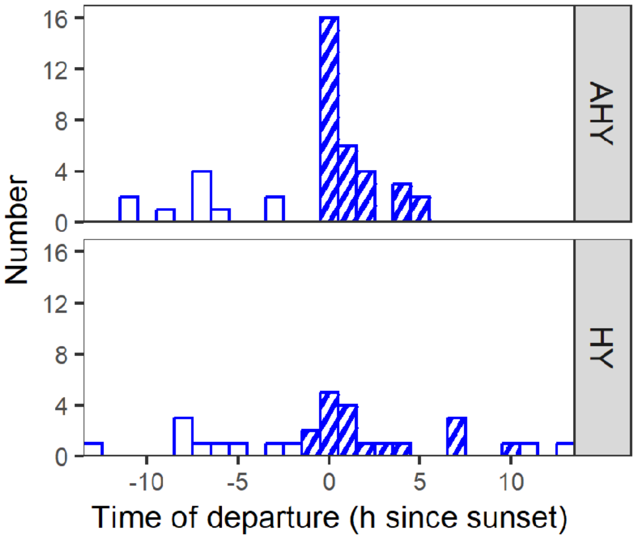
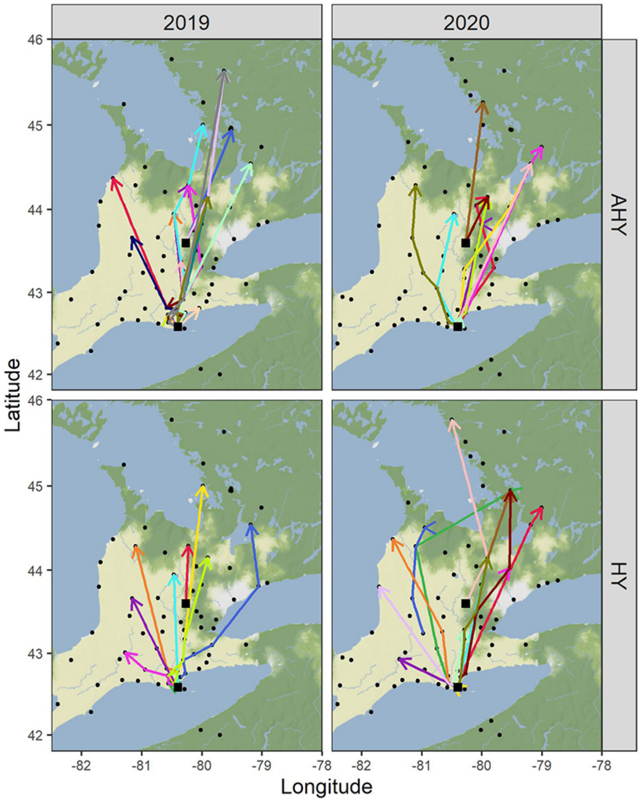


Fig. 4. Prebreeding movement paths of AHY and HY American Tree Sparrows (*Spizelloides arborea*) tagged in 2019 and 2020. Individuals are represented by different colors, arrows indicate the final detections in the orientation of travel, black circles show active stations with no detections, and black squares show the tagging locations. Detections of two sparrows north of 50°N and one sparrow of unknown age were excluded. © Stadia Maps © OpenMapTiles © OpenStreetMap © Stamen Design.



were 93 nocturnal relocation events when birds (n = 62) were on the move at night, and the majority (96%) of the inter-station movements occurred in the northerly direction (Fig. 4). These nocturnal relocation events occurred from 19 February–4 May 2019 (median = 17 April 2019) and 4 February–25 May 2020 (median = 4 April 2020). All but three relocation events occurred during the 22 February–17 May pre-breeding migration season (two prior, one post), and big days for relocation were 22 April 2019 (n = 12) and 3–4 April 2020 (n = 14). Most individuals relocated on a minimum of one to two different nights. Although six individuals relocated on a minimum of three different nights when considering all the data, within the spatiotemporal scope of the recurrent events analysis, this number reduced to three (Fig. 5).

In the recurrent events analysis, nocturnal relocation events were strongly associated with weather conditions, with the daily hazard of departure increasing with higher temperature, higher pressure, and less cloud cover (Table 2; Fig. 6). The hazard of departure also increased with a lower u component of wind (i.e., a more easterly component), or alternatively, birds avoided departure in stronger westerlies. In addition to the weather effects, the daily hazard of departure was greater in 2020 than in 2019. Neither day of year, precipitable water, snow depth, v wind, nor age class were retained in the selected model, although there was no snow

Fig. 5. Event plot showing the nocturnal relocation events (green shape) for 62 American Tree Sparrows (*Spizelloides arborea*) in 2019 and 2020. Green triangles indicate nocturnal departures from the capture site whereas green circles indicate other relocation events. The gray lines show the period from capture to the terminal event when birds were detected at 44–45°N (final green circle) or the end of the study period on day 124 (black circles).

