Euphagus carolinus (Rusty Blackbird) from two different breeding populations in northeastern North America exhibit chain migration yet use the same region for stopover

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ABSTRACT
Bird populations within the same species may follow different migratory strategies and phenology depending on their breeding location and latitude, and migratory strategies may be influenced by important stopover sites. Understanding these strategies and identifying important stopover sites is crucial for the conservation of species with regionally varying population trends. In this study, *Euphagus carolinus* (Rusty Blackbird) from 2 populations in eastern North America were affixed with NanoTag (Lotek) transmitters and tracked using the Motus Wildlife Tracking System to determine migratory routes and connectivity, stopover locations, and wintering areas. During fall migration, birds tagged at Observatoire d'oiseaux de Tadoussac, Québec and breeding sites in New England maintained separate migratory routes north of 43° latitude, as indicated by positive Mantel statistics of migratory connectivity, before converging on stopover areas in the Chesapeake and Delaware Bays region of the mid-Atlantic U.S. Migratory strategy differed between the 2 populations: birds from New England spent ~2 months longer at breeding latitudes than birds from Québec, and Québec birds spent more time at fall stopover sites and wintering latitudes. Birds from both populations made >1-week stopovers during spring and fall migrations and made long-distance (up to 645 km) nocturnal flights. The few winter detections suggested that *E. carolinus* from New England wintered at more southern latitudes than birds from Québec. Land cover data around stopover sites indicated that *E. carolinus* were positively associated with percent cover of wooded wetlands, croplands, and hay/pasture. Results from this study could help identify and protect regionally important stopover and wintering areas for *E. carolinus*, a species that has experienced dramatic long-term population declines linked to habitat loss in the nonbreeding range.

Keywords: automated radio-telemetry, chain migration, migratory connectivity, Motus, Rusty Blackbird, stopover

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LAY SUMMARY

- Once common in North America, *Euphagus carolinus* (Rusty Blackbird) populations have declined by >90% over the past century.
- Loss of forested wetlands on wintering grounds and stopover sites may have contributed to the decline.
- *Euphagus carolinus* congregate in large numbers at some stopover and wintering areas, so identifying and protecting these areas may help the population recover.
- Birds were captured at two sites, in Québec and New England, outfitted with NanoTag (Lotek) transmitters, and tracked during migration and winter using Motus, a continent-wide network of receiving stations.
- Results from the tracking show that both populations use the Chesapeake and Delaware Bays area extensively for stopovers.
- Stopovers also occurred in the St. Lawrence Plain east of Lake Ontario and along the New England coast.
- *Euphagus carolinus* from the two populations differed in migratory strategy: birds from New England spent more time at breeding latitudes, while birds from Québec spent more time at fall stopover sites.
- Regional land managers could use Motus detections from this study to identify critical stopover sites for *E. carolinus* from multiple populations.

***Euphagus carolinus* (Quiscale rouilleux) provenant de deux populations reproductrices distinctes dans le nord-est de l'Amérique du Nord présente une migration en chaîne mais utilise la même région comme halte migratoire**

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RÉSUMÉ
Les populations d’oiseaux au sein d'une même espèce peuvent adopter des stratégies et phénologies migratoires différentes selon leur lieu et latitude de nidification et ces stratégies peuvent être influencées par d’importantes haltes migratoires. La compréhension de ces stratégies et l’identification des haltes migratoires importantes est cruciale pour la conservation des espèces dont les tendances démographiques varient régionalement. Dans cette étude, des Quiscales rouilleux (*Euphagus carolinus*) provenant de deux populations de l’est de l’Amérique du Nord ont été munis de nano-émetteurs et suivis à l’aide du Système de surveillance faunique Motus afin de déterminer les trajets, la connectivité et les haltes migratoires, ainsi que les sites d’hivernage. Pendant la migration automnale, les oiseaux de l’Observatoire d’oiseaux de Tadoussac, Québec et de la Nouvelle-Angleterre ont maintenu une connectivité migratoire distincte au nord du 43° parallèle, comme mesuré positivement par le test Mantel de connectivité migratoire, avant de converger vers des haltes migratoires dans les régions des baies de Chesapeake et de Delaware des états américains côtiers. La stratégie migratoire diffère entre les deux populations, les oiseaux de la Nouvelle-Angleterre passant plus de temps aux latitudes de reproduction, et les oiseaux de Québec passant plus de temps aux haltes automnales et aux latitudes d’hivernage. Les oiseaux des deux populations ont effectué des haltes de plus d'une semaine lors des migrations de printemps et d'automne et des vols nocturnes sur de longues distances (jusqu'à 645 km). Peu de Quiscales rouilleux hivernants ont été détectés, mais les oiseaux de la Nouvelle-Angleterre ont été détectés hivernant à des latitudes plus méridionales que les oiseaux de Québec. Les données sur l’occupation des terres autour des haltes et zones d’hivernage indiquent que le Quiscale rouilleux est associé à un pourcentage de couverture de zones humides boisées, de terres cultivées, de foin et de pâturages. Le Quiscale rouilleux a connu un déclin spectaculaire de sa population au cours du siècle dernier, principalement en raison de la perte d’habitat en dehors de son aire de nidification. L’identification et la protection des haltes migratoires et des aires d'hivernage d’importance régionale pourraient contribuer à stabiliser les populations de Quiscales rouilleux.

Mots-clés : télémetrie automatisée, migration en chaîne, connectivité migratoire, Motus, quiscale rouilleux, halte migratoire

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INTRODUCTION

Migratory birds in North America employ a diversity of annual time-budgeting strategies, thought to optimize survival and reproductive capacity (Newton 2008). Strategies vary from largely sedentary species that move short distances during the nonbreeding season in response to regional weather conditions and/or food availability, to species that breed at boreal and Arctic latitudes and migrate to South America. Some populations within the same species may follow different strategies leading to patterns such as "leap-frog" migration, where northern breeding populations migrate greater distances and winter at more southern latitudes than southern breeding populations; or "chain" migration, where northern breeding populations winter at the northernmost latitudes and the geographic structure of populations is maintained during the nonbreeding season (Fraser et al. 2018, Rueda- Hernández et al. 2023). Alternatively, populations from different breeding regions may mix throughout the wintering range. Migratory connectivity measures the degree of segregation between breeding populations during migration and winter (Marra et al. 2006, Bégin-Marchand et al. 2021). Understanding the degree of migratory connectivity and spatial structure of migratory routes and wintering areas for species of conservation concern is of critical importance, especially for species whose population trends may vary regionally (Webster and Marra 2005, Marra et al. 2006). Additionally, in some species individuals within the same population may follow different migratory strategies based on age or sex (Woodworth et al. 2016).

Stopover locations may play an important role in shaping migratory strategies of some species, in particular those that take advantage of seasonally abundant food resources (e.g., shorebirds in Delaware Bay; Dunne et al. 1982). In turn, the migratory strategy may influence the selection of stopover locations, as longer distances and non-stop migratory flights require larger fuel loads (Smetzer and King 2018). Geographic barriers to migration such as waterbodies for landbirds, continental land masses for waterbirds, and other expanses of unsuitable habitat also influence stopover site selection (Buler and Moore 2011). Stopover may be as short as a brief break from flying to rest or feed, or may be more than a month in duration and sometimes include molt (Smetzer and King 2018, Tonra and Reudink 2018, Morales et al. 2022, Poirier et al. 2024). Advancements in tracking technology have revealed that prolonged migratory stopovers (>1 week) are more common than previously thought among many groups of birds, including waterfowl, shorebirds, and passerines (McKinnon and Love 2018, Smetzer and King 2018). Identification and protection of key stopover areas for species of conservation concern could be important for recovery of these species, especially if they concentrate at stopover sites or form flocks during migration. Additionally, multiple species may utilize important stopover sites, especially those near geographic barriers to migration (Buler and Moore 2011).

In this study, we used the Motus Wildlife Tracking System (hereafter Motus; Taylor et al. 2017), a continent-wide network of automated VHF receivers, to examine migratory strategy, connectivity, and stopover locations of *Euphagus carolinus* (Rusty Blackbird), a species of conservation concern in eastern North America. *Euphagus carolinus* populations declined by >90% over the past century for reasons that are still unclear (Greenberg and Droege 1999, Greenberg and Matsuoka 2010, Evans 2021). Habitat loss in the nonbreeding range from large-scale conversion of floodplain forests to agricultural lands may have driven the decline, but other factors such as methylmercury accumulation, agricultural blackbird-control programs, blood parasites, competition with other blackbird species, loss and degradation of boreal wetlands, habitat fragmentation, and climate change may be limiting the species' ability to rebound (Hamel 2009, Barnard et al. 2010, Greenberg and Matsuoka 2010, Edmonds et al. 2010, Powell et al. 2010, McClure et al. 2012, Luepold et al. 2015). Christmas Bird Count (CBC) annual indices suggest that *E. carolinus* populations declined

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steeply until the 1990's and have since rebounded slightly during 1993-2021 (Meehan et al. 2022). Breeding Bird Survey data suggest a similar long-term decline and show that populations were stable during 2011–2021 (Smith et al. 2023a). Ten-year trends from eBird data differed, and were strongly negative during winters 2011–2021 (Fink et al. 2023). *Euphagus carolinus* are currently listed as a species of "Special Concern" under the Species at Risk Act in Canada, a "Species of Concern" by the U.S. Fish and Wildlife Service, a "Vulnerable" species by the International Union for Conservation of Nature, and a "Common Bird in Steep Decline" by Partners in Flight (Environment Canada 2015, Rosenberg et al. 2016, U.S. Fish and Wildlife Service 2021, BirdLife International 2024). Identification of important migratory stopover and wintering sites is an objective for recovery of *E. carolinus*, since the species is known to concentrate at such locations for extended periods of time where they would be vulnerable to direct effects of habitat loss or degradation (Environment Canada 2015, Wright et al. 2018).

Euphagus carolinus breed continent-wide in the boreal forest of North America and migrate to wintering sites in the Mississippi Alluvial Valley and Southeastern Coastal Plain (Hamel and Ozdenerol 2009, Avery 2020). During all seasons, *E. carolinus* are associated with forested wetlands, where they primarily feed on aquatic invertebrates and nuts found in damp soil and shallow water (Greenberg et al. 2011, DeLeon 2012, Newell et al. 2003, Mettke-Hofmann et al. 2015, Evans et al. 2021). Foraging conditions at stopover and wintering sites may depend on precipitation and water levels of floodplain forests, and abundance data during stopovers and winter suggest high variability between years (Luscier et al. 2010, Newell 2010, DeLeon 2012, Wright et al. 2018a, Kolbe and Grinde 2019). Previous stable isotope, tracking, and genetic studies have shown a geographic divide in *E. carolinus* populations, where birds breeding west of James Bay (Ontario) winter in the Mississippi Alluvial Valley and birds breeding east of James Bay (Québec) winter on the Southeastern Coastal Plain (Hobson et al. 2010, Johnson et al. 2012, Wright et al. 2018a, 2021, Wilson et al. 2021). Population declines estimated from Christmas Bird Count data were similar between the Lower Mississippi Alluvial Valley and Southeastern Coastal Plain Bird Conservation Regions (Niven et al. 2004).

