

Research Article

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Comparing fall migration of three *Catharus* species using a radio-telemetry network

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Abstract: Migration routes vary greatly among small passerine species and populations. It is now possible to determine the routes over great distances and long periods of time with emerging monitoring networks. We tracked individual Swainson's Thrush (*Catharus ustulatus*), Bicknell's Thrush (*Catharus bicknelli*) and Gray-cheeked Thrush (*Catharus minimus*) in northeastern Quebec and compared their migration routes and paces across an array of radio-telemetry stations in North America. Swainson's Thrush migrated further inland than the other two species. Individuals from all three species slowed their migration pace in the southeastern United States, and Swainson's Thrush was more likely to stopover than Bicknell's Thrush. Although individuals were tagged in a small area within or close to their breeding range, the results document the variability of migration routes between species with similar ecological characteristics and provide detailed material to be used for migration studies with broader taxonomic or ecological scope.

Keywords: *Catharus bicknelli*, *Catharus minimus*, *Catharus ustulatus*, Motus network, migration pace

1 Introduction

Bird migration is influenced by factors intrinsic or extrinsic to the species [1]. Migration routes may vary greatly within and among different species depending on their genetic

and evolutionary history [2–6], their breeding origins [7–10], and their morphology [11–13]. While some species use a wide range of routes and stopover areas during migration, some species converge into specific areas, which makes them more vulnerable to competition or changes in the quality or availability of this habitat [14, 15].

Our knowledge regarding bird migration has greatly improved over the last decade, especially due to emerging technologies and networks [16, 17]. For instance, satellite telemetry enables ornithologists to identify the main migratory flyways for large birds [18–20]. However, until recently, tracking devices were not light enough to be carried by smaller species. New tracking technologies like geolocators, light-weighted radio-transmitters and GPS tracking devices have led to detailed migrations routes of a few species of passerines [6, 17, 21–24]. The Motus wildlife tracking system [25], hereafter, 'Motus', is a coordinated radio-telemetry network consisting of receiving stations (Figure 1B) distributed across the American continent (www.motus.org). Motus has an unprecedented capability to provide detailed information on broad-scale movements, simultaneously for many different individuals and species [25–28]. Although limited by the position of the receiving stations, Motus enables the effective measurement of location, direction, and pace of migration without having to recapture the birds [26, 27, 29–31].

Swainson's Thrush (*Catharus ustulatus*), Bicknell's Thrush (*C. bicknelli*) and Gray-cheeked Thrush (*C. minimus*) are neotropical migrants, breed in boreal forests and migrate almost exclusively at night [32–36]. Migration tracking of these thrushes was often limited to a specific area or relies on few individuals to determine their North American fall migration route [24, 36, 37]. Breeding and wintering ranges of Swainson's Thrush and Gray-cheeked Thrush cover most of boreal North America and northern South America, respectively [33, 34]. Bicknell's Thrush are restricted to high-altitude boreal forests in eastern North America during the breeding season [32, 38] and the Greater Antilles in winter [32, 39].

Here, we compared the migratory routes and paces of

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Swainson's, Gray-cheeked and Bicknell's Thrushes across the Motus radio-telemetry network in North America. Because of its restricted wintering and breeding ranges and smaller migration distance, we hypothesized that individuals Bicknell's Thrush would be detected more frequently by receiving stations located along the coast of the Atlantic Ocean and would exhibit a faster migration pace than Swainson's and Gray-cheeked Thrush.

2 Methods

2.1 Radio tracking

We captured Bicknell's and Swainson's Thrushes on their breeding habitat in northeastern Quebec during the pre-nesting period at Forêt Montmorency (FM; 47.33°N, 71.18°W) and Monts-Valin national park (MV; 48.62°N, 70.80°W; FM-MV). We captured Gray-cheeked Thrush and other individuals Swainson's Thrush close to their breeding habitat during the fall migration at the Observatoire d'oiseaux de Tadoussac (OOT; 48.15°N, 69.67°W), located in the south of the Labrador peninsula, which is the breeding origin of most individuals migrating in this specific area [40].

We conducted field work from 2015 to 2017, but one breeding site (MV) was sampled only in 2017. During the breeding period, nets were opened 1 hour before sunrise for 6 hours, followed by a 4-hour period starting 1 hour before sunset for approximately 21 days of tagging per year. During migration, tags were deployed from mid-September to mid-October and nets were opened from 0530 to 0700 am (EST) for approximately 30 days of sampling per year.