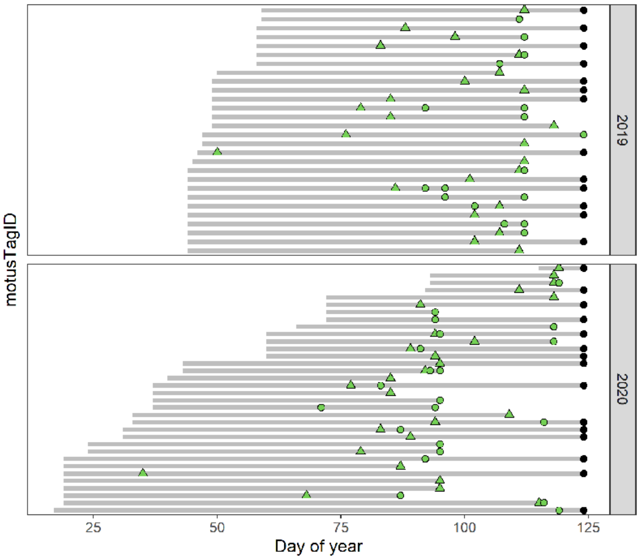


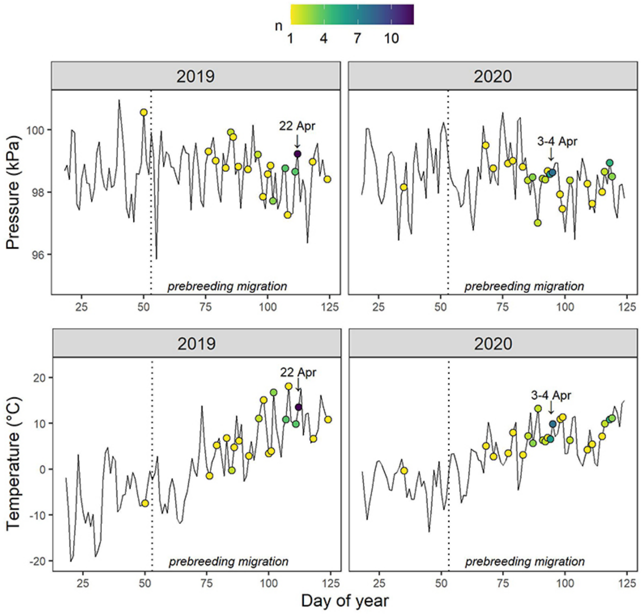
Table 2. Parameter coefficients (β ± robust SE) of the top Cox regression model of recurrent relocation events in American Tree Sparrows (*Spizelloides arborea*) using the spring data. The hazard ratio (HR) equals exp(β).

Parameter	β ± SE	HR	z	p
Year (2020)	0.540 ± 0.177	1.716	3.045	0.002
Pressure	0.622 ± 0.201	1.863	3.089	0.002
Temperature	0.224 ± 0.033	1.251	6.779	< 0.001
Cloud cover	-0.018 ± 0.006	0.983	-2.916	0.004
u wind	-0.079 ± 0.029	0.924	-2.702	0.007

cover (and therefore no snow cover variability) after 9 March 2019 and 1 March 2020 (day of year 68 and 61, respectively). For reference, daily u wind varied from -7.9 to 15.9 $m \cdot s^{-1}$ with an average of 2.3 $m \cdot s^{-1}$ (light westerly component). Daily v wind varied from -10.3 to 9.7 $m \cdot s^{-1}$ with an average of 0.5 $m \cdot s^{-1}$. V winds greater than a threshold of 5 $m \cdot s^{-1}$, which we assumed were likely to provide favorable tailwinds for northward migration, occurred on 13% of the possible dates. Although day of year was not retained in the top model, when included as the only covariate, the hazard for departure increased with day of year (β = 0.034 ± 0.007, z = 5.177, p < 0.001).

Nine birds (7 HY and 2 AHY) were detected in southern Ontario in the fall, during or after postbreeding migration (Fig. 7). In eight of these birds, all detections occurred during fly-bys between 17 October and 20 November. There were 38 nocturnal fly-bys during 13 nocturnal relocation events compared to only two diurnal fly-bys during two diurnal relocation events. These diurnal fly-bys began at 06:01 and 09:39, respectively. The ninth bird arrived at Old Cut on 8 November 2019 at 06:40, where it remained intermittently until leaving on 1 January 2020 at 07:50:00. This HY bird had been captured and tagged at this location. In the fall, no birds were detected outside of our study region, despite decent Motus coverage to the east and south (Fig. A1.1).

Fig. 6. Daily counts of nocturnal relocation events (symbols) by American Tree Sparrows (*Spizelloides arborea*) in relation to atmospheric pressure and temperature in 2019 and 2020 until day of year 124. In general, nocturnal relocation events occurred more frequently on days with higher pressure and temperature. Big days for movement occurred on 22 April 2019 (n = 12) and 3–4 April 2020 (n = 14). The vertical dashed lines indicate the onset of the prebreeding migration season as defined by eBird Status and Trends.



