Research Square

Preprints are preliminary reports that have not undergone peer review.
They should not be considered conclusive, used to inform clinical practice,
or referenced by the media as validated information.

Migratory passerines share localized movement strategies but differ in activity timing and habitat use during post-breeding stopover

Barbara Frei

frei.bb@gmail.com

Environment and Climate Change Canada

Ana C. Morales

Environment and Climate Change Canada

Marcel A. Gahbauer

Environment and Climate Change Canada

Kyle H. Elliott

McGill University

Research Article

Keywords: diel activity, migratory stopover, migratory behaviour, radio telemetry, stopover ecology

Posted Date: July 7th, 2026

DOI: https://doi.org/10.21203/rs.3.rs-9815932/v1

License: This work is licensed under a Creative Commons Attribution 4.0 International License.
Read Full License

Additional Declarations: No competing interests reported.

Abstract

Background

Stopover is a critical stage of migration during which birds rest and refuel between bouts of active flight. Many migratory bird species may use the same high-quality sites during post-breeding migration, thus competition for the resources needed to sustain migration may be intense. Species may reduce this competition by partitioning their use of space, time, or habitat during stopover.

Methods

We deployed radio nanotags on individuals of five bird species during post-breeding migration and used high-resolution telemetry tracking to track movements at a stopover site. We examined species-specific partitioning across three axes, including: movement behaviour (space), daily activity (time), and fine-scale habitat use (habitat) during the stopover period.

Results

Across species, individuals generally exhibited similar highly localized movements typical of restricted spatial activity during intensive foraging. An aerial insect forager (Blue-headed Vireo) had a much shorter daily activity period followed by other insectivores (warblers) and then omnivores (thrush and sparrow). Habitat use was best explained by vegetation characteristics at the smallest spatial scale considered (25 m) with species responding differently to canopy height, structural heterogeneity, and forest cover.

Conclusion

These patterns indicate that while migratory passerines share broadly similar spatial movement strategies during stopover, niche partitioning occurs in activity timing and microhabitat preferences. We show the importance of heterogeneity in forest cover and structure and suggest the conservation of this under-recognized habitat for birds during the critical migratory period.

Background

Stopovers, defined as *an interruption of migratory endurance flight to minimize immediate and/or delayed fitness cost* [1], are the dominant and yet still poorly understood periods of time in the migration process, when birds stop to rest and refuel at largely unknown and unexperienced locations for varying amounts of time [2]. This usually includes a first search and settle period [3] followed by more targeted movements when habitat is selected to favour specific habitat characteristics and to maximize refueling potential. Stopover home range size, local movements, daily activity, and habitat associations are a

function of multiple factors, including species, season, climate, individual conditions, and site conditions, and are expected to differ from the far better-known breeding season ecology [2, 4, 5].

As birds settle across the landscape for stopover events during migration, factors at multiple scales influence spatial decisions, leading to a hierarchical decision-making process [2, 6, 7]. Migration pathways are dictated by geographic features (mountains, waterways and waterbodies, etc.) which distribute birds unequally across the landscape. Such barriers, along with anthropogenic drivers such as artificial light at night (ALAN) influence large-scale bird movements and spatial distribution of stopover hotspots [8, 9]. Once birds broadly settle into an area for migratory stopover, less is known about finer-scale habitat associations and movements. Migratory birds present a higher plasticity in their habitat choices during migration stopovers than during the breeding period [10], meaning that their habitat use during migration may differ from their better-known breeding habitat associations.