We fixed a lightweight Lotek Avian Nanotag (Figure 1A) using a "8"-shaped harness made beforehand with nylon elastic thread [41, 42]. The harness and the transmitter weighed ~1.5 g, which represented ~3% of the body mass of individuals and does not affect the long-term behavior and survival rate of individuals [41, 43, 44]. Each nanotag transmitted at 166.800 Hz and had a single signature signal, with a burst interval between 5 to 20 seconds and an estimated lifespan between 180 to 500 days (Table S1.)

Telemetric monitoring was provided by Motus, a coordinated radio-telemetry network [25]. We selected the active receiving stations across the network between August and November, inclusively. The number and location of receiving stations varied from 347 in 2015, 333 in 2016 and 382 in 2017 (Figure 2). We downloaded data from the Motus website (www.motus.org) on March 5, 2019. False-positive detections were removed methodically

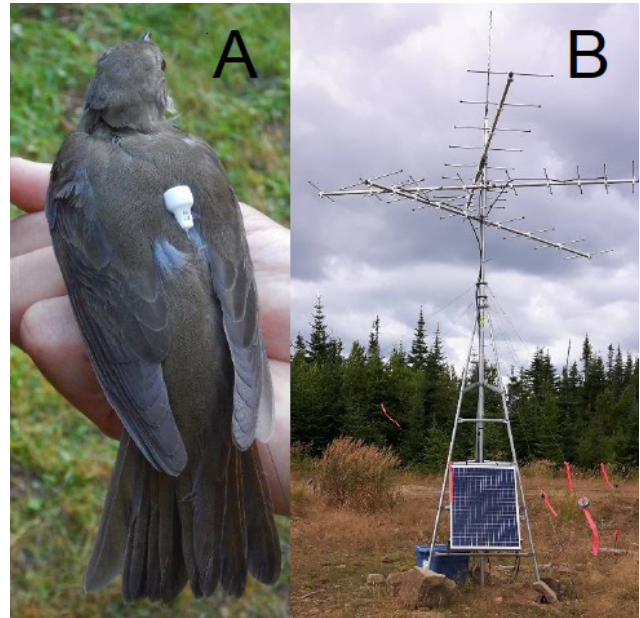


Figure 1. (A) Lotek avian nanotag fixed on a Gray-Cheeked Thrush tagged at Observatoire d'oiseaux de Tadoussac ©Mikaël Jaffré. (B) Receiving station of the Motus network located at Forêt Montmorency ©André Desrochers.

according to the Motus user guidelines using the *motus* package [45]. Furthermore, we removed all detections with movement rates >150 km hr⁻¹ between two separate receiving stations separated by >200 km. In total, 256 transmitters were deployed and 236 had valid detections in the Motus network (Table 1).

2.2 Migration routes

We performed a Mantel test [46] to measure the association between similarity in spatial patterns of detection across the radio-telemetry array and species similarity, thus determining whether two individuals of the same species had more similar detection histories than two individuals of different species. The Mantel test is commonly used in community ecology, but its limited use so far in migration ecology [9, 47, 48] warrants a brief description. To perform the Mantel test, we built a 'Receiving Site' matrix with columns representing each receiving site from the Motus network and rows representing each individual bird. Each cell of the matrix contained a Boolean value for detection or the absence thereof. To compare species, we used an additional 'Species' matrix, again with rows representing individual birds, but columns representing species with a combination of two Boolean dummy variables. We converted both matrices distinctly into a triangular matrix, each cell of the matrix representing a pairwise Bray-Curtis dissimilarity index between individuals [49].