Stable-isotope analysis

Overall, δ^2H_f values differed among the three groups of birds with sufficient data (2019 AHY, 2020 HY, 2020 AHY; $F_{2, 40} = 6.63$ p = 0.003) but were similar between capture locations (p = 0.68; model $r^2 = 0.251$). Based on post hoc Tukey tests, δ^2H values were higher in 2019 AHY than in 2020 HY birds (diff = 10.8, p = 0.003), slightly lower in 2020 HY than in 2020 AHY birds (diff = -6.1, p = 0.074), and similar in 2019 AHY and 2020 AHY birds (diff = -4.8, p = 0.263). The larger difference between age classes in a single year than between years in a single age class suggests that age class may be a more important determinant of δ^2H_f than year. Lower δ^2H_f values among HY birds suggest that their feathers formed at a more northwesterly location than in AHY birds. However, likely origins spanned a broad region of the western breeding range, and differences among years and age classes were subtle (Fig. 8).

Fig. 7. Fall movement paths of American Tree Sparrows (*Spizelloides arborea*; n = 8) tagged in 2019 and 2020. Individuals are represented by different colors. Colored squares indicate the first detections in the fall, arrows indicate the final detections in the orientation of travel, black circles show active Motus stations with no detections, and black squares show the tagging locations. A ninth bird was only detected at Old Cut. © Stadia Maps © OpenMapTiles © OpenStreetMap © Stamen Design.

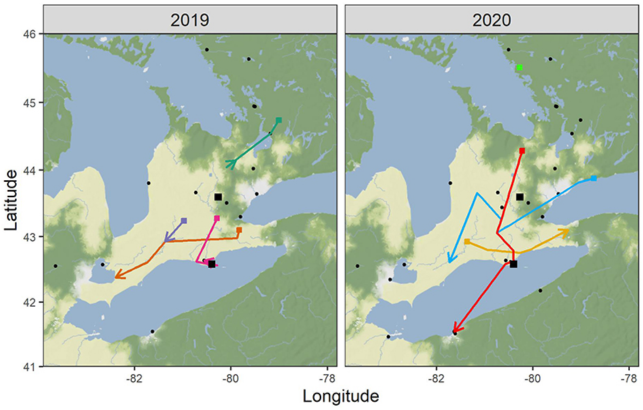
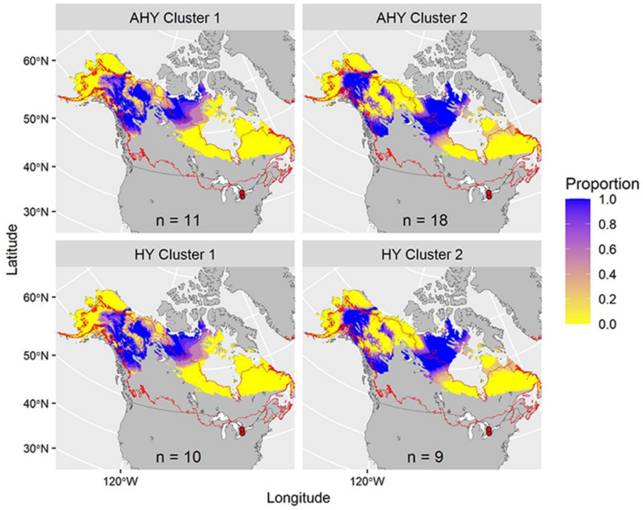


Fig. 8. Geographical assignments by age class (AHY, HY) and cluster for American Tree Sparrows (*Spizelloides arborea*). The scale of the map shows the proportional number of individuals assigned at a given cell, proportional to the maximum number of individuals in a given panel. The Boreal Forest (shapefile from Brandt 2009) is shown with a red outline. Capture sites are shown by the red circles. The map is based on a Lambert Conformal Conic projection.



DISCUSSION

To fill the information gap on the movement ecology of American Tree Sparrows, we tracked the landscape-level movements of individual birds from nonbreeding through to the early stages of pre-breeding migration using the Motus Wildlife Tracking System. Following capture, birds interspersed periods of residency with punctuated movements biased northwards. Early movements appeared to be dispersive and were largely contained to the study region of southwestern Ontario (~40,000 km²). Movements increased in frequency with day of year, and by the end of April, all birds had left the study region. Nine birds (15%) retained their tags, returned to the study region, and were detected by Motus stations in the fall. This suggests broad fidelity to a nonbreeding area, which is consistent with banding data (Brewer et al. 2018). Because only one bird returned to its tagging location for a period of residency, there was little evidence of precise nonbreeding site philopatry. In addition to providing new information about the migratory movements of a temperate wintering songbird, we found support for phenological tracking of mild conditions via weather-driven movements that mainly occurred at dusk or during the night.