One, if not the most, important constraint during migration for birds is to acquire enough food to meet energetic requirements, particularly for long-distance migrants [2, 4, 5]. Food requirements and energetic conditions may drive small-scale habitat selection [11], foraging behaviours [12, 13], and movements [11]. As many migratory bird species may use the same high-quality sites during post-breeding migration in early autumn, competition for the resources needed to sustain migration can be intense and may influence refueling success [14, 15]. Species may reduce competition by partitioning their use of space, time, or habitat [16–19]. While such “Hutchinsonian” niche partitioning has been widely demonstrated in resident taxa with knowledge of the distribution of resources, such as breeding warblers, it is unclear if partitioning commonly occurs during brief visits to novel habitats, such as migration stopovers for passerines (in shorebirds see Bellefontaine and Hamilton 2023[20]). In autumn, when migratory populations swell to include juvenile birds and thus increase interspecific competition, many species of insectivorous, granivorous and frugivorous songbirds coexist for days to weeks at stopover sites. Dietary plasticity, and even foraging plasticity [21], is frequent and widespread in landbirds during migration [22]. Thus, niche partitioning likely happens in other dimensions than diet, such as space, time or microhabitat.

To develop comprehensive conservation planning for migratory birds we need a better understanding of habitat relationships and stopover ecology [23]. While recent technological advances have catalyzed significant advances to our understanding of migratory flight [5, 24], our understanding of the stopover period has advanced much less [1]. Current knowledge of stopover is mainly based on the proximate study of departure decisions [1]. Our overall aim was to quantify stopover movement, activity, and habitat use for migratory birds during fall stopover and identify associations with intrinsic (i.e., species’ ecology and individual condition) and extrinsic (seasonality, time to departure) factors. To do so, we used two years of fall stopover data on telemetry tracked individuals of several migratory species with differing natural histories and biology (i.e., diet, migration strategy, size) in a peri-urban green space of one of Canada’s largest cities. For the billions of songbirds that migrate southward from the boreal forest each fall, the cities in southern Canada are the first human barrier they encounter, including those that are funneled through the ‘Montreal Gap’ between the Great Lakes and the Gulf of the St. Lawrence. Our

objectives were to: (1) quantify individual migratory bird movement during stopover to compare across species and individual condition/timing, (2) compare species-specific daily activity from telemetry-tracked individuals and explore activity trends across seasonality and stopover duration, and (3) identify species-specific habitat associations during fall stopover. We predicted that leaner individuals would have higher average movement rates as they searched for food [11] and that individuals with longer stopovers would have lower average movement rates as once they settled into an optimal area they would remain there. We also predicted that daily activity would start earlier and end later for frugivore species than for insectivorous species that may be constrained to foraging during times when insects are active [25, 26]. Lastly, we predicted a unimodal relationship with forest cover and canopy height (i.e., lower use when forest cover/canopy height is very low or very high) and a positive relationship with canopy structural heterogeneity across most species [23, 27, 28].

Methods

Radio-tagging and tracking migratory birds during post-breeding migration

The study took place on the western tip of the island of Montreal (45.43◦N, 73.94◦W; ~3.75 million people in Montreal) at the McGill Bird Observatory (MBO), within a peri-urban green space characterized by a mix of shrubland, mature deciduous forests, hawthorn tracts, sumac stands, small wetlands, and an old apple orchard [29]. The site is an important stopover site for several migratory birds [30], including neotropical moult migrants [27, 31–33]. We focused on five different species of migratory birds that were commonly captured during post-breeding migration and represented a suite of ecological traits (Table S1): Blue-headed Vireo (*Vireo solitarius*), Hermit Thrush (*Catharus guttatus*), Magnolia Warbler (*Setophaga magnolia*), Yellow-rumped (Myrtle) Warbler (*S. coronata)*, and Song Sparrow (*Melospiza melodia*). Birds were captured and radio-tagged at the MBO during their 2022–2023 fall migration monitoring period (1 August – 7 November). The radio-tags used were Lotek VHF nanotags (registered with the Motus Wildlife Tracking System) and each of the tags operated on the same frequency of 166.380 MHz and emitted a unique digital code to allow us to uniquely identify the individual. Birds were captured using 30 mm mist nets and banded with numbered aluminum leg bands. Tags were attached to each bird using a figure eight leg-loop harness made from nylon-elastic thread [34]. Standard banding measurements were taken, including: sex, age based on plumage and skull ossification, mass, fat, and wing chord length. Birds were identified, aged, and sexed by experienced banders using the identification guide by Pyle et al. (1997)[35]. Birds were banded under Animal Use Protocol 2007–5447 from McGill University, radio-tagged under Animal Use Protocol 22BF01 and 23BF01 from Environment and Climate Change Canada, and federal banding permits 10743B and 10743T issued by the Canadian Wildlife Service.