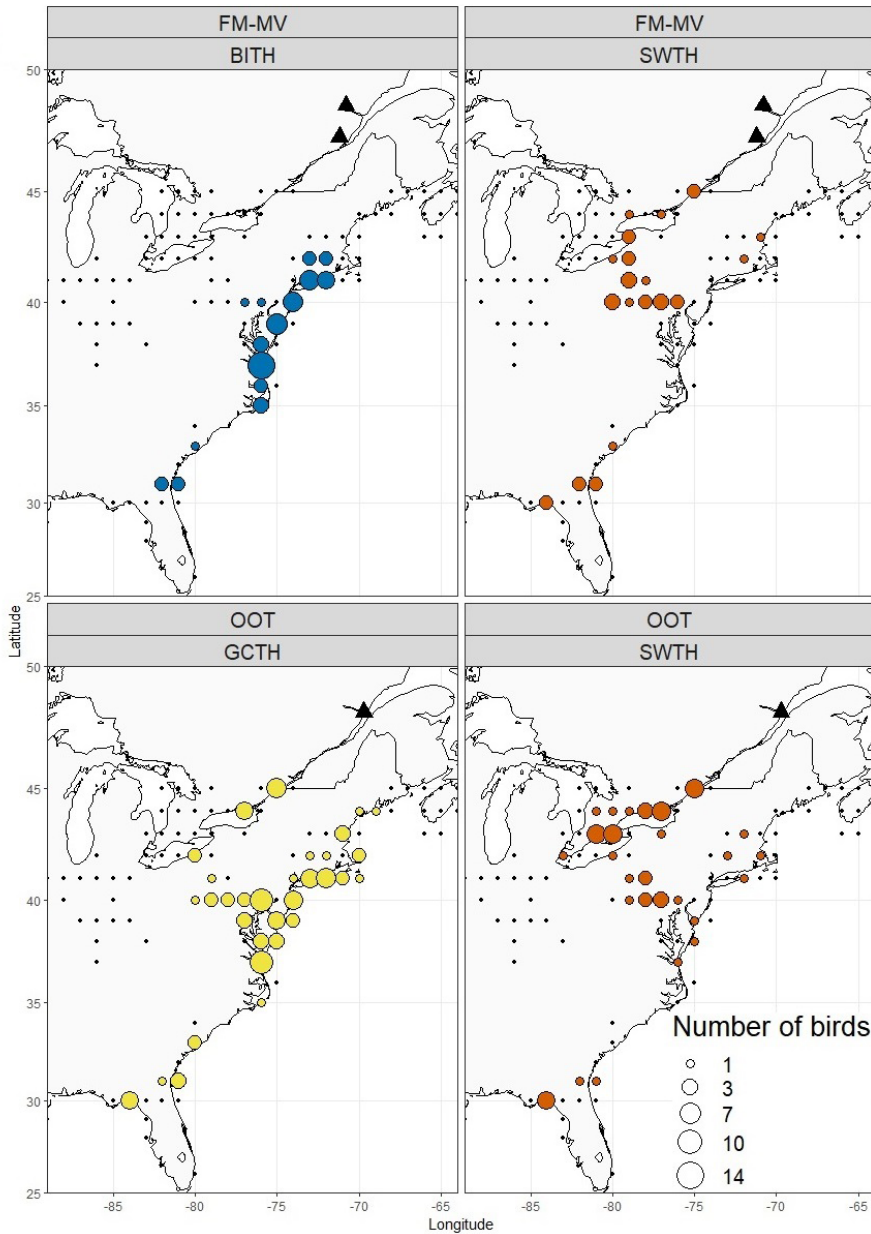


Figure 2. Number of individuals detected between 45°N and 30°N per species (BITH: Bicknell’s Thrush; GCTH: Gray-cheeked Thrush; SWTH: Swainson’s Thrush) and location of Motus receiving stations (all years combined) with no detection (smaller black points). Receiving stations were grouped by rounded coordinates to nearest degree. Black triangles are the tagging location (FM-MV or OOT).

Table 1. Number of transmitters deployed per species, year and tagging location detected in the Motus network (BITH: Bicknell’s Thrush; GCTH: Gray-cheeked Thrush; SWTH: Swainson’s Thrush).

Tagging Location	Migrating site (OOT)		Breeding site (FM-MV)		Total
	SWTH	GCTH	SWTH	BITH	
Species					
2015	29	8	28	24	89
2016	17	18	19	15	69
2017	21	33	22	22	98
Total deployed	67	59	69	61	256
Total detected	62	56	61	57	236

We calculated the Pearson correlation between the values in the two triangular matrices and compared it with an empirical distribution of correlation coefficients obtained with 10 000 random permutations of the detection matrix. We used a partial Mantel test to control for the year of capture [46, 49], and grouped the receiving stations spatially by rounding their geographic coordinates, from 0.5 to 10 degrees. We retained the spatial grouping yielding the highest contrast among species. We performed Mantel tests with the R package *vegan* [50].