Following capture, American Tree Sparrows remained near their capture site for variable lengths of time, departing over a protracted period from early February to late April. During capture site residency, variable detection rates were consistent with the movement of birds into and out of the detection range of the nearby Motus station during routine diurnal foraging and flocking activities interspersed with nocturnal inactivity. Such intermittent coverage is typical of Motus data (e.g., Crewe et al. 2019). About a third of the birds permanently departed their capture sites during daylight hours, which suggests localized dispersal during routine diurnal movements. Diurnal landscape-level relocations have also been documented in Motus-tracked Snow Buntings, which are a nomadic wintering species occupying the same study region as ours (McKinnon et al. 2019). In contrast to Snow Buntings, most departure events by American Tree Sparrows occurred during or after dusk and before dawn, suggesting that they had initiated pre-breeding migration. Typically, in songbirds, nocturnal flight behavior occurs during migration seasons, as birds engage in multi-hour, long distance migratory flights or shorter relocation flights within migratory stopover landscapes (Taylor et al. 2011). However, migratory movements also occur outside of strict migration seasons (Terrill 1987), including in American Tree Sparrows (Niles et al. 1969). Some of the early movements made by American Tree Sparrows in our study, especially those followed by relocations many weeks later, could be less migratory in nature. Because many sparrows remained in the study region to be detected on subsequent nights, our results suggest that nocturnal flights were relatively short in duration. More extensive tracking data for American Tree Sparrows will be needed to determine if short nocturnal flights persist throughout their entire migratory journey to breeding locations.

Nocturnal movements by American Tree Sparrows were strongly associated with mild weather conditions characterized by clear conditions (e.g., relatively high temperature, low cloud cover, and high barometric pressure). These results support the hypothesis of phenological tracking of climate, whereby birds advance their range northward as environmental conditions improve over the spring. Movement during favorable weather may improve visibility of navigational and habitat cues, may enhance flocking cohesion, and may reduce exposure to adverse abiotic conditions while in flight or when settling in a new patch of habitat. Movement at night could provide further benefits via reduced predation risk from diurnal predators and visibility of celestial bodies for navigation, all of which are key factors thought to favor nocturnality of migratory flights (Alerstam 2009). Relocation events were not associated with the v component of wind, which suggests that birds were not more likely to relocate in favorable winds for northward migration (i.e., +v wind). This lack of responsiveness to favorable winds for northward migration, which contrasts with prior studies focused on departures from stopover sites (Schmaljohann and Eikenaar 2017), could be because of the short duration and more dispersive nature of relocation flights in the nonbreeding range. In addition, westerlies dominate in our region and conditions for favorable northward migration were relatively infrequent. On the other hand, relocation events were associated with easterlies, which typically coincide with the passage of low pressure systems to the south and the arrival of unfavorable weather. This could indicate that birds moved north to avoid risking exposure to oncoming precipitation. Interestingly, the relocation event noted by Niles et al. (1969) suggested a southward escape response to harsh winter weather, whereas our study suggests a northward tracking of mild conditions.

By the time nocturnal movements were underway, our study region was mostly snow free. As a result, daily snow depth was neither important nor relevant for predicting nocturnal relocation events. Although snow depth did not drive landscape relocations, local snow cover may still regulate habitat use, local movement, and behavior in winter. American Tree Sparrows carry large fat reserves in winter, which could be an adaptation for greater fasting capacity in the event of low food availability (Rogers 2015). Based on occupancy models of Project Feeder Watch data, American Tree Sparrows tended to occupy sites with more snow, and they increased localized movement in the form of supplemental feeder visits during periods of abnormally cold conditions—but interestingly not greater snow depth (Zuckerberg et al. 2011). This suggests that icy conditions may be particularly challenging for American Tree Sparrows, being ground-based seedeaters in winter. Icy conditions were also implicated in the winter movement-mortality event reported by Niles et al. (1969).

Stable-isotope analysis of feathers combined with Motus data revealed some new insights into migratory connectivity. Nonbreeding American Tree Sparrows in southern Ontario likely originate from a broad region of the species' western breeding range, from southern Nunavut west to central Alaska. Breeding origins south and east of Hudson's Bay were less likely. Likely origins were loosely associated with the northern edge of boreal zone, as expected for this treeline-associated species. Motus data showed many birds heading northeasterly and along the east shore of Georgian Bay (Lake Huron) during pre-breeding migration, which may suggest a migratory route around rather than across the Great Lakes. Limited Motus coverage north of southern Ontario means we were not able to determine migration routes with any certainty. Prior banding data suggested that Ontario birds may derive from western populations with a northwest-southeast oriented migration, or maritime populations with a northeast-southwest oriented migration (Brewer et al. 2018). Our stable-isotope analyses support a western rather than maritime origin for birds wintering in southwestern Ontario. Finally, stable-isotope analyses suggest a more northerly origin of HY birds compared to AHY birds in 2020. Age-based differential migration or molt migration has been documented in other northern breeding birds (Marquiss et al. 2012, Hannah et al. 2020a); however, further research is needed to evaluate whether this is a general feature of American Tree Sparrow life history.