Recent tracking studies, now possible with the miniaturization of tracking devices, have shown that stopover is an important component in the migratory strategy of *E. carolinus* (Johnson et al. 2012, Wright et al. 2018a, 2021, Grinde et al. 2021). To date, most published tracking data have come from the population wintering in the Mississippi Alluvial Valley (Johnson et al. 2012, Wright et al. 2018a, 2021), with only one GPS track representing the eastern population. Tracked birds stopped at multiple sites for extensive periods of time (>7 days, up to 58 days) during fall migration alternating with long distance (>300 km) migratory flights (Johnson et al. 2012, Wright et al. 2018, 2021). Spring migration was more rapid than the leisurely fall migration, but most birds still made at least one prolonged stopover (>7 days) in spring (Johnson et al. 2012, Wright et al. 2020). The lengthy stopovers made by *E. carolinus* have been likened to staging behavior of shorebirds, and there is evidence of molt-migration during spring stopover (Wright et al. 2018a, 2018b). *Euphagus carolinus* often concentrate into large flocks during stopover, so identifying and protecting key stopover sites could have high conservation value (Environment Canada 2015).

In this study, we affixed NanoTag (Lotek) transmitters to *E. carolinus* from northeastern North America and tracked their movements during both spring and fall migrations and winter using Motus. The recent proliferation of automated Motus radio-telemetry receivers now enables tracking of small birds at continental scales without having to recapture individual birds, which has been necessary for similar studies using GPS tags or geo-locators (McKinnon and Love 2018, Smetzer and King 2018). We combined data from birds captured at 2 locations: Observatoire d'Oiseaux de Tadoussac, Québec (hereafter

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Québec) where birds were captured during fall migration in years 2017–2020, and New Hampshire and Maine (hereafter New England) where birds were captured at nest sites during the 2018, 2019, and 2021–2023 breeding seasons. While birds tagged in New England represent a regional breeding population, birds captured and tagged at Québec during fall migration could have nested over a vast area of the eastern boreal forest (Brisson-Curadeau et al. 2020). The objectives of this study were (1) to determine migratory routes, stopover locations, and wintering areas of *E. carolinus* in eastern North America; (2) to compare migratory strategies of birds from the 2 regions; (3) to determine the degree of spatial and temporal migratory connectivity between the 2 origins during migration; and (4) to identify land cover characteristics of stopover locations. We predicted that eastern *E. carolinus* would migrate to wintering sites in the Southeastern Coastal Plain, based on the geographic divide formed by the Appalachian Mountains described in other studies, but did not predict further geographic segregation in wintering populations. We predicted that the more southern New England breeding population would arrive at their breeding grounds earlier in the spring than birds tagged in Québec, and that fall migration would begin earlier for Québec birds. We predicted birds from Québec would spend more time at fall and spring stopover sites than birds from New England. Finally, we predicted that *E. carolinus* stopover locations would be positively correlated with percent cover of wooded wetlands from satellite imagery.

METHODS

Study Areas and Capture Methods

[LEVEL HEADING 3] **Québec**

Observatoire d'oiseaux de Tadoussac (48.1591°N, –69.6623°W) is located in the south of the Labrador peninsula in La Haute-Côte-Nord region, Québec, Canada. The bird observatory is a member of the Canadian Migration Monitoring Network, and standardized banding and migration monitoring surveys have been conducted there since 1993. The banding station is situated 55 m above sea level on the dunes of Tadoussac, a sandy marine terrace adjacent to the estuary of the St. Lawrence River and is surrounded by boreal forest. The water barrier created by the estuary concentrates migratory birds following the coastline through the region (Ibarzabal 1999, Gagnon et al. 2011). The habitat immediately surrounding the banding station is open and sandy, with patches of stunted boreal vegetation. Due to the openness of the vegetation at the site, most migrants (including *E. carolinus*) are observed passing over or through the site rather than using the habitat for stopover. Based on daily migration surveys, flocks of *E. carolinus* typically migrate through the site in the early morning following the passage of cold fronts and are infrequently observed under other circumstances.

From 2017 to 2020, we captured *E. carolinus* during fall migration between September 13 and October 5 using a mist-net configuration to target this species (Table 1 and Supplementary Material Table S1). We deployed 9-m, 32-mm mesh mist nets in 2 squares surrounding a playback speaker and opened nets daily from 0530 to 0700 (EDT). We attached Lotek Avian NanoTags (Lotek Wireless, Inc., Newmarket, ON, Canada) to the captured birds with leg-loop harnesses (Rappole and Tipton 1991) made from 1.0-mm elastic thread with a polyester liner.

[LEVEL HEADING 3] **New England**

The New England study area encompasses the Upper Androscoggin watershed in Coos County, New Hampshire and Oxford County, Maine, USA and the Upper Kennebec watershed in Franklin County, Maine. The study area extends between 44.4889°N and 45.1681°N in latitude and between –70.8579°W and –71.3379°W in longitude. The terrain is

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mountainous, with *E. carolinus* nesting at elevations of 350–820 meters above sea level (m.a.s.l.). Extensive forests cover ~90% of the watersheds, evenly divided between coniferous, deciduous and mixed forest types (Publicover et al. 2003). Forest management for various wood products is the predominant land use. The landscape includes numerous ponds and lakes, with some exceeding 200 ha; wetlands, many of which are beaver influenced, occupy roughly 3.6% of the watershed's area (Publicover et al. 2003).

From 2019 to 2023, we captured adult *E. carolinus* near their nests in 6-m, 60-mm mesh mist nets and we removed nestlings from the nest by hand (Table 1 and Supplementary Material Table S1). Capture and tagging activities occurred when nestlings were 7–10 days old in late May–June. In 2022 we captured 2 adult females and 1 juvenile from unknown nest sites in early July as they foraged along a roadside within the study area. We attached Lotek NanoTags in a similar fashion to those at Québec, but used 1.5-mm stretch bead cord (Stretch Magic, Pepperell Braiding Company, Pepperell, MA, USA) in 2018, 2019, and 2021 and a combination of 1.5-mm stretch bead cord and ear loop elastic cord from Single-use Masks (Jiangsu Excellence Medical Supplies Co., Ltd., Changzhou, China) in 2022 and 2023 (see Supplementary Material Table S1 for ages and sexes of tagged birds by site and year and Supplementary Material Table S2 for models, burst intervals, and lifespans of NanoTags used).

In 2018, we deployed three archival "store-on-board" GPS tags (PinPoint-50, Lotek Wireless, Inc., Newmarket, ON, Canada) on adult males. These tags attempted fixes once every 3–4 days during migration and once every 15 days during the winter, with points split between before and after sunrise to capture roosting and foraging locations.

Motus Data Filtering

We analyzed all data in R statistical software version 4.3.3 (R Core Team 2024). We downloaded NanoTag detection data from the Motus Wildlife Tracking System server using the R package *motus* 6.0.1 (Birds Canada 2023) on January 2, 2024. We filtered the detection data to eliminate false detections following methods suggested in the Motus R book (Crewe et al. 2018). We discarded all runs of 2 detections and graphically evaluated runs of 3 or more detections. To visualize detections of tagged birds, we developed a series of plots and tables (including lat/long position by date, map of detections, table of transitions between receivers, and plots of signal strength by time and antenna) using the application *shiny* 1.7.4 (Chang et al. 2022). We removed tags detected only at the capture locations from the dataset.

Identification of Stopovers

Once we had eliminated presumed false detections, we identified start and end times of stopovers and migratory flights. Since previous research has shown that *E. carolinus* make regional-scale movements during stopovers (10–35 km; Wright et al. 2018a), we did not define criteria a priori to automatically identify stopover periods. Rather, we used latitude by date plots and transition tables to identify periods of time greater than one day for which there was little change in latitude in a migratory direction (south in fall, north in spring). We defined stopovers as a minimum of two detections separated by at least 24 hours that were at a similar latitude and within 100 km distance between receivers. We did not consider stopovers of <24 hr, to distinguish between brief pauses between migratory movements and the decision to spend multiple days at one location (Bayly et al. 2018). We calculated stopover duration as the time difference in days between the first and last detection of the stopover.

Many of the *E. carolinus* tagged at Observatoire d'oiseaux de Tadoussac unexpectedly remained at or near the capture site for days to weeks after capture. We

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analyzed these stopovers at Tadoussac separately from stopovers identified elsewhere along the migration route, since they may have been influenced by the tagging process.

Identification of Migratory Flights

We took a similar approach for identifying migratory flights to that for identifying stopovers, and rather than defining criteria a priori, identified time periods for which there were sequential detections at multiple receivers in a migratory direction within a ~24-hr period. These migratory flights appeared as vertical lines in the plot of latitude by date in the shiny application. In cases, when a series of detections at a stopover site immediately preceded detections at other receivers indicating a migratory flight, we recorded a known departure time for that flight. The maximum duration considered a migratory flight was 27.6 hr; however, this flight and others likely included some periods of stopover.

To estimate flight speed during migratory flights, we calculated the distance between the first and last receiver of each flight and the difference in time between the first detection at the first receiver and the first detection at the last receiver. We included only flights exceeding 30 km and 30 min in the flight speed estimates, since estimated speeds of shorter flights are more influenced by simultaneous detections between receivers and differences in antenna geometry than estimates for longer flights. We excluded flights exceeding 12 hr in duration from flight speed estimates to reduce the likelihood of including periods of stopover. The distances and durations reported are considered minima, since we did not identify obvious start or end times for many flights.

Statistical Methods

[LEVEL HEADING 3] Stopovers at Tadoussac

For *E. carolinus* that stopped over at Tadoussac after capture and had known stopover durations based on clear departure events detected by local Motus receivers, we used the banding data in a global linear model to test effects of age, sex, body condition (residual of a model of mass by age and sex), handling time (min, release time-capture time), and capture date (day of year) on stopover duration. We used a backward stepwise selection approach using second order Akaike's Information Criterion for small sample sizes (AIC_c) and the dredge function in R package *MuMIn* 1.47.1 (Bartoń 2022) to select a final model. We tested fat score independently since birds captured in 2020 lacked scores.

[LEVEL HEADING 3] Stopovers elsewhere

We compared stopover duration between birds from New England and Québec and between fall and spring using an analysis of variance (ANOVA) on models both with and without an interaction between site and season. Unlike stopovers at Tadoussac, which included presumed arrival and known departure times, most stopovers elsewhere lacked Motus receiver detections that indicated arrival or departure times and dates. The GPS tag recorded a point once every 4 days during migration. Thus, it is best to interpret stopover durations at sites other than Tadoussac as minimum stopover durations.