Tag burst rate varied among the species, ranging from ~ 4.3 s for Hermit Thrush to ~ 14.9 s for Magnolia Warblers. Due to smaller birds being constrained using smaller tags with shorter battery lives, longer

burst intervals were employed to allow for maximal battery life while still allowing for hand-held tracking. Tags were detected by an array of permanent and 'pop-up' Motus automated telemetry towers, including at the MBO (45.4307◦N, − 73.9385◦W), at the McGill University Macdonald Campus (45.4079◦N, − 73.939◦W), at the Bois-de-la-Roche nature park (45.4403◦N, − 73.9407◦W), and in a suburban area to the south of the study site (45.4109◦N, − 73.9301◦W). While detections at the towers allowed us to identify bird departures from the site and (when detected) provided some information of bird movements and general locations (i.e., which antenna direction of strongest signal), they did not provide robust location data. For this we used daily manual tracking starting the day after the bird's initial capture and tagging, until the bird was confirmed to have departed from the site or was not detected either by the towers or through manual tracking for > 5 days. Using a 3-element Yagi and a receiver (Lotek SRX 800 or Lotek SRX 1200) tagged birds were tracked and their daily locations were recorded as a GPS point when the signal was at least 130 dB (Lotek SRX 800) or 200 dB (Lotek SRX 1200) at a gain (precision) between 9 and 40 dB.

Quantifying individual movements from tracking data

We quantified individual bird movement from tracking data by calculating the median step length (distance between subsequent tracked locations), net displacement (the shortest straight-line distance between starting and final tracked position), and cumulative distance (sum of all step lengths for tracked locations of an individual). From this we also quantified a straightness index, defined as net displacement divided by the cumulative distance [36, 37]. We compared median step length and straightness index resulting from telemetry tracking data across the five study species using Kruskal-Wallis tests. We also used a general additive model (GAM) to model individual straightness index as a function of stopover length and fuel load on arrival, and a general additive mixed model (GAMM) to model individual step lengths as a function of stopover length and fuel load of arrival, accounting for individual variation as a random effect. See Supplementary Information for details on stopover length and fuel load calculations.

Change point activity analysis

The onset and end time of diel activity were determined using radio telemetry data collected by the Motus station deployed at the McGill Bird Observatory (MBO). Proximity to receiving antenna, transmitter orientation, and environmental obstructions can affect received signal strength, causing high signal strength variation when a tagged individual is active and low signal strength variation during periods of inactivity. Changes in signal strength variation can then be used to determine when a bird becomes active in the morning and quiescent in the evening. Following Morbey et al. (2020), we applied change point analysis to extract the time of activity onset and end based on the characteristic increase and decrease of signal variation respectively. Change points in signal variation were determined using the package "changepoint" [39], for the six-hour period centered on local sunrise for activity onset and sunset for activity end. Sunrise and sunset times were determined for the study site using the function

getSunlightTimes in the suncalc package [40]. For further details on change point extraction methods see Supplemental Information.

To test for differences among the five species for onset and end activity change points we used GAMMs, including (1) species as a categorical fixed effect, (2) species-specific smooth term of days until departure as a measure of proximity to migration departure and (3) day of year (DOY) to account for seasonal trends independent of departure timing in activity rates. To account for individual variation, we included bird ID as a random effect. Onset and end activity models were checked for concurvity between smooth predictor variables, checked that models met assumptions using the DHARMa package [41] and tested model fit using the Hosmer-Lemeshow test from the ResourceSelection package [42]. We compared estimated marginal means of both onset and end of activity among species using Tukey-adjusted pairwise comparisons using the eemmeans package [43].