To test whether species migrated at similar distances from the coast, we retained receiving stations between latitudes 45°N and 35°N, i.e. roughly between north of the Great Lakes and south of North Carolina. We rounded the geographic coordinates to the nearest degree to group receiving stations close to each other and calculated the geodesic distance to the Atlantic coast. We fitted a Gaussian linear mixed model with individual bird as a random effect and tested hypotheses with an analysis of deviance (Type II Wald Chi square test) from the R package *car* [51], with Bicknell's Thrush as the reference level. To compare individual variability in migration routes among species, we performed a Bartlett's test of homogeneity of variances for the median distance (log) to coastline. To test whether breeding origin had an effect on migration routes, we performed all analyses a second time with a data subset designed to compare Swainson's Thrush tagged at FM-MV vs. those tagged at OOT.

2.3 Migration pace

Lotek Avian nanotags do not record ground speed, thus we inferred the migration pace between consecutive detections from different receiving stations (hereafter, 'steps'), based on the time elapsed between the last detection of a receiving station and the first detection of the next receiving station, and the distance between these two receiving stations [27]. We assigned geographical coordinates to each step based on latitude and longitude midpoints between receiving stations and retained steps separated from at least 30 minutes. We retained receiving stations south of 47°N, i.e. south of the southernmost tagging location and compared the three species regardless of their tagging location, assuming that it had no effect on migration pace below this latitude.

We performed an analysis of deviance from the R package *car* [51] from a binomial generalized mixed model (GLMM), with individual bird as a random effect, to test whether latitude (scaled) and species had an effect on the probability of stopover. Migrating birds may fly at

ground speed approximately between 15 and 50 km/h [24, 35, 52, 53]. Given this uncertainty, we ran GLMMs with ground speed thresholds of 5 to 60 km/h, below which the response variable was interpreted as a stopover [27]. For parameter estimation, Bicknell's Thrush was chosen as the reference level.

3 Results

3.1 Different migration routes

We detected 34 Gray-cheeked Thrush, 25 Bicknell's Thrush, 30 (OOT), and 14 (FM-MV) Swainson's Thrush at least once between latitudes of 45° N and 35° N (Figure 2). Spatial patterns of detection were significant between Swainson's, Gray-cheeked and Bicknell's Thrush (Mantel test, $R = 0.14$, $p = 0.00001$). Interspecific differences in spatial migration patterns were scale-dependent (Figure S1). Spatial patterns of detection were not significant between Swainson's Thrush tagged at FM-MV and those tagged at OOT. Inter-individual variances of the median distance (log) to coastline were nearly different between Swainson's and Gray-cheeked Thrushes (Bartlett's test $K\text{-squared} = 3.61$, $p = 0.06$); but more contrasted between Bicknell's ($s^2 = 0.43$) and Gray-cheeked Thrushes ($s^2 = 1.76$; Bartlett's test $K\text{-squared} = 11.73$, $p < 0.001$), and between Bicknell's and Swainson's Thrushes ($s^2 = 0.95$; Bartlett's test $K\text{-squared} = 4.24$, $p = 0.04$, Figure 3). Inter-individual variances of both tagging location (FM-MV: $s^2 = 0.62$; OOT: $s^2 = 1.11$) were similar (Bartlett's test $K\text{-squared} = 1.37$, $p = 0.24$). Bicknell's Thrush migrated closer to the Atlantic coast (20.63 ± 27.64 km) than Gray-cheeked Thrush (120.3 ± 23.54 km) and Swainson's Thrush (283.6 ± 21.14 km; Wald $\chi^2 = 62.38$, $p < 0.001$), while Gray-cheeked Thrush migrated closer to the coast than Swainson's Thrush. Differences between Swainson's Thrush from both breeding origins were not significant.

3.2 Different migration pace

South of the southernmost tagging location (47°N), we observed 102, 109 and 57 migration steps from Gray-cheeked Thrush (range: 0.2-164.8 km hr⁻¹, median: 12.09 km hr⁻¹), Swainson's Thrush (range: 0.04-132.44 km hr⁻¹, median: 4.71 km hr⁻¹) and Bicknell's Thrush (range: 0.39-86.74 km hr⁻¹, median: 3.72 km hr⁻¹) respectively. Migration pace of all three species exhibited a bimodal distribution, with a cut-off point at roughly 35 km hr⁻¹ (Figure S2.). Results were similar regardless of the ground

speed threshold (Table S2.). At a ground speed threshold of 30 km hr⁻¹, all three species were increasingly likely to stopover as they progressed south ($= -1.22 \pm 0.45$, $p = 0.01$, Figure 4). When controlling for latitude, Bicknell's Thrush was less likely to make stopovers than Swainson's Thrush ($= 0.96 \pm 0.48$, $p = 0.05$). We found no significant differences in stopover probability between Gray-cheeked and Bicknell's Thrush.