[LEVEL HEADING 3] Migratory strategies

To evaluate migratory strategies of *E. carolinus* captured in Québec and New England, we fit a generalized additive mixed effects model (GAMM) using R package *mgcv* 1.8-42 (Wood 2011) to assess differences in latitude by date between the two populations. Previous research has shown that *E. carolinus* make both long, non-stop migratory flights and prolonged stopovers during migration (Wright et al. 2018a, 2021), which would yield a nonlinear step-shaped pattern in latitude by date for each bird if detections were constant. Additionally,

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detection data spanned the full calendar year, and it was desirable to combine data from different seasons so that predicted values at the beginning and end of the migratory seasons, when birds were stationary at breeding and wintering areas, would fall within the range of the observed data. The flexible nature of GAMMs can accommodate these nonlinear patterns. The dataset used in the GAMM model was a reduced version of the Motus detection data that included only the final detection of an individual each day (UTC time zone). We included locations from the New England GPS tag.

We used a cyclical cubic regression spline to model latitude by day of year for each population across the full calendar year, allowing the smoother to take a different shape for each population by using an interaction term between date and population; we opted not to fit a global smoother between the two populations (Pedersen et al. 2019). We included a random effect smooth term to account for uneven detection rates of each bird and fit this term as a factor smooth to allow for different patterns in migratory strategy (e.g., stopovers at different latitudes) between individuals of the same population. A continuous autocorrelation structure accounted for temporal autocorrelation in detections of the same individual at lag one, while allowing for gaps in detections. A random intercept term for year accounted for differences in migration timing by year. We based the structure of the model on guidance provided in Pedersen et al. (2019) as shown in Equation (1) in package *mgcv* syntax. We fit separate models of the same structure on a reduced dataset including only individuals of known age and sex as additional cyclical smoothed terms (e.g., Sex + s(Date, by Sex, bs = ”cc”)).

Latitude ~ Site + s(Date, by Site, bs = ”cc”, m = 2) + s(TagID, Date, bs = ”fs”, m = 1) + s(Year, bs = ”re”) , correlation = corCAR1(form = ~Date|yearID) (1)

We evaluated model terms in the GAMM model of latitude by date by fitting global and reduced models and comparing model fit using AIC_c on the *lme* component of the model with R package *AICcmodavg* 2.3-1 (Mazerolle 2020). Further evaluation of model fit involved examining plots of residuals and applying the *gam.check* function in package *mgcv*. We calculated predicted values and 95% confidence intervals from the final model for each population and date (at the population level excluding random effects) and evaluated these values to determine differences in migratory strategy between the 2 populations.

[LEVEL HEADING 3] **Migratory connectivity**

To test for spatial migratory connectivity of *E. carolinus* from the 2 capture sites (Québec and New England), we used a moving window of latitude to measure migratory connectivity en route during fall migration (Bégin-Marchand et al. 2020, 2021). This method works well for aggregating detections of individuals when the detection data are irregular and incomplete, as is the case with Motus data across a network of receivers with uneven spatial density. We used a window of 2° in latitude, created grid cells of 0.1° latitude by 0.1° longitude within each window, and built a detection matrix that recorded the presence or absence of each individual in each grid cell. A second matrix included a row for each individual detected in the latitude window and a column for each capture site filled with ones or zeros to assign individuals to sites. We then converted each matrix to a Bray-Curtis dissimilarity matrix using R package *vegan* 2.6.4 (Okansen et al. 2022) and calculated a Mantel statistic with bootstrapped 95% confidence intervals between the 2 dissimilarity matrices using R package *ecodist* 2.1.3 (Goslee and Urban 2007). Using this method of computing the Mantel statistic within latitude bands enables us to measure connectivity of birds from the two capture locations during migration without knowing exact locations of wintering areas, stopover sites, or breeding locations (Québec birds only).

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To test for temporal migratory connectivity of *E. carolinus* during fall migration, we used a similar method as for spatial connectivity, but instead of using latitude by longitude grid cells for the detection matrix we used week of the year, and for each individual we recorded week/s of detection within each latitude window of two degrees (Bégin-Marchand et al. 2021). We then calculated a Mantel statistic with confidence intervals as above.

[LEVEL HEADING 3] **Land cover at stopover sites**

To determine nonbreeding habitat associations of *E. carolinus*, we compared land cover classifications surrounding Motus receivers that detected *E. carolinus* during migratory stopovers to land cover surrounding receivers that did not detect *E. carolinus* over a multiple-day period. We downloaded 2021 land cover data from satellite imagery of 30-m spatial resolution from the National Land Cover Database (NLCD; Dewitz 2023). To eliminate receivers outside of the nonbreeding range, we used the coordinates of receivers that detected *E. carolinus* during migration to create a convex hull polygon using R package *sf* 1.0-14 (Pebesma 2018) and included only the receivers without stopover detections that were inside the polygon. We created buffers of 15-km and 5-km radii around each receiver and calculated percent cover of each NLCD class within the buffers. The 15-km radius represented the theoretical detection range of a 9-element Yagi antenna typical of most Motus receivers (Taylor et al. 2017), while the 5-km radius reflected an assumption of reduced NanoTag detectability during stopovers than on high-altitude migratory flights (Crewe et al. 2019). We excluded several stopover locations in Canada as the NLCD dataset includes only the U.S., and Canadian land cover classification lacked a category for wooded wetlands, previously identified as the most important land cover class for nonbreeding *E. carolinus* (Luscier et al. 2010, Wright et al. 2021). We examined correlations between land cover classes, and merged "Developed, Open Space" with "Developed, Low Intensity" and "Developed, Medium Intensity" with "Developed, High Intensity" classes. We also merged unclassified offshore areas with "Open Water". We added elevation for each receiver. The resulting dataset included 26 receivers with detections during stopover, 201 receivers without detections, 13 land cover classes, and elevation.

We used binomial generalized linear models to model probability of *E. carolinus* occurrence at Motus receivers during stopover with land cover classes and elevation as predictors. We examined correlation tables and plots of predictor variables and response and fit individual binomial models of occurrence for each variable. Predictors selected for a global candidate model showed positive correlations with *E. carolinus* occurrence and a model P value of <0.15. Variables with negative relationships were only included in the candidate model if they were biologically plausible (e.g., elevation, % open water, % developed). We fit the candidate model with all selected variables, then assessed model coefficients, standard errors, and P values for each variable. We compared AIC_c values of the candidate model and all reduced models using the dredge function in R package *MuMIn* 1.47.1 (Bartoń 2022) and selected variables for the final model that appeared in more than half of the models with $\Delta AIC_c < 2$.

RESULTS

Summary of Detections and Migratory Routes

One hundred eighty-one different Motus receivers detected 100 of the 177 tagged *E. carolinus* away from the capture site (Figure 1, Table 1, and Supplementary Material Table S3). In fall, many birds from Québec traveled southwest along the St. Lawrence River before turning south, some making it as far west as Lake Ontario. Other birds from Québec took a more easterly route through southern New England. Birds from breeding sites in northern

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New England traveled through inland and coastal New England before heading southwest parallel to the coast. Notably, the "Deer Pond Farm" receiver in the Hudson River Valley of western Connecticut detected seven individuals from each capture site (Supplementary Material Table S1). Most birds from Québec and New England detected farther south converged in the Delaware and Chesapeake Bays area, where several receivers detected similar numbers of individuals from both populations (see "Patuxent River Park" and "Newtowne Neck State Park" in Supplementary Material Table S3). There were few Motus receivers and thus few birds detected south of the Chesapeake Bay, but existing receivers detected ten birds in South Carolina and Georgia in late fall and winter, eight from New England and two from Québec. The routes detected during spring migration generally resembled fall routes of birds from the same origin; however, some routes of individual birds differed between spring and fall.

Stopovers at Tadoussac

Of the 71 *E. carolinus* tagged in Québec with subsequent detections during migration, 62 (87%) stopped over for 24 hr or more in the area surrounding Observatoire d'oiseaux de Tadoussac. Twenty-eight (45%) of the birds stopping over were detected consistently by the omnidirectional antenna at the banding site ("Tadoussac2" receiver), which has an estimated range of only 500 m for unobstructed tags (Taylor et al. 2017). Others were intermittently or seldom detected by local receivers before departure.

For the 58 *E. carolinus* with known departures from the Tadoussac area, the mean stopover duration was 11.6 ± 6.5 days (SD, range: 1–41 days) and none of the variables tested predicted stopover duration strongly. Fat scores of birds captured and tagged in Québec were low overall (mean = 0.89; score 0 = 25, score 1 = 21, score 2 = 16, score 3 = 1) and there was no effect of fat score on stopover duration ($R^2 = 0.05$, $n = 32$, $P = 0.12$). Analysis of the global model of stopover duration by age, sex, body condition, handling time, and capture date ($AIC_c = 376.0$, $n = 58$, $R^2 = 0.08$) indicated that only sex and capture date should be included in a reduced model ($AIC_c = 370.6$, $n = 58$, $R^2 = 0.09$), but neither was strongly predictive of stopover duration. Mean stopover duration was approximately 3 days shorter for males compared to females ($\beta = -3.17$, SE = 1.69, $P = 0.066$) and duration was shorter for birds captured at later dates ($\beta = -0.22$, SE = 0.11, $P = 0.047$).

Stopovers Elsewhere

We identified migratory stopovers for *E. carolinus* from both New England ($n = 10$) and Québec ($n = 17$) using the Motus detection data and identified 4 stopovers from the New England GPS tag (Figure 2, Supplementary Material Table S4). We detected stopovers in both fall ($n = 24$) and spring ($n = 7$) migrations. The mean stopover duration was 6.4 ± 4.9 days (SD, range: 1–21 days) and did not differ significantly between New England (mean 5.2 ± 3.6 days SD) and Québec (7.4 ± 5.7 days SD, $F_{1,28} = 1.7$, $P = 0.21$) origins. There was some evidence that stopover duration was longer in spring (9.8 ± 5.4 days SD) than fall (5.4 ± 4.3 days SD) ($F_{1,28} = 5.0$, $P = 0.033$). There was no support for the interaction between site and season ($F_{1,27} = 0.07$, $P = 0.787$).

Euphagus carolinus stopovers were geographically clustered (15 of 31) in the Chesapeake and Delaware Bays region and birds from both New England and Québec stopped in this region in both fall and spring (Figure 2). Other stopovers were scattered across New England (mostly New England birds) and the Great Lakes basin east of Lake Ontario and along the St Lawrence River (Québec birds; Figure 2). Several receivers detected multiple *E. carolinus* individuals during stopovers (Figure 2, Supplementary Material Table S2).