Age class was not a major driver of relocation timing in American Tree Sparrows in our study. In general, age and sex are expected to be important intrinsic drivers of migration phenology in songbirds. This is supported from theoretical models of optimal pre-breeding migration timing (Kokko et al. 2006, Morbey and Hedenström 2020) and comparative analyses showing that males migrate earlier than females (i.e., protandry), but more so among after-second-year birds than among second-year birds (Deakin et al. 2024). The ordering of pre-breeding migration timing by sex and age is also supported by species-specific studies of temperate wintering Snow Buntings (McKinnon et al. 2016). In addition to sex differences in timing, specimen collections of temperate wintering songbirds suggest that males tend to overwinter farther north than females (Baumgartner 1942). An important limitation of our study is the lack of sex information, due to the monomorphic nature of this species and a limited sample of feathers analyzed for genetic sexing. Future research on American Tree Sparrows should include the collection of intrinsic biological markers, such as feather, claw, or blood samples, for DNA-based sex identification to better characterize the interactive effects of age and sex on winter movements, habitat use, and phenology.

Although the proportional hazard model accounted for a significant amount of the variation in nocturnal movement event timing, much residual variation remained. Thus, in addition to the climate variables we considered, American Tree Sparrows may use additional ecological features or alternative weather conditions as cues to initiate migratory movements, and these may occur at different spatiotemporal scales and different lags. In terms of omitted extrinsic factors, seed availability may be an important factor to consider in future studies, because resource tracking is likely to be an important driver of movement strategies (Abrahms et al. 2021). We also did not track body condition, which is known to be an important correlate of migratory departure decisions (Schmaljohann and Eikenaar 2017). Future studies could use automated feeding and weighing stations to get at the interactive effects of food, body condition, and weather on movement decisions.

The American Tree Sparrow has experienced precipitous range-wide declines in recent decades and is currently a species of conservation concern (Rosenberg et al. 2016, COSEWIC 2024). Given the limited information on many aspects of the ecology of this species (Naugler et al. 2020), results from this study will help to fill some important knowledge gaps. Our Motus tracking results suggest that individuals wintering in southern Ontario reside in the region for a minimum of six months, or half of the annual cycle. Therefore, until specific mechanisms for these declines are better understood, management actions directed at reducing mortality on the nonbreeding grounds seem beneficial. Much of southern Ontario, where this study took place, along with parts of southern Québec, represent the bulk of the nonbreeding range for this species in Canada (Fink et al. 2023). Within this region, agricultural land use has changed dramatically whereby areas once dominated by pasture and forage have been replaced by intensive row crops (Fyson et al. 2024), resulting in the extensive loss of overwintering habitat (Naugler et al. 2020). Because of attraction by residential bird feeders during winter, collisions with windows (Dunn 1993, Kummer and Bayne 2015) and predation by domestic cats (Blancher 2013, Pyott et al. 2024) are also potential sources of mortality.

American Tree Sparrows face additional threats after departing from the nonbreeding grounds in southern Ontario. Frequent climate extremes in recent decades, especially during spring, have disproportionately impacted the mid-latitudes in the Northern Hemisphere (Horton et al. 2015, La Sorte et al. 2016). Given that American Tree Sparrows are exposed to these conditions during northward migration in early spring, this period of the annual cycle could also pose risks to American Tree Sparrow survival. Mitigating the effects of climatic extremes will be difficult until further insights into the timing, routes, and stopover habitats used during migration are better understood. Our stable-isotope analysis indicates that birds overwintering in southern Ontario likely come from a broad extent of the breeding range, suggesting that migratory connectivity is likely low. This result emphasizes the wide range of jurisdictions responsible for management of the breeding range for this species (i.e., at least five provinces, territories, and states). Given what little is known about habitat use, local abundance, and distribution, collaborative surveys across portions of its vast northern breeding range will be necessary to understand how these habitats may be changing, especially in response to rapid climate change.

Author Contributions:

YEM: conceptualization, Motus data analysis, lead writer. KAH: project principal investigator, conceptualization, writing. JNC: conceptualization, field work, editing. JWK: analysis and write-up of stable-isotope data, editing. SM: conceptualization, field work, editing.

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Data Availability:

Relevant data and code are available on Dryad: https://doi.org/10.5061/dryad.cc2fqz6hk.