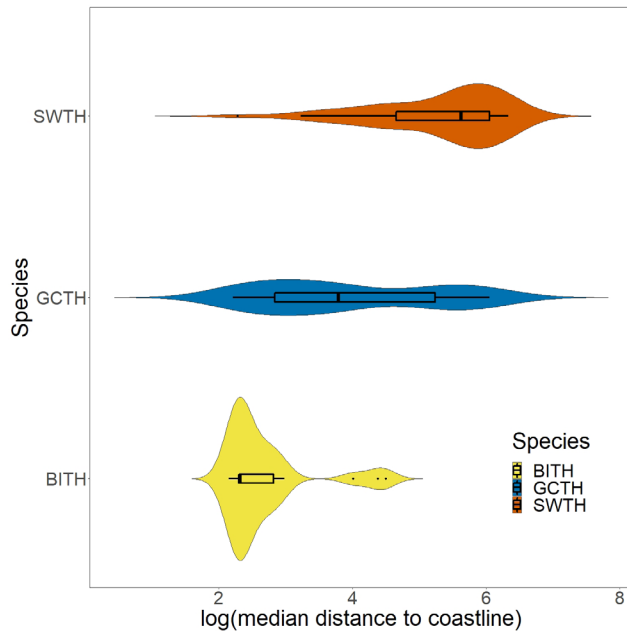


Figure 3. Individual variation of the median distance (log) to coastline (BITH: Bicknell's Thrush; GCTH: Gray-cheeked Thrush; SWTH: Swainson's Thrush).

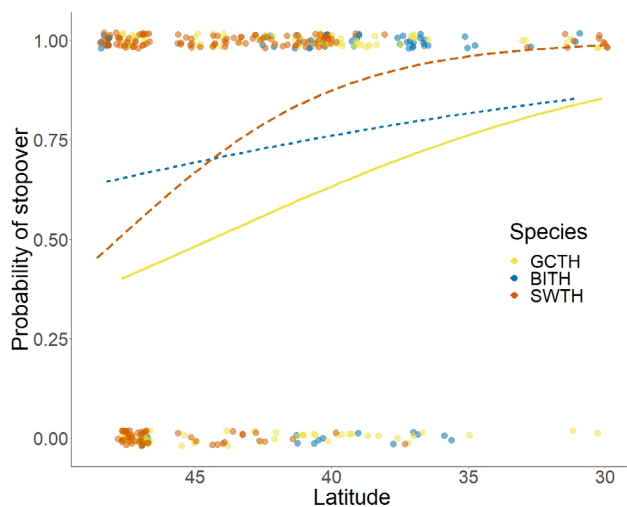


Figure 4. Probability of stopover according to latitude (°N) among Gray-cheeked Thrush (GCTH), Bicknell's Thrush (BITH) and Swainson's Thrush (SWTH). X axis is reversed to facilitate visualisation of southward progression.

4 Discussion

We found substantial interspecific differences in the detection histories across the radio-telemetry array between three species of *Catharus* thrushes. Swainson's Thrush tended to migrate mostly inland along the St. Lawrence River and the Great Lakes, while Bicknell's Thrush and Gray-cheeked Thrush migrated mostly along the Atlantic coast. Individuals from all three species had a propensity to stopover as they approached the southern states of North America, and Bicknell's Thrush was less likely to stopover than Swainson's Thrush. We recognize that the individuals tracked come from a small area within or close to the breeding range of each species and hence, our results are not representative of the entire species. However, the apparent differences in migration routes and migration pace raise interesting questions.