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Migratory Flights

We identified 122 migratory flights of *E. carolinus* from the Motus detection data, with mean distance of 147 km (range: 9–645 km) and mean duration of 3.7 hr (range: 0.07–27.6 hr) (Supplementary Material Table S5). We recorded 15 flights exceeding 300 km. Mean flight speed was 59.6 ± 25.7 km hr^{-1} for flights >30 km, >30 min, and <12 hr (n = 96). The most frequent flight speed estimates ranged from 45 to 65 km hr^{-1} (Supplementary Material Figure S1A). Forty-eight of 50 (96%) known departures occurred between sunset and sunrise, with 1 departure before sunset and 1 after sunrise (Supplementary Material Figure S1B). Mean departure time was 3.7 ± 2.5 hr (SD) after sunset, but most frequent departure times were 1.5 to 3.5 hr after sunset (Supplementary Material Figure S1B). Of the 50 flights with known departure times, 38 were of birds leaving the capture site in Québec after stopover. While departure times were almost exclusively nocturnal, at least 29 of 122 (24%) total flights continued into the morning after sunrise.

Wintering Locations

Motus receivers detected 4 *E. carolinus* (three from Québec, one from New England) during the winter months (December–February) and the New England GPS tag recorded locations through the winter (Table 1, Figure 3). Receivers on the Delmarva peninsula in Delaware and Maryland detected two Québec birds periodically throughout the winter at ~38° latitude (Figure 3). One of these birds (tag ID 35071) triggered 5 different receivers on 20 days in total between November 24 and February 21. The second bird triggered three receivers on 11 days in total during November 23 to March 25. A South Carolina receiver detected a Québec bird (tag ID 26855) on December 15 and 16 and a Québec spring migrant on March 25.

Motus receivers detected only one *E. carolinus* tagged in New England during the winter months; a single detection on December 1 in South Carolina (tag ID 66477, Figure 3). The GPS-tagged New England bird arrived on wintering grounds in North Carolina around November 5–7 and departed around March 10–13. During the entire winter, the largest distance between GPS fixes was only 600 m. Five New England birds were detected in late fall as they arrived on migratory flights between November 14 and 26 in coastal South Carolina and Georgia (Figures 1 and 3). Inland receiving stations in South Carolina detected 2 other New England birds, 1 on November 13, and 1 on March 14. Eight of the 29 (28%) *E. carolinus* from New England detected by the Motus array were found south of 35° latitude, while only 2 of 71 (3%) birds from Québec were detected as far south.

Migratory Strategy

The cyclical GAMM of latitude by date revealed marked differences in migratory strategy and annual cycle between *E. carolinus* captured in Québec during fall migration and those captured in New England during the breeding season (Figure 4). The smoothed interaction term for latitude by date and capture site was highly explanatory suggesting the differences in latitude by date result from a different migratory pattern, rather than simply a difference in latitude (Supplementary Material Table S6). Birds tagged in New England spent ~50% of the year (mid-April through mid-October) at breeding latitudes (Figure 4). Birds from Québec were not detected near their boreal breeding territories but likely arrived in mid- to late-May. During fall migration, birds from Québec had already completed at least 1 leg of their journey before arriving at Tadoussac between September 10 and October 4 (mean = September 23). This suggests that birds from Québec spent almost 2 months less time at breeding latitudes than birds from New England.

There were noticeable differences in migration timing between *E. carolinus* from the 2 capture sites. During fall migration, birds from Québec were detected at higher latitudes at any given date on average, though there was considerable overlap in latitude between the two

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populations in October and November (Figure 4). In the spring, *E. carolinus* from New England initiated migration earlier than birds from Québec (Figure 4). There was no effect of age in models using the reduced dataset of known age and sex, but a term for sex suggested that male *E. carolinus* wintered at higher latitudes on average than females (Supplementary Material Table S7, Supplementary Material Figure S2). This result is based on only a few wintering individuals, so should be interpreted with caution.

Migratory Connectivity

Patterns of spatial and temporal migratory connectivity of *E. carolinus* during fall migration indicated that migratory routes of birds from both capture sites converged south of 43° latitude, but birds from Québec passed through these latitudes at later dates than birds from New England. *E. carolinus* from both capture sites were present in the 43° latitude window (42–44°) concurrently, but were detected in different grid cells spatially (Figure 5). In the 42° latitude window, birds from both populations were detected in the same geographic areas during the same weeks. As birds moved farther south between 42° and 37° latitude, Mantel statistics for temporal connectivity differed from zero suggesting birds from New England and Québec passed through latitude bands at different times. Mantel statistics for spatial connectivity did not differ from zero south of 42° except for some small differences at the 39° and 38° latitude bands. We did not have enough detections to test for migratory connectivity south of 37° latitude or during winter.

Land Cover at Stopover and Wintering Sites

The binomial models of *E. carolinus* occurrence by land cover classes revealed that percent cover of wooded wetlands, cropland, and hay/pasture were positively related to occurrence in both 15-km and 5-km buffer sizes and elevation had a weak negative relationship to stopover occurrence at the 15-km scale (Table 2). The global candidate models included open water at 15-km and elevation at 5-km, but these variables were eliminated from the final model based on multi-model inference using AIC_c. After wooded wetlands, percent cover of croplands had the next strongest relationship with *E. carolinus* occurrence based on the individual models; however, percent cover of wooded wetlands and croplands were somewhat correlated at both 15-km ($r = 0.27$, $P < 0.001$) and 5-km ($r = 0.34$, $P < 0.001$) buffer sizes.

DISCUSSION

The Motus detection data confirmed that the migratory behavior of *E. carolinus* in eastern North America was generally similar to western North American individuals, and tagged birds made prolonged (>1 week) stopovers on both spring and fall migrations, were primarily nocturnal migrants, and made long, non-stop migratory flights >300 km (Johnson et al. 2012, Wright et al. 2018a, 2021). *Euphagus carolinus* captured in New England and Québec revealed differences in migratory strategy and timing between the two populations. Boreal-breeding *E. carolinus* captured at Québec spent ~2 months less time at breeding latitudes than did individuals breeding in New England and spent more time at spring and fall stopover sites and wintering latitudes. The annual time budget of Québec birds was similar to GPS-tagged *E. carolinus* from the western boreal forest, with extended periods of time spent in migratory stopover rather than breeding latitudes (Wright et al. 2021). Increased time spent in stopover could present an elevated risk to these populations, where birds rest and refuel in unfamiliar environments (Newton 2006). For southern breeding birds able to spend longer periods of time at breeding latitudes, the prolonged growing season may provide ample time and food resources to undergo pre-basic molt and accumulate fuel prior to the onset of migration (Avery 2020). Birds breeding at more northerly latitudes with a shorter growing season may rely more heavily on areas along the migratory route for molt and fat accumulation. The

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effects of climate change may alter the migratory strategies of these populations differently, as birds at higher latitudes may take advantage of longer growing seasons and delay the onset of fall migration or arrive at breeding latitudes earlier in spring (Brisson-Curadeau et al. 2020). Changes in phenology of food resources at spring and fall stopover sites and wintering areas may also affect these populations differently (Fontaine et al. 2015).

Our results suggest that *E. carolinus* follow a pattern of chain migration in eastern North America, maintaining latitudinal structure throughout the nonbreeding season (Smith et al. 2003). While detections during the winter months were limited by the lack of Motus receivers in inland Virginia and North Carolina, there was some evidence that birds breeding at the southern extremity of the breeding range (New England), were more likely to winter at the southern extremity of the Southeastern Coastal Plain wintering range in South Carolina and Georgia. Additionally, the GAMM of latitude by date suggested that birds from Québec remained farther north than birds from New England throughout most of the year, with some overlap during fall stopover in the Chesapeake and Delaware Bays area and spring migration when New England birds migrated north earlier. Measurements of spatial and temporal migratory connectivity during migration indicated that *E. carolinus* from Québec and New England maintained separate routes at higher latitudes, but converged in the mid-Atlantic region with birds from New England moving through earlier than birds from Québec. For this analysis, note that Québec birds likely originated from a much larger breeding area than birds from New England, and thus should be more likely to exhibit greater variation in migratory route, timing and wintering localities than New England birds. It has been suggested that short-distance and "chain" migrants such as *E. carolinus* may be more resilient and able to respond to changing climate and resource phenology than "leap-frog" migrants (Fontaine et al. 2015). However, strong spatial structure in the nonbreeding range may affect resilience of populations differentially (Marra et al. 2006).

Though several Motus studies have documented stopover biology at capture locations in eastern North America (e.g., Dossman et al. 2016, Wright et al. 2018a, Poirier et al. 2024), few studies have documented stopovers in regions away from the capture site (Smetzer and King 2018, Smith et al. 2023b). We demonstrated that the detection of migratory stopovers is now possible with proliferation of Motus receivers in eastern North America, though geographic gaps in receiver coverage still exist. Stopover was an important component of migration for *E. carolinus* from both Québec and New England. Both populations were detected on prolonged (>7 days) stopovers during both spring and fall migrations, placing the species among the growing list of passerines that exhibit this behavior now that methods exist for detecting these stopovers (Smetzer and King 2018). The number of stopovers detected was surprisingly high given the broad geographic spacing of receivers in the Motus array, and the limited antenna range for detecting birds on the ground compared to migrants aloft (Crewe et al. 2019).

The Chesapeake and Delaware Bays region has been shown to be an important stopover area for nocturnal migrants in eastern North America, based on traffic observed in doppler weather radar (Buler and Dawson 2014, Guo et al. 2023), and is a well-known stopover area for shorebirds during spring migration (Dunne et al. 1982). Both populations of *E. carolinus* converged on the Chesapeake Bay and Delaware Bay areas during both fall and spring migration. Of the 27 stopovers detected by Motus receivers, 14 were in the Chesapeake and Delaware Bays area, highlighting the importance of this region for eastern *E. carolinus*. Weekly abundance data from eBird Status and Trends models confirm that the Chesapeake and Delaware Bays region hosts large numbers of *E. carolinus* during November and March–April (Fink et al. 2023). The importance of this region to *E. carolinus* has not been previously documented. Given the species' preference for floodplain forests during the nonbreeding season, it is logical that this region, where major river systems enter the coastal

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plain, would provide an abundance of suitable habitat (Avery 2020). Other regions where *E. carolinus* stopovers were detected include New England and the eastern Great Lakes Basin, regions with lower densities of Motus receivers but high relative abundance of *E. carolinus* in eBird data during both spring and fall migration (Fink et al. 2023).

Land cover around receivers that detected stopovers suggested wooded wetlands, croplands, and hay/pastures were selected for at two spatial scales, despite not knowing precise stopover locations from Motus detections. These findings were consistent with habitat associations reported for *E. carolinus* during stopover and winter in other studies (Hamel et al. 2009, Luscier et al. 2010, Wright et al. 2020, 2021, Evans et al. 2021). We could not find other examples of studies that used Motus detections to describe land cover around stopover sites, but our results suggest this method would work for other species. Given the enhanced detection from the Motus network when transmitters are aloft (Crewe et al. 2019), detections during stopover likely occurred when *E. carolinus* were most mobile, such as during movements between roosting and foraging areas, relocations to other stopover sites, and during arrivals to and departures from the stopover site (Wright et al 2018a). These results suggest that Motus detection data can be combined with land cover and/or eBird data at local scales to predict areas and dates with high probabilities of *E. carolinus* stopover. Ground-truthing these predictions with field surveys could reveal important regional stopover sites for *E. carolinus*.