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APPENDIX 1

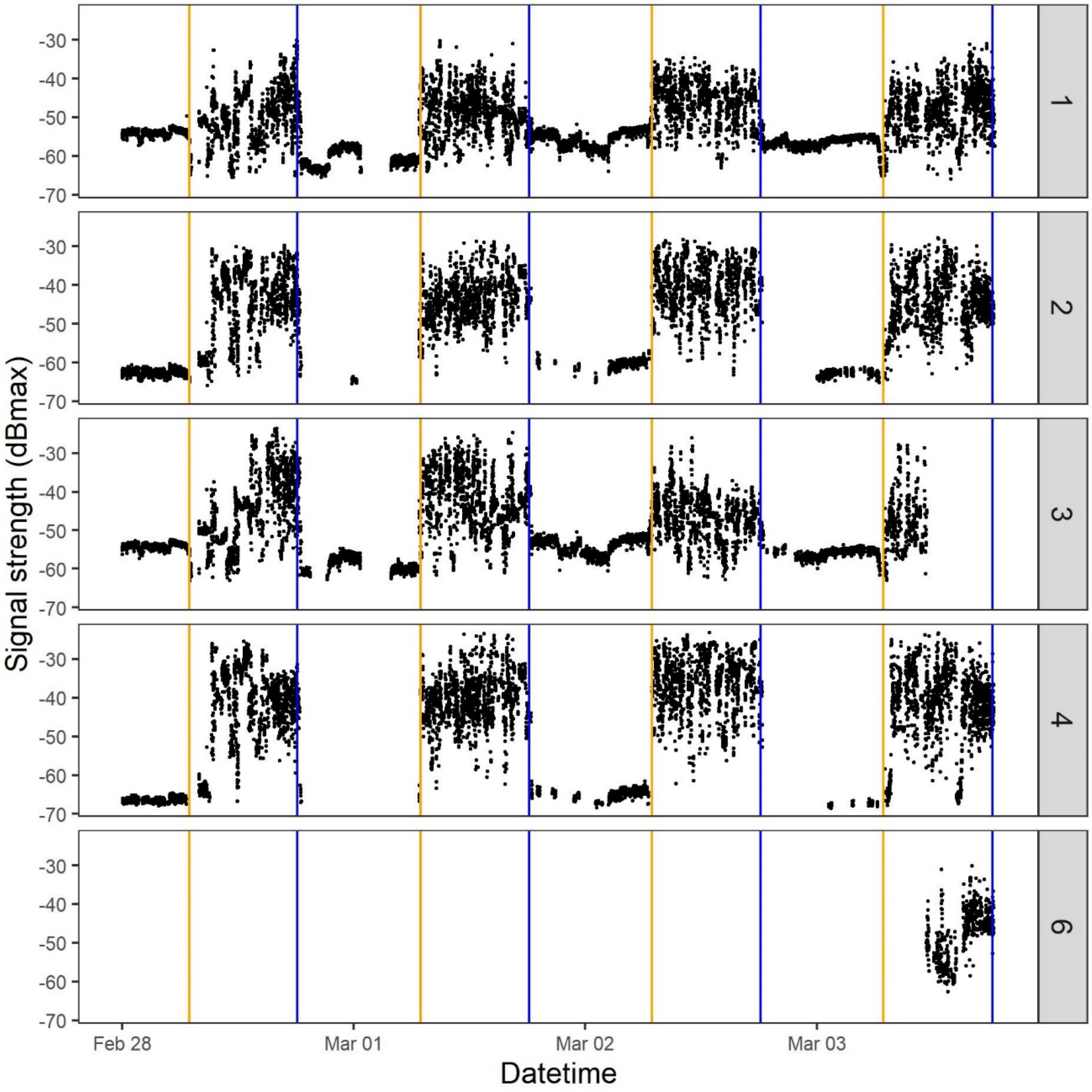

Fig. A1.1. Exemplar Motus detection data for a single bird at the Old Cut Motus station. Shown are signal strength (dB relative to the digital maximum) versus time on five dates at each of five antennas. Also shown are sunset (blue vertical lines) and sunrise (orange vertical lines). At night, low signal strength variability or no data suggest that birds are roosting. High signal strength variability during the day indicates that birds are moving and presumably engaging in routine diurnal activities like foraging and flocking. Gaps in the detection histories occur because detection is imperfect.