Resource selection function during post-breeding migration

We compared 'used' vs. available' habitat using a resource selection function (RSF) for all tracked locations during the fall stopover period for four of the five focal species. We omitted the Song Sparrow from the analysis as a large number of individuals moved to an adjacent agricultural areas which we found was not well characterized by the habitat layers used. To build our model we extracted spatially available data including: mean and standard deviation (SD) of vegetation height (1 m resolution) from OpenForest [44], and both high (> 3 m) and low (< 3 m) vegetation layers (1 m resolution) from the 2023 Indice Canopée Metropolitan [45]. Unused locations were derived at a 1:5 ratio by creating random locations within 300 m of the used location at a random angle and distance. We extracted data at four buffers (25m, 50m, 100m, 200m) and first ran a scale of effect sensitivity analysis using general linear mixed effect models (GLMMs) on all four predictor variables and species as a random effect to inform a data driven spatial scale for the RSF. We checked for collinearity using Variance Inflation Factor (VIF; variables with VIF values > 10 were considered to have problematic collinearity and were removed) among predictor variables. We ranked the models using Akaike's Information Criterion for small sample size (AICc) to determine the data-driven scale of effect [46].

Once the scale of effect was determined, we ran species-specific RSF models with habitat predictors using General Additive Models (GAMs) as we had no *a priori* expectations of linear effects. After checking for concurvity, we ran species-specific Generalized Additive Mixed-effect Models (GAMMs) including individuals as random effects. Random variance for individuals collapsed to zero variance indicating no detectable among-individual variation in baseline selection, therefore final models were fit without individual-level random effects. We ensured models met with all assumptions using the DHARMa package [41] and tested model fit using the Hosmer-Lemeshow test from the ResourceSelection package [42]. We considered $\alpha = 0.05$ as significant and $\alpha = 0.1$ as marginally significant.

Results

Individual movement from tracked birds differs marginally between species

Over the 2022–2023 post-breeding migration period 101 individual birds were tracked to 704 individual locations. This included five Blue-headed Vireos (25 locations), 42 Hermit Thrushes (356 locations), 18 Magnolia Warblers (99 locations), 22 Yellow-rumped Warblers (108 locations), and 14 Song Sparrows (110 locations). Overall, all tracked migratory birds showed evidence of tortuous, localized movement during fall stopover with a mean straightness index of 0.30 (± 0.03 SE). Straightness index did not vary across species (Kruskal-Wallis chi-squared = 4.78, p-value = 0.31, Fig. S1). Likewise, straightness index did not significantly differ across species-specific stopover lengths (p = 0.23–0.82 depending on species) or fuel load (p = 0.23) on arrival. The median step length between tracked displacements of migratory birds during stopover varied marginally among species (Kruskal-Wallis chi-squared = 8.79, p-value = 0.06; Fig. S2). Step distance as a function of stopover length was significant for Blue-headed Vireo (p = 0.04), Yellow-rumped Warbler (p < 0.01), and Song Sparrow (p < 0.01), and generally showed smaller step lengths with longer stopovers (Fig. 1) when accounting for individual differences (deviance explained = 25.7%). As with the straightness index, fuel load on arrival was not significantly related to step length (p = 0.51)