Based on the pattern of Motus detections in this study and lengths of migratory flights and stopovers reported in this study and others, *E. carolinus* from both New England and Québec likely made extensive undetected stopovers between the capture sites and the mid-Atlantic region (Wright et al. 2018a, 2021). For instance, tagged birds were detected leaving the capture sites late-September to mid-October but went largely undetected until early to mid-November, when many were detected on long-range migratory flights and stopovers in the mid-Atlantic region. This suggests that many *E. carolinus* from both origins stopped over for extended periods of time (~1 month) at latitudes between ~43°N and ~47°N but went mostly undetected during that time. For New England birds detected in coastal South Carolina and Georgia, there were undocumented stopovers of 5–16 days between the last detections in the Chesapeake Bay area and arrival along the coast. In cases when distances between Motus detections are relatively short, but elapsed time between detections indicates a stopover occurred, it may be possible to use a combination of Motus detection geometry (bearings of migratory flights, flight speed, and detection times), eBird data, and land cover data to predict possible locations of unobserved stopovers. Based on our familiarity with the dataset, we believe this method could reveal additional stopover sites in New England, where Motus receiver density was relatively high, that could be ground truthed by field surveys or future tracking studies.

The *E. carolinus* stopovers at Tadoussac subsequent to tagging were unexpected, and we hypothesize that the capture and tagging process caused birds to remain multiple days at Tadoussac rather than at other stopover sites in the region. Alternatively, the Tadoussac area may be a previously unknown stopover site for *E. carolinus*. The latter seems unlikely considering the site has been monitored by daily migration monitoring surveys since 1993 and is a popular birdwatching location, yet there has been no indication of *E. carolinus* using the area for stopover (Savard et al. 2011; CBM, PC, and AT, personal observation). Almost half of the birds stopping over were in the immediate vicinity of the banding station based on detections made by an omnidirectional antenna, which has a maximum estimated range of 500 m for flying birds (Taylor et al. 2017). If *E. carolinus* regularly stopped over within several hundred meters of the station, it seems unlikely they could have escaped detection for so long. Birds were captured by using playback in the early morning and were carrying little to no fat, suggesting they were arriving after nocturnal migratory flights. Once captured, the

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birds were separated from the flock they were travelling with, and flocks presumably continued on to their destination while the captured birds were processed and affixed with nano-transmitters. We suspect that the *E. carolinus* captured at Observatoire d'oiseaux de Tadoussac were ready to make a stopover on the date of their capture, but would have stopped at another site had they not been captured. For instance, 3 stopovers were detected in the vicinity of Saint-Roch-des-Aulnaies, QC, only ~100 km or ~2 hr flight time from Tadoussac. Effects of tracking devices on migration patterns have been infrequently reported in ornithological studies, primarily due to difficulties in tracking control groups, but could alter migratory timing and stopover substantially when present (Green et al. 2019, Brlík et al. 2020). Tagged *E. carolinus* have been shown to make stopovers subsequent to capture in 2 other studies using Motus data, but both studies were conducted at known stopover sites and potential tagging effects were not discussed (Wright et al. 2018a, Grinde et al. 2021). Manual tracking in Tadoussac with handheld receivers could further our understanding of how *E. carolinus* use the site.

The cyclical GAMM fit to predict mean *E. carolinus* latitude by date was a useful method for identifying differences in phenology between birds from the 2 capture sites. While confidence intervals around the predicted values do not encompass the full range of individuals observed, we recognize that these intervals represent the location of the mean individual from each population given the data. There were wide ranges of arrival, capture, and departure dates from Québec, which was expected given the location of the site along the St Lawrence River, a migratory barrier where migrants from the vast eastern boreal forest are known to concentrate (Gagnon et al. 2011). There were few winter detections of birds from either capture site and none from breeding latitudes of birds from Québec, so predicted values for these time intervals are less reliable than those from the migratory periods. The differences in annual time budgets between birds from New England and Québec could have conservation and management implications, and may be influenced by climate change if migratory passage dates are related to temperature (Brisson-Curadeau et al. 2020).

Conclusions

This study collected detailed information on migratory behavior and routes of *E. carolinus* from eastern North America and provides important insights for conservation of this declining species in the region. Migratory strategies of birds tagged in New England, at the southern extremity of the breeding range, varied notably from those tagged in Québec, with birds from New England spending two months longer at the breeding grounds than birds from Québec. This could have important management implications as birds from Québec rely more heavily on stopover and wintering habitats. We determined that *E. carolinus* made prolonged stays at stopover sites during both spring and fall migration, and identified the Chesapeake and Delaware Bays area as an important stopover region for birds from both capture sites. Wooded wetlands, cropland, and hay/pasture were the land cover classes most associated with stopover probability. Combined with Motus detection and eBird data, land cover could be used to identify important stopover locations for *E. carolinus* in the east. There were few Motus receivers in inland Virginia and North Carolina where many *E. carolinus* likely wintered, so future Motus studies on *E. carolinus* in the east would benefit from increased Motus coverage in this area (Fink et al. 2023). Documenting migratory routes of *E. carolinus* from Newfoundland would be an important next step in understanding migratory connectivity of *E. carolinus* in the east, as these birds have been considered a separate subspecies and are genetically isolated from populations breeding in continental eastern North America (Avery 2020, Wilson et al. 2021).

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Ethics statement
All handling of birds at OOT was performed under standards on the welfare of animals from the Canadian Council on Animal Care (CCAC) and approved by every institution's CCAC committee: (Canadian Wildlife Service: OOT) and by the Canadian Wildlife Service Bird Banding Office and in NH under the University of Maine Inter-Institutional Agreement for Care and Use of Vertebrate Animals (IACUC).

Conflict of interest statement
The authors have no conflicts of interest to declare. This work has not been submitted elsewhere.

Author contributions
P.C., C.R.F, and J.A.T conceived the project; C.B.M. and L.B. designed field methods and conducted the research. C.B.M., J.A.T., and J.W. developed the analysis methods; J.W. analyzed the data and wrote the first draft of the paper; C.R.F, A.T., J.F.T., and J.A.T. contributed substantial materials, resources, and funding.

Data availability
Analyses reported in this article can be reproduced using the data and code provided by Walker et al. (2024).

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LITERATURE CITED

Avery, M. L. (2020). Rusty Blackbird (*Euphagus carolinus*), version 1.0. In *Birds of the World* (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bow.rusbla.01

Barnard, W. H., C. Mettke-Hofmann, and S. M. Matsuoka (2010). Prevalence of hematozoa infections among breeding and wintering Rusty Blackbirds. *The Condor* 112:849–853.

Bartoń, K. (2022). MuMIn: Multi-Model Inference. R package version 1.47.1, https://CRAN.R-project.org/package=MuMIn

Bayly, N. J., K. V. Rosenberg, W. E. Easton, C. Gomez, J. A. Y. Carlisle, D. N. Ewert, A. Drake, and L. Goodrich (2018). Major stopover regions and migratory bottlenecks for Nearctic–Neotropical landbirds within the Neotropics: A review. *Bird Conservation International* 28:1–26.

Bégin-Marchand, C., A. Desrochers, J. A. Tremblay, and P. Côté (2020). Comparing fall migration of three Catharus species using a radio-telemetry network. *Animal Migration* 7:1–8.

Bégin-Marchand, C., A. Desrochers, P. D. Taylor, J. A. Tremblay, L. Berrigan, B. Frei, A. Morales, and G. W. Mitchell (2021). Spatial structure in migration routes maintained despite regional convergence among eastern populations of Swainson's Thrushes. *Movement Ecology* 9:23.

Birds Canada (2023). motus: Fetch and use data from the Motus Wildlife Tracking System. https://motusWTS.github.io/motus.

BirdLife International (2024). Species factsheet: *Euphagus carolinus*. http://datazone.birdlife.org/species/factsheet/rusty-blackbird-euphagus-carolinus on 23/01/2024.

Brlík, V., J. Koleček, M. Burgess, S. Hahn, D. Humple, M. Krist, J. Ouwehand, E. L. Weiser, P. Adamík, J. A. Alves, et al. (2020). Weak effects of geolocators on small birds: A meta-analysis controlled for phylogeny and publication bias. *Journal of Animal Ecology* 89:207–220.

Brisson-Curadeau, É., K. H. Elliott, and P. Côté (2020). Factors influencing fall departure phenology in migratory birds that bred in northeastern North America. *The Auk: Ornithological Advances* 137:ukz064.

Buler, J. J., and F. R. Moore (2011). Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. *Journal of Ornithology* 152:101–112.

Buler, J. J., and D. K. Dawson (2014). Radar analysis of fall bird migration stopover sites in the northeastern US. *The Condor: Ornithological Applications* 116:357–370.

Chang, W., J. Cheng, J. Allaire, C. Sievert, B. Schloerke, Y. Xie, J. Allen, J. McPherson, A. Dipert, and B. Borges (2022). shiny: Web Application Framework for R. R package version 1.7.4, https://CRAN.R-project.org/package=shiny.

Crewe T. L., Z. J. Crysler, and P. D. Taylor (2018). Motus R Book. https://motuswts.github.io/motus/

Crewe, T. L., J. E. Deakin, A. T. Beauchamp, and Y. E. Morbey (2019). Detection range of songbirds using a stopover site by automated radio- telemetry. *Journal of Field Ornithology* 90:176–189.

DeLeon, E. E. (2012). Ecology of Rusty Blackbirds wintering in Louisiana: Seasonal trends, flock composition and habitat associations. Dissertation, Louisiana State University, Baton Rouge, LA, USA.

Dewitz, J. (2023), National Land Cover Database (NLCD) 2021 Products: U.S. Geological Survey data release, https://doi.org/10.5066/P9JZ7AO3.

Accepted Manuscript

Downloaded from https://academic.oup.com/condor/advance-article/doi/10.1093/ornithapp/duae066/7930274 by guest on 02 January 2025

Dossman, B. C., G. W. Mitchell, D. R. Norris, P. D. Taylor, C. G. Guglielmo, S. N. Matthews, and P. G. Rodewald (2016). The effects of wind and fuel stores on stopover departure behavior across a migratory barrier. *Behavioral Ecology* 27:567–574.

Dunne, P., D. Sibley, C. Sutton, and W. Wander (1982). Aerial surveys in Delaware Bay: Confirming an enormous spring staging area for shorebirds. *Wader Study Group Bull*etin 35:32–33.

Edmonds, S. T., D. C. Evers, D. A. Cristol, C. Mettke-Hofmann, L. L. Powell, A. J. McGann, J. W. Armiger, O. P. Lane, D. F. Tessler, P. Newell, K. Heyden, and N. J. O'driscoll (2010). Geographic and seasonal variation in mercury exposure of the declining Rusty Blackbird. *The Condor* 112:789–799.