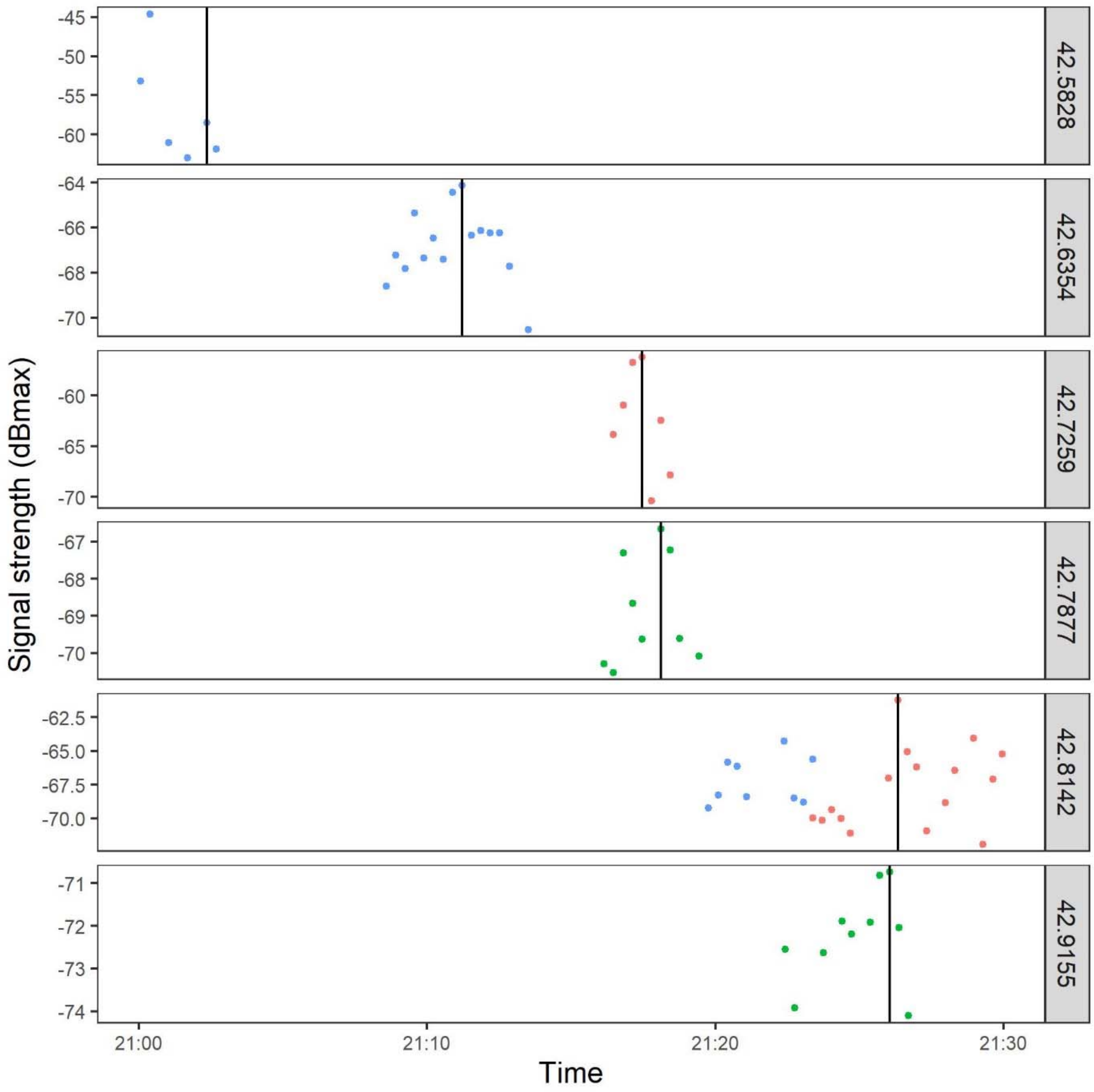

Fig. A1.2. Exemplar Motus detection data for a single bird showing its departure from Old Cut (top panel) and nocturnal fly-bys at five Motus stations (lower panels). Shown are signal strength (dB relative to the digital maximum) versus time at each of six stations sorted by latitude. Within a panel, different colors represent different antennas. Fly-bys are isolated and short sequences of detections at a single Motus station and antenna. They show a pattern of increasing then decreasing signal strength, although the data are noisy. Fly-bys likely characterize a nocturnal flight. In this example, the ordering of fly-bys by latitude indicates that the nocturnal flight is northward.