The Bicknell's Thrush has a restricted and more easterly wintering range than Swainson's and Gray-cheeked Thrushes. Hence, the Bicknell's Thrush likely adopts a more coastal route that reduces the overall migration distance, creating an approximately straight line between the breeding and wintering grounds. Furthermore, the weak individual variability regarding the median distance to coastline for Bicknell's Thrush suggests that this coastal route is likely the unique migration route for this species, which is likely to have a potential impact on the species' annual survival [54]. We expected that Bicknell's Thrush would be different from the two other species, but contrary to our predictions, most individuals of Gray-cheeked Thrush also migrated along the Atlantic coast. We could not accurately determine whether migrating individuals had the same breeding location, which is known to have an influence on migration routes [6–9], but the individuals captured in migration likely originate from the Labrador peninsula [40]. Gray-cheeked Thrush exhibited more variability than the Bicknell's Thrush, as some individuals migrated towards the Great Lakes. Breeding Gray-cheeked Thrush from Newfoundland showed similar variability in their migration routes [55], suggesting that breeding origin among eastern populations does not greatly influence migration routes of this species. Intraspecific differences in migration routes might be explained by other factors like age [56–59], sex [13, 60], body condition [61] or evolutionary history [5, 6]. We did not have enough data to examine those hypotheses and more individuals from other populations across the entire breeding range are needed to understand this variability. In addition to that suggestion, breeding origin had no impact on migration routes for Swainson's Thrush captured at both tagging locations. As we hypothesized, Swainson's Thrush had

a more continental route than Bicknell's Thrush, but the difference with Gray-cheeked Thrush merits further investigation. According to another study, Gray-cheeked Thrush and Swainson's Thrush showed differences in their migration routes closer to their wintering grounds— Gray-cheeked Thrush being more likely to cross large bodies of water like the Gulf of Mexico or the Caribbean Sea [37, 62]. In the northern part of their fall migration, the Appalachian Mountains might influence migration routes for some species of passerine [63–65]. Swainson's Thrush might reach the east coast further south and bypass the north of the Appalachian Mountains. A more developed network of receiving stations in the Appalachian Mountain range (e.g. Green Mountains, White Mountains, Allegheny) during the year of the study would have allowed to test the effect of topography on the migratory routes of these three species, but again, more individuals from distinct populations across the entire breeding range is needed to understand the influence of landscape features on the migration routes of these species.

We interpret the bimodal distribution of individual migration paces as evidence of stopovers. Migrating thrushes spent more time outside than inside the Motus detection range. Hence, for migration pace to reflect the actual ground speed, we need to assume that movement paths between consecutive detections were quasi linear [27]. Based on those observations and caveats, we conclude that the Gray-cheeked Thrush stopped less often or for a shorter period of time than the Swainson's Thrush. This hypothesis is consistent with a recent study documenting Gray-cheeked Thrush flights exceeding 3000 km without refueling [26, 62].

Part of the latitudinal pattern of stopovers could be due to sampling bias, caused by geographic variation in the density of the Motus receiving stations. Distances among receiving stations tend to be greater in southeastern North America than further to the North towards the Great Lakes and the east coast of the United States (e.g. New Jersey to Vermont). A denser array of receiving stations will tend to enable the calculation of exceptionally slow or fast speeds, depending on the occurrence and length of stopovers or other variables likely to influence migration pace. Assuming constant ground speed, stopovers will exert a greater negative influence on movement rates, which would increase probability of detecting stopover, if receiving stations are nearby. This bias will be accentuated in the case of longer stopovers. However, our results are contrary to this expectation, and we conclude that if anything, the greater distances among towers to the South have weakened our estimates. Contrary to our results, other studies conducted in Europe suggest

an increase in migration pace and refueling rate along migratory route [66, 67]. Although our approach did not allow us to identify a specific stopover site or habitat, our results could illustrate the importance of stopover in southeastern of the United States. Other fall migration studies have noticed that migrating birds had undertaken an overwater flight across the Gulf of Mexico or the Caribbean Sea [37, 55]. This could result in an important need to rest and refuel before undertaking a long flight [68, 69]. The quality of these stopover areas might have a significant impact on individuals' survival [68, 70, 71] and more investigation should be addressed.

Limits of the study

During the period of the study, the Motus network was at its early stages, and had spatial and temporal gaps. The array was heterogeneous and skewed by an overrepresentation of receiving stations on the east coast of North America and along the St. Lawrence River and Great Lakes. A wider coverage of migration corridors would have allowed to distinguish with greater accuracy the differences in migratory routes and better estimate migration pace. Motus remains an effective and low-cost technology that has the potential to track a large number of passerines, over long distances through the American continent without having to recapture the birds [25]. The development of the network by adding more receiving stations, especially towards the west and south, would likely help enhance the efficiency and accuracy of this technology. Lastly, acknowledging that our result cannot be projected to the entire species, the interspecific differences that we found within our sample might allude to important differences within populations or other species of *Catharus*.

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