Timing of daily activity differs significantly between species

A total of 734 activity onset changepoints were extracted for 86 individuals and 697 activity end changepoints were extracted for 95 individuals. Total number of individuals, changepoints, and timing of activity is outlined in Table S2. Both daily onset and end activity GAMMs met model assumptions, showed good fit and did not show concurvity between predictor variables. The onset of daily activity relative to sunrise differed significantly among species. Average activity for Blue-headed Vireo began ~ 15 minutes after sunrise, significantly later than Hermit Thrush (β = −42.23 ± 9.92 SE, $p < 0.001$), Magnolia Warbler (β = −39.45 ± 16.16 SE, $p = 0.015$), Yellow-rumped Warbler (β = −31.07 ± 10.24 SE, $p = 0.003$), and Song Sparrow (β = −38.85 ± 10.36 SE, $p < 0.001$), which all began activity before sunrise (Fig. 2A). Among the other four species most pairwise differences were non-significant except for Yellow-rumped Warbler and Hermit Thrush, with the latter having the earliest onset morning activity of all species (Fig. 2A). The relationship between activity onset and days to departure differed among species, with a significant effect only detected for Hermit Thrush (edf = 1.00, F = 4.44, $p = 0.036$), with activity onset growing earlier as departure approached (Fig S3). There was also a significant nonlinear seasonal effect of day of year (edf = 4.84, F = 3.24, $p = 0.033$), with the onset of morning activity growing later in the season (Fig. S4). The model explained a modest proportion of the variance in activity onset (adjusted $R^2 = 0.125$; n = 559).

The timing of the end of the daily activity period relative to sunrise differed significantly among the five focal species. Compared to Blue-headed Vireo (which ended activity ~ 49 minutes before sunset), activity ended later in all other species: Hermit Thrush (β = 58.07 ± 6.78 SE, $p < 0.001$), Magnolia Warbler (β = 55.42 ± 11.84 SE, $p < 0.001$), Yellow-rumped Warbler (β = 54.31 ± 6.99 SE, $p < 0.001$), and Song Sparrow (β = 68.61 ± 7.31 SE, $p < 0.001$). Pairwise comparisons of estimated marginal means indicated that all other species ended their activity significantly later than Blue-headed Vireos, with Song Sparrows ending activity latest, and Magnolia Warbler, Yellow-rumped Warbler, and Hermit Thrush being intermediates (Fig. 2B) Species-specific relationships between end of activity and days to departure from the stopover site were generally weak. Only the Blue-headed Vireo showed a significant effect (edf = 1, F = 6.13, $p = 0.014$), indicating a linear change in activity ending earlier as departure approached (Fig. S5). Unlike activity onset, there was no evidence of a strong seasonal effect independent of departure timing ($p = 0.23$). Overall, the model explained a moderate proportion of variation in activity end (adjusted R^2 = 0.266; $n = 629$), indicating that timing of end-of-day activity varied primarily by species, while temporal effects related to departure or season were minor.

Migratory bird habitat use during stopover

Across all species, the smallest spatial scale (25 m) showed by far the strongest fit to the data (77 AICc unit difference to the next spatial scale of 50 m). Response to habitat covariates varied among species. Hermit Thrush showed strong nonlinear responses to both mean canopy height (edf = 3.90, $p < 0.001$) and canopy height SD (edf = 3.80, $p < 0.001$), with a weaker but significant forest cover (edf = 2.78, $p = 0.013$). Generally, predicted habitat use probabilities for Hermit Thrush showed a preference for areas with mean canopy height of 5–20 m, increases in use with canopy height heterogeneity, and decreases in habitat use when forest cover increased beyond 50% (Fig. 3). Yellow-rumped Warbler habitat use was not associated with mean canopy height but exhibited significant nonlinear effects of canopy height SD (edf = 3.88, $p = 0.005$) and forest cover (edf = 3.24, $p = 0.007$). Predicted habitat use for Yellow-rumped Warbler demonstrated a preference for areas with greater canopy height homogeneity (lower SD) and peak use around 75% forest cover (Fig. 3). For Magnolia Warbler, probability of use was significantly influenced by mean canopy height (edf = 2.35, $p = 0.025$) and forest cover (edf = 3.29, $p = 0.007$), while canopy heterogeneity was not significant. Predicted habitat use for Magnolia Warblers demonstrated a preference for areas with 50% forest cover, and decreasing preference when mean canopy height was > 20 m (Fig. 3). In contrast, Blue-headed Vireo exhibited only marginally (α = 0.1) supported effects of canopy height heterogeneity (edf = 3.83, $p = 0.058$) and forest cover (edf = 3.72, $p = 0.063$), with no significant response to mean canopy cover (Fig. S6). Deviance explained varied among species, from 10.3% for Magnolia Warbler to 20.4% for Blue-headed Vireo, with intermediate values for the other species. Overall, patterns suggest that migratory passerines differ in the relative importance of canopy height and forest during fall stopover, with some species (Hermit Thrush) responding strongly to both forest cover and structural complexity, whereas others (Yellow-rumped Warbler, Magnolia Warbler) showed more selective or weaker responses.