Evans, B. S., L. L. Powell, D. W. Demarest, S. M. Borchert, and R. S. Greenberg (2021). Flock size predicts niche breadth and focal wintering regions for a rapidly declining boreal-breeding passerine, the Rusty Blackbird. *Diversity* 13:62.

Fink, D., T. Auer, A. Johnston, M. Strimas-Mackey, S. Ligocki, O. Robinson, W. Hochachka, L. Jaromczyk, C. Crowley, K. Dunham, A. Stillman, I. Davies, A. Rodewald, V. Ruiz-Gutierrez, and C. Wood (2023). eBird Status and Trends, Data Version: 2022; Released: 2023. Cornell Lab of Ornithology, Ithaca, New York. https://doi.org/10.2173/ebirdst.2022

Fontaine, J. J., R. J. Stutzman, and L. Z. Gannes (2015). *Leaps, Chains, and Climate Change for Western Migratory Songbirds*. Nebraska Cooperative Fish & Wildlife Research Unit -- Staff Publications. http://digitalcommons.unl.edu/ncfwrustaff/177

Fraser, K.C., A. Roberto-Charron, B. Cousens, M. Simmons, A. Nightingale, A. C. Shave, R. L. Cormier, and D. L. Humple (2018). Classic pattern of leapfrog migration in Sooty Fox Sparrow (*Passerella iliaca unalaschcensis*) is not supported by direct migration tracking of individual birds. *The Auk: Ornithological Advances* 135:572–582.

Gagnon, F., J. Ibarzabal, J. P. L. Savard, M. Belisle, and P. Vaillancourt (2011). Autumnal patterns of nocturnal passerine migration in the St. Lawrence estuary region, Quebec, Canada: A weather radar study. *Canadian Journal of Zoology* 89:31–46.

Goslee, S. C., and D. L. Urban (2007). The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22:1–19.

Geen, G. R., R. A. Robinson, and S. R. Baillie (2019). Effects of tracking devices on individual birds–a review of the evidence. *Journal of Avian Biology* 50:jav01823.

Greenberg, R., and S. Droege (1999). On the decline of the Rusty Blackbird and the use of ornithological literature to document long- term population trends. *Conservation Biology* 13:553–559.

Greenberg, R., and S. M. Matsuoka (2010). Rangewide ecology of the declining Rusty Blackbird Rusty Blackbird: Mysteries of a species in decline. *The Condor* 112:770–777.

Greenberg, R., D. W. Demarest, S. M. Matsuoka, C. Mettke-Hofmann, D. Evers, P. B. Hamel, J. Luscier, L. L. Powell, D. Shaw, M. L. Avery, and K. A. Hobson (2011). Understanding declines in Rusty Blackbirds. In *Boreal Birds of North America: A Hemispheric View of Their Conservation Links and Significance* (J. V. Wells, Editor). *Studies in Avian Biology* 41:107–126.

Grinde, A. R., A. Bracey, and S. Kolbe (2021). *Mapping Avian Movement in Minnesota*. University of Minnesota, Duluth, MN, USA.

Guo, F., J. J. Buler, J. A. Smolinsky, and D. S. Wilcove (2023). Autumn stopover hotspots and multiscale habitat associations of migratory landbirds in the eastern United States. *Proceedings of the National Academy of Sciences USA* 120:e2203511120.

Downloaded from https://academic.oup.com/condor/advance-article/doi/10.1093/ornithapp/duae066/7930274 by guest on 02 January 2025

Accepted Manuscript

Hamel, P. B., and E. S. R. A. Ozdenerol (2009). Using the spatial filtering process to evaluate the nonbreeding range of Rusty Blackbird *Euphagus carolinus*. In *Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics* (T. Rich, C. Arizmendi, D. Demarest, and C. Thompson, Editors). Partners in Flight, McAllen, TX, USA. pp. 334–340.

Hamel, P. B., D. I. De Steven, T. Leininger, R. A. Wilson (2009). Historical trends in Rusty Blackbird nonbreeding habitat in forested wetlands. In *Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics* (T. Rich, C. Arizmendi, D. Demarest, and C. Thompson, Editors). Partners in Flight, McAllen, TX, USA. pp. 341–353.

Hobson, K. A., R. Greenberg, S. L. V. Wilgenburg, and C. Mettke-Hofmann (2010). Migratory connectivity in the Rusty Blackbird: Isotopic evidence from feathers of historical and contemporary specimens. *The Condor* 112:778–788.

Ibarzabal, J. (1999). Tadoussac: un site de migration des oiseaux de proie. *Le Naturaliste Canadien* 123:11–18.

Johnson, J. A., S. M. Matsuoka, D. F. Tessler, R. Greenberg, and J. W. Fox (2012). Identifying migratory pathways used by Rusty Blackbirds breeding in southcentral Alaska. *The Wilson Journal of Ornithology* 124:698–703.

Kolbe, S., and A. Grinde (2019). *Rusty Blackbird stopover use in the St. Louis River Estuary: 2019 Minnesota Ornithologists' Union Savaloja Grant Report*. Natural Resources Research Institute, University of Minnesota Duluth, MN, USA.

Luepold, S. H. B., T. P. Hodgman, S. A. McNulty, J. Cohen, and C. R. Foss (2015). Habitat selection, nest survival, and nest predators of Rusty Blackbirds in northern New England, USA. *The Condor: Ornithological Applications* 117:609–623.

Luscier, J. D., S. E. Lehnen, and K. G. Smith (2010). Habitat occupancy by Rusty Blackbirds wintering in the lower Mississippi Alluvial Valley. *The Condor* 112:841–848.

Marra, P. P., D. R. Norris, S. M. Haig, M. Webster, J. A. Royle, K. Crooks, and M. Sanjayan (Editors) (2006). *Migratory Connectivity*. Conservation Biology Series, Cambridge, UK.

Mazerolle, M. J. (2020) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-1. https://cran.r-project.org/package=AICcmodavg.

McClure, C. J., B. W. Rolek, K. McDonald, and G. E. Hill (2012). Climate change and the decline of a once common bird. *Ecology and Evolution* 2:370–378.

McKinnon, E. A. and O. P. Love (2018). Ten years tracking the migrations of small landbirds: Lessons learned in the golden age of bio-logging. *The Auk: Ornithological Advances* 135:834–856.

Meehan, T. D., G. S., LeBaron, K. Dale, A. Krump, N. L. Michel, and C. B. Wilsey (2022). Trends in relative abundance for birds wintering in the continental USA and Canada: Audubon Christmas Bird Counts, 1966–2021, version 4.0. National Audubon Society, New York, NY, USA.

Mettke-Hofmann, C., P. B. Hamel, G. Hofmann, T. J. Zenzal Jr., A. Pellegrini, J. Malpass, M. Garfinkel, N. Schiff, and R. Greenberg (2015). Competition and habitat quality influence age and sex distribution in wintering Rusty Blackbirds. *PLoS One* 10:e0123775.

Morales, A., B. Frei, G. W. Mitchell, C. Bégin-Marchand, and K. H. Elliott (2022). Reduced diurnal activity and increased stopover duration by molting Swainson's Thrushes. *Ornithology* 139:ukab083.

Newell, P. J. (2013). Winter ecology of the Rusty Blackbird (*Euphagus carolinus)*. Ph.D. Thesis, University of Georgia, Athens, GA, USA.

Accepted Manuscript

Downloaded from https://academic.oup.com/condor/advance-article/doi/10.1093/ornithapp/duae066/7930274 by guest on 02 January 2025

Newton, I. (2006). Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* 147:146–166.
Newton, I. (2008). *The Migration Ecology of Birds*. Academic Press, London, UK.
Niven, D. K., J. R. Sauer, G. S. Butcher, and W. A. Link (2004). Christmas Bird Count provides insights into population change in land birds that breed in the boreal forest. *American Birds* 58:10–20.
Oksanen, J., G. Simpson, F. Blanchet, R. Kindt, P. Legendre, P. Minchin, R. O'Hara, P. Solymos, M. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. Hill, L. Lahti, D. McGlinn, M. Ouellette, E. Ribeiro Cunha, T. Smith, A. Stier, C. Ter Braak, J. Weedon (2022). vegan: Community Ecology Package. R package version 2.6-4, <https://CRAN.R-project.org/package=vegan>
Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *The R Journal* 10:439–446.
Pedersen, E. J., D. L. Miller, G. L. Simpson, and N. Ross (2019). Hierarchical generalized additive models in ecology: An introduction with mgcv. *PeerJ* 7:e6876.
Publicover, D., D. Weihrauch, J. Erikson, and K. Kimball (2003). *Ecological Atlas of the Upper Androscoggin River Watershed*. Appalachian Mountain Club, Boston, MA, USA.
Poirier, V., K. H. Elliott, and B. Frei (2024). Peri-urban forest margins are important stopover sites for moult-migrating songbirds. *Journal for Nature Conservation 77*:126539.
R Core Team (2024). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
Rappole, J. H., and A. R. Tipton (1991). New harness design for attachment of radio transmitters to small passerines. *Journal of field Ornithology* 62:335–337.
Rosenberg, K. V., J. A. Kennedy, R. Dettmers, R. P. Ford, D. Reynolds, J. D. Alexander, C. J. Beardmore, P. J. Blancher, R. E. Bogart, G. S. Butcher, et al. (2016). Partners in Flight Landbird Conservation Plan: 2016 Revision for Canada and Continental United States. Partners in Flight Science Committee.
Rueda- Hernández, R., C. M. Bossu, T. B. Smith, A. Contina, R. Canales del Castillo, K. Ruegg, and B. E. Hernández- Baños (2023). Winter connectivity and leapfrog migration in a migratory passerine. *Ecology and Evolution* 13:e9769.
Savard, J. P. L., M. Cousineau, and B. Drolet (2011). Exploratory analysis of correlates of the abundance of Rusty Blackbirds (*Euphagus carolinus*) during fall migration. *Ecoscience* 18:402–408.
Smetzer, J. R., and D. I. King (2018). Prolonged stopover and consequences of migratory strategy on local-scale movements within a regional songbird staging area. *The Auk: Ornithological Advances* 135:547–560.
Smith, R. B., T. D. Meehan, and B. O. Wolf (2003). Assessing migration patterns of Sharp-shinned Hawks *Accipiter striatus* using stable- isotope and band encounter analysis. *Journal of Avian Biology* 34:387–392.
Smith, A. C., Hudson, M-A. R. Aponte, V. I., English, W. B., and C. M. Francis (2023a). North American Breeding Bird Survey - Canadian Trends Website, Data-version 2021. Environment and Climate Change Canada, Gatineau, Quebec, Canada.
Smith, A. D., F. J. Sanders, K. L. Lefevre, J. M. Thibault, K. S. Kalasz, M. C. Handmaker, F. M. Smith, and T. S. Keyes (2023b). Spring migration patterns of red knots in the Southeast United States disentangled using automated telemetry. *Scientific Reports* 13:11138.