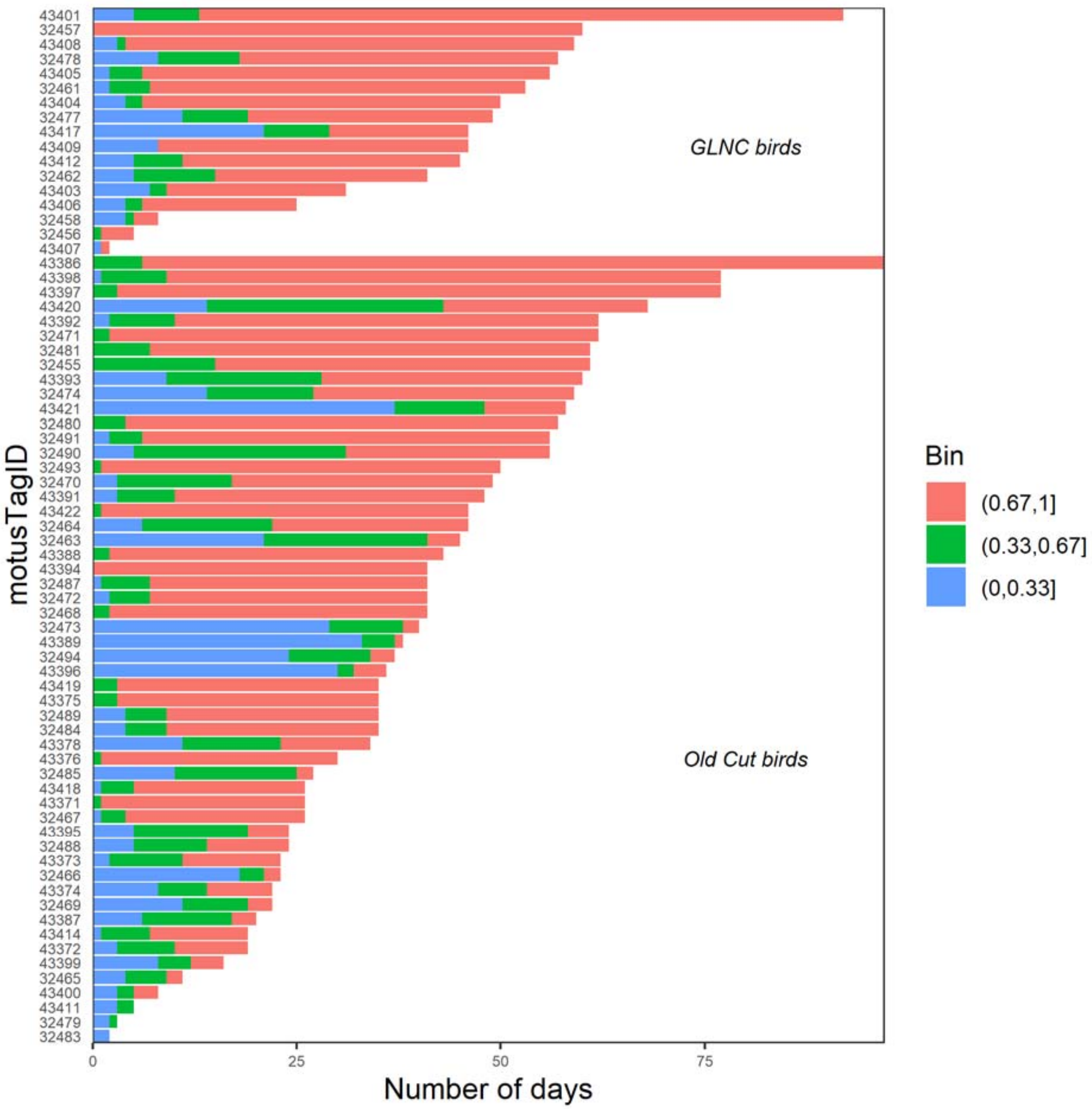

Fig. A1.3. A representative of data coverage between sunrise and sunset for American Tree Sparrows tracked by Motus (n = 71). The stacked bars show the number of days with diurnal detections. The colors represent different hourly detection rates. Red indicates that tags were detected at least once during 67-100% of the hourly periods of a given day; green indicates that tags were detected during 33-67% of the hourly periods; and blue indicates that tags were detected during fewer than 33% of the hourly periods. Tags are sorted by capture site (GLNC birds above and Old Cut birds below) and number of days with detections.

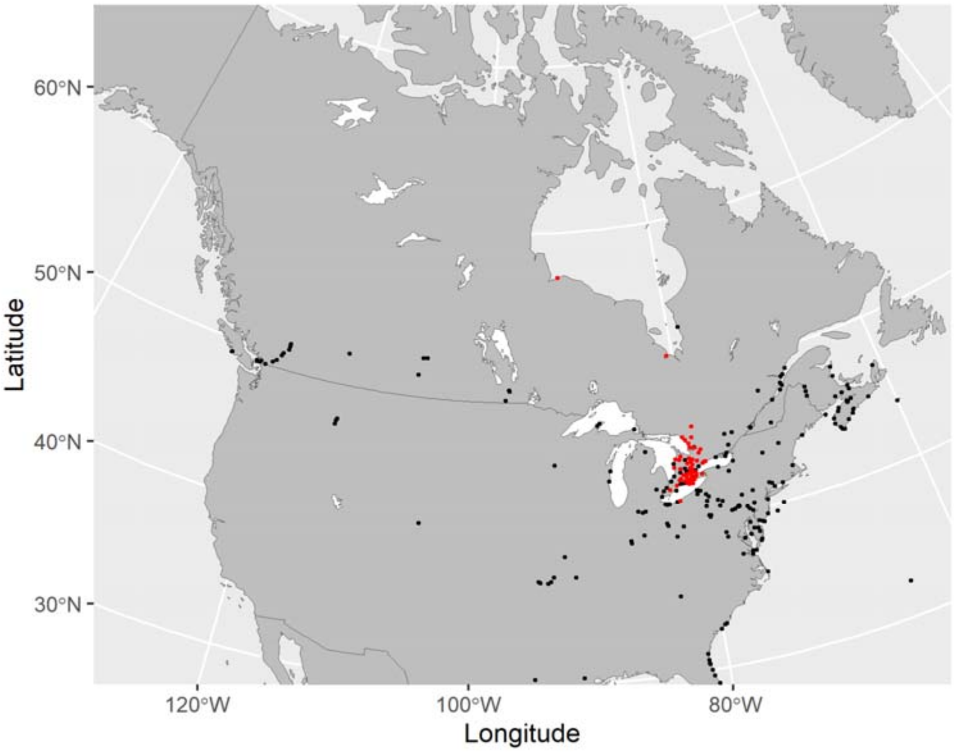

Fig. A1.4. Locations of active (black circles) and used (red circles) Motus stations in North America during the temporal extent of our study of American Tree Sparrows. Stations were active for at least 100 days within the 12 February 2019 to 21 November 2020 period. The map is based on a Lambert Conformal Conic projection.