Accepted Manuscript

Downloaded from https://academic.oup.com/condor/advance-article/doi/10.1093/ornithapp/duae066/7930274 by guest on 02 January 2025

Taylor, P. D., T. L. Crewe, S. A. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. M. Francis, C. G. Guglielmo, D. J. Hamilton, and R. L. Holberton (2017). The Motus Wildlife Tracking System: A collaborative research network to enhance the understanding of wildlife movement. *Avian Conservation and Ecology* 12:8.

Tonra, C. M., and M. W. Reudink (2018). Expanding the traditional definition of molt-migration. *The Auk: Ornithological Advances* 135:1123–1132.

U.S. Fish and Wildlife Service (2021). Birds of Conservation Concern 2021. United States Department of the Interior, U.S. Fish and Wildlife Service, Migratory Birds, Falls Church, VA, USA. http://www.fws.gov/birds/management/managed-species/birds-of-conservation-concern.php

Walker, J., C. Bégin-Marchand, A. Terrigeol, J.-F. Therrien, P. Côté, L. Burford, C. R. Foss, and J. A. Tremblay (2024). Data from: *Euphagus carolinus* (Rusty Blackbird) from two different breeding populations in northeastern North America exhibit chain migration yet use the same region for stopover. *Ornithological Applications* 127:duae000. https://doi.org/10.5061/dryad.n2z34tn6s [Dataset].

Webster, M.S. and P. P. Marra (2005). The importance of understanding migratory connectivity and seasonal interactions. In *Birds of Two Worlds: The Ecology and Evolution of Temperate-Tropical Migration* (R. Greenberg and P. P. Marra, Editors). John Hopkins University Press, Baltimore, MD, USA.

Wilson, R. E., S. M. Matsuoka, L. L. Powell, J. A. Johnson, D. W. Demarest, D. Stralberg, and S. A. Sonsthagen (2021). Implications of historical and contemporary processes on genetic differentiation of a declining boreal songbird: The Rusty Blackbird. *Diversity* 13:103.

Wood, S. N. (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society* 73:3–36

Woodworth, B. K., A. E. Newman, S. P. Turbek, B. C. Dossman, K. A. Hobson, L. I. Wassenaar, G. W. Mitchell, N. T. Wheelwright and D. R. Norris (2016). Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. *Oecologia* 181:413–422.

Wright, J. R., L. L. Powell, and C. M. Tonra (2018a). Automated telemetry reveals staging behavior in a declining migratory passerine. *The Auk: Ornithological Advances* 135:461–476.

Wright, J. R., C. M. Tonra, and L. L. Powell (2018b). Prealternate molt-migration in Rusty Blackbirds and its implications for stopover biology. *The Condor: Ornithological Applications* 120:507–516.

Wright, J. R., L. L. Powell, S. N. Matthews, and C. M. Tonra (2020). Rusty Blackbirds select areas of greater habitat complexity during stopover. *The Condor*: *Ornithological Applications* 122:duaa040.

Wright, J. R., J. A. Johnson, E. Bayne, L. L. Powell, C. R. Foss, J. C. Kennedy, and P. P. Marra (2021). Migratory connectivity and annual cycle phenology of Rusty Blackbirds (*Euphagus carolinus)* revealed through archival GPS tags. *Avian Conservation and Ecology* 16:20.

Accepted Manuscript

Downloaded from https://academic.oup.com/condor/advance-article/doi/10.1093/ornithapp/duae066/7930274 by guest on 02 January 2025

Table 1. Number of NanoTags deployed on *Euphagus carolinus* (Rusty Blackbird) by site and year, and number of tags detected during fall migration (August to November), winter (December to February), and the following spring (March to May) from Motus detection data downloaded on January 2, 2024. Detection dataset for New England birds tagged in 2023 lacks winter and spring migration data and may be incomplete for fall (*).

Deployments			**Detections**		
Site	**Year**	**Deployed**	**Fall**	**Winter**	**Spring**
New England	2019	12	8	0	3
	2021	20	10	0	3
	2022	17	6	1	2
	2023	13	5*	0*	0*
New England	**Total**	**62**	**29**	**1**	**8**
Québec	2017	21	12	1	3
	2018	30	23	0	0
	2019	13	7	0	0
	2020	51	29	2	10
Québec	**Total**	**115**	**71**	**3**	**13**
Total		**177**	**100**	**4**	**21**

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Table 2. Model terms, coefficients with standard errors, *z*, and *P* values from a binomial GLM of probability of occurrence of *E. carolinus* stopover near Motus receivers based on percent cover of land cover classifications in buffers of 15-km and 5-km around receivers. Stopover selection was positively related to percent cover of wooded wetlands, cropland, and hay/pasture at both scales.

Model	Term	Estimate	SE	*z* value	*P*
15-km buffer	Intercept	–3.09	0.46	–6.75	<0.001
	Wooded Wetlands	7.46	2.86	2.61	0.009
	Cropland	3.87	1.39	2.79	0.005
	Hay/Pasture	8.81	2.36	3.73	<0.001
	Elevation (scaled)	–0.67	0.34	–1.95	0.051
5-km buffer	Intercept	–3.49	0.44	–7.95	<0.001
	Wooded Wetlands	8.72	2.81	3.10	0.002
	Cropland	4.16	1.38	3.01	0.003
	Hay/Pasture	6.91	2.09	3.29	<0.001

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Figure 1. Detections and tracks of *E. carolinus* by Motus receivers during fall (left) and spring (right) migration, September 2017 to December 2023. Birds tagged at Observatoire d'Oiseaux de Tadoussac, Québec are shown in orange; birds from New England in purple. Red points and tracks are from a GPS tag affixed to a New England male in 2018. Yellow points are capture locations and gray points are locations of Motus receivers lacking detections. Size of the points (ndetect) indicates the number of individuals detected. Routes from both populations overlapped in the mid-Atlantic region.

Figure 2. Stopover locations of *E. carolinus* detected by Motus receivers (mean coordinates for stopovers detected by multiple receivers) and a GPS tag during fall (October to November, left) and spring (March to May, right) migration. Size of each point depicts stopover duration in days, and the color represents capture site, New England or Observatoire d'oiseaux de Tadoussac, Québec. Capture sites are marked with yellow points, and gray points are Motus receivers that did not detect stopovers. Note that points are partially transparent and that overlapping stopovers occurred at some sites during each season. Stopovers were geographically clustered in the Chesapeake and Delaware Bays area for both populations.

Figure 3. Winter Motus detections of *E. carolinus* affixed with nano-transmitters in New England or Observatoire d'oiseaux de Tadoussac, Québec, including the wintering location of a New England bird with a GPS tag. Detections from late fall and early spring south of the Virginia area are shown in black. New England birds were detected at more southern locations than birds from Québec, though the sample size was small and Motus receivers were sparse in key parts of the wintering range.

Figure 4. Predicted values (smoothed line) from a cyclical GAMM model of latitude by date and capture site for *E. carolinus* captured in New England and Québec, with shaded 95% confidence intervals. Detections (one point per individual per day), migratory flights (vertical lines) and stopovers (horizontal lines) identified from the Motus data are included. Data from a GPS tag deployed in New England are included in green. The bottom panel is the same plot with fall migration enlarged. Birds from New England spent ~2 months longer at breeding latitudes than birds from Québec.

Figure 5. Mantel *R* statistic testing connectivity between *E. carolinus* during fall migration in windows of 2° latitude, centered at the median latitude (°). Spatial connectivity is shown by the solid line, and temporal connectivity by the dashed line. Vertical lines are bootstrapped 95% confidence intervals around the Mantel *R* statistic. *Euphagus carolinus* showed little to no spatial connectivity below 42° latitude, but temporal connectivity suggests that the timing of fall migration differed by latitude.

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Figure 1

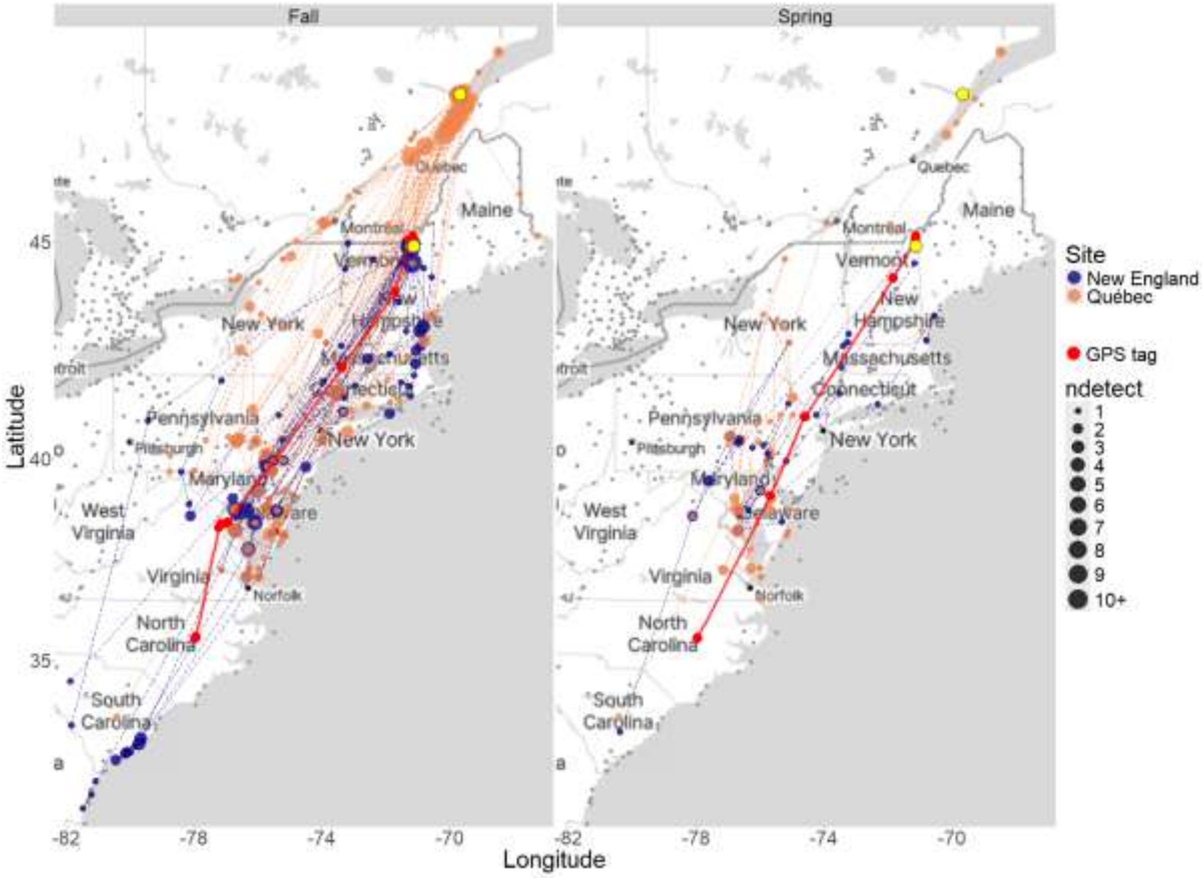

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Figure 2

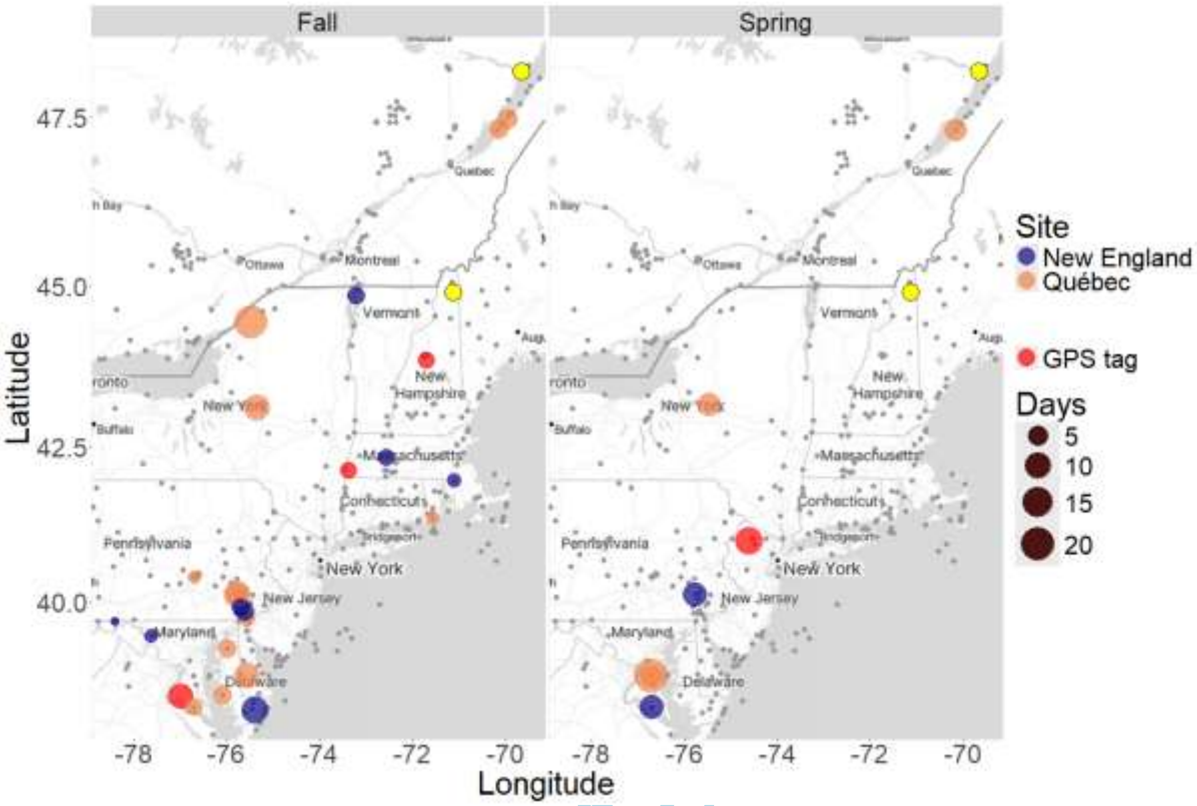

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Figure 3

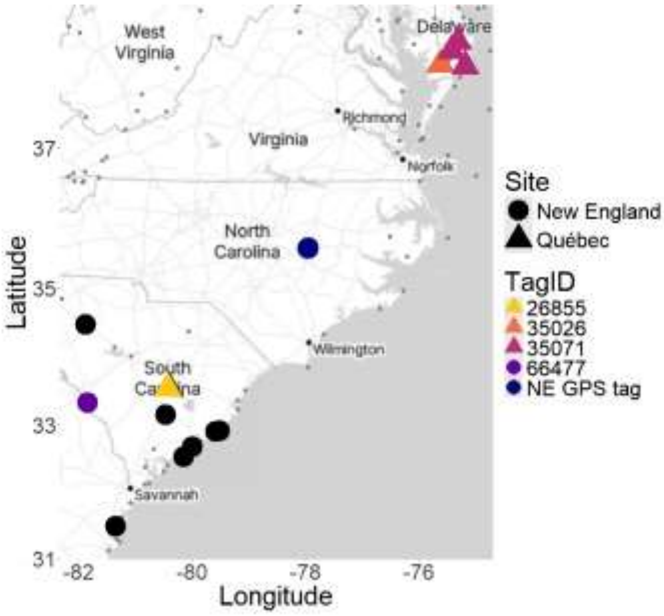

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Figure 4

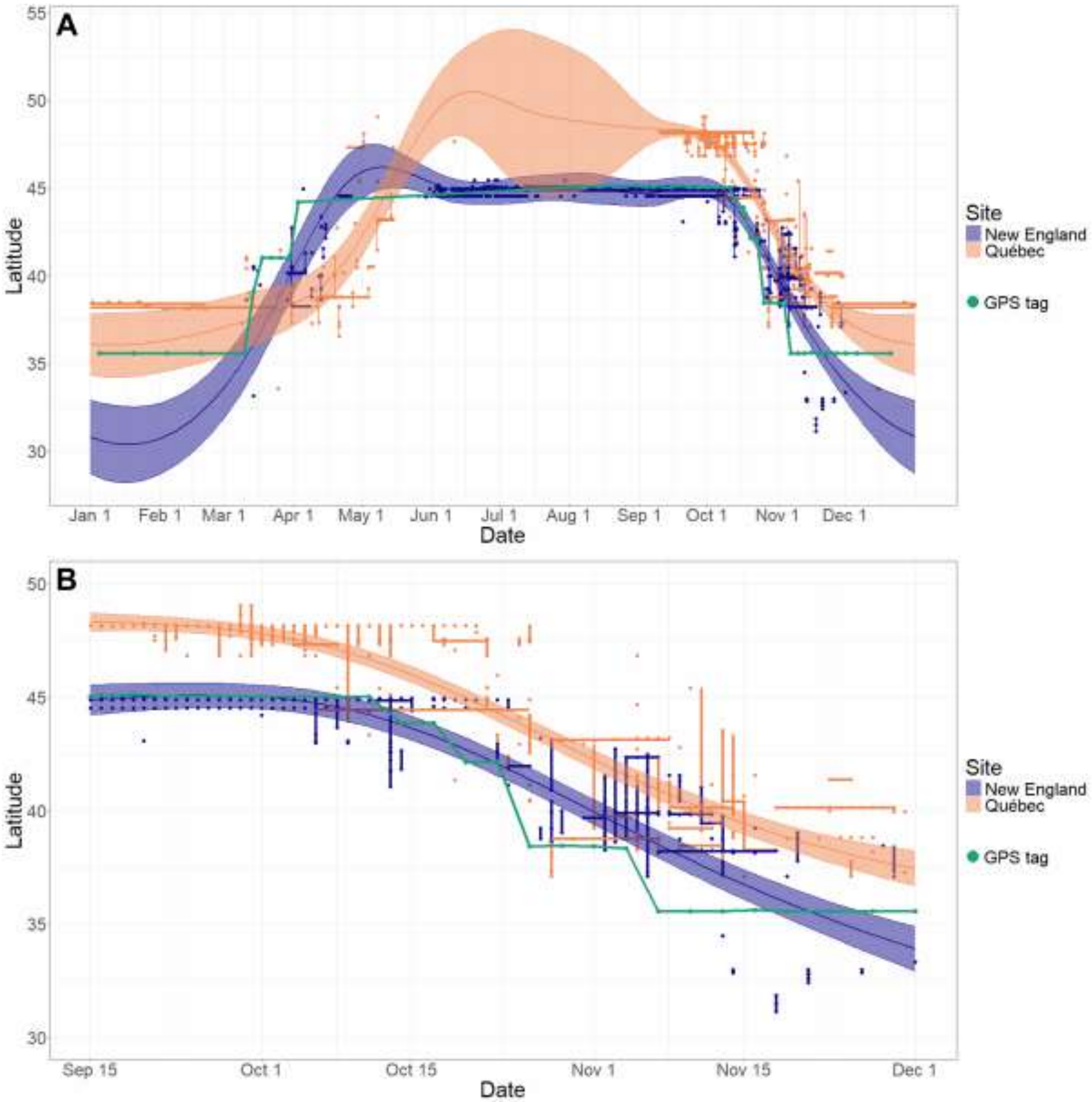

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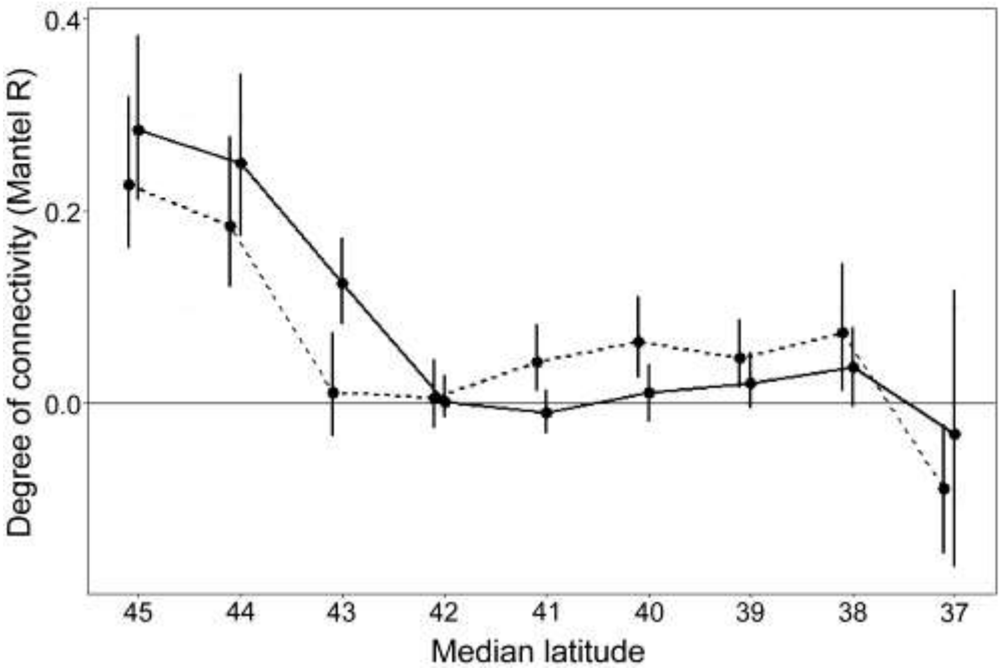
Figure 5



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