Discussion

We found evidence of clear niche partitioning across two axes (time and microhabitat) across a suite of migratory bird species during post-breeding stopover in a large peri-urban green space. Individual movements were localized and tortuous with variation driven by extrinsic rather than intrinsic factors, with limited differences between species. Temporal activity (morning onset and evening cessation) patterns differed strongly among species, with larger differences for evening cessation of activities suggesting late-day constraints are a stronger influence of temporal niche differentiation. Habitat use during fall stopover occurred at the finest spatial scale considered (25 m), with species-specific responses to vegetation structure and forest cover. Thus, despite the large number of individual migrants of multiple species funnelling through limited stopover sites near a large urban center just south of the boreal ecozone, interspecific competition may be limited by niche partitioning in activity periods and microhabitats.

Localized movements during stopover similar across species but differ with stopover duration

Movement patterns across all species of migratory birds in our study indicated higher tortuosity for primarily localized exploratory movements typical of refueling stopover events. This behaviour likely reflects a strategy to maximize foraging efficiency and maximizing energy intake while minimizing energy output and possible predation risk [1, 3, 4]. Despite differences in the foraging ecology (insectivorous vs. frugivores vs. granivores) and migration strategies (short vs. medium vs. long-distance migrants), general movements (quantified using the straightness index) varied only marginally between species and did not significantly differ overall. This suggests that general factors such as resource distribution and habitat structure may play a stronger role in driving movement than species-specific ecology, leading to basic spatial movement being broadly similar among migratory passerines occupying the same landscape. Despite not being statistically different, Magnolia Warbler (long-distance migrant) had the highest straightness index and demonstrated more linear movements compared to the other species. Longer-distance migrants are under higher pressure to minimize total migration time to cover larger distances, and as such employ a ‘time-minimization’ strategy that requires faster refueling, sometimes leading to higher movements to locate food resources [47, 48].

Our findings support our prediction that individual movements of migratory birds may change across the course of the stopover duration, with three of the five species (Blue-headed Vireo, Yellow-rumped Warbler, and Song Sparrow) demonstrating shorter displacements with longer stopovers. These patterns may reflect behavioural adjustments during the stopover period, with earlier exploration leading to higher movements, and the longer an individual stays during stopover movements become more focused and restricted. Similar trends have been observed in some of the few studies where individual migrants have been tracked during stopover. Tracked Ovenbirds (*Seiurus aurocapilla*) during spring and fall migration at a large urban park in New York City, USA found that linearity (i.e., straightness) indices and displacement distances were significantly lower beyond the fourth day of stopover [49]. Similar trends were found

during spring stopovers for Wilson's Warblers (*Cardellina pusilla*) in Arizona, USA with linear displacement dropping after two days [50]. Unlike our predictions, fuel load on arrival was not significantly related to either movement patterns we measured [11, 51].

Species-specific diel activity patterns may be related to foraging niche

In contrast to daily movement, diel activity patterns differed strongly among species. While species varied in both activity onset and cessation, differences were larger during cessation, suggesting that late-day constraints (e.g., low-light foraging or risk tolerance) may be a stronger influence of niche differentiation. Most species initiated activity before sunrise (15–28 minutes before sunrise; Table S2), with Hermit Thrush starting the earliest while Blue-headed Vireos began activity later than all other species (12 minutes after sunrise; Table S2). Similarly, with Blue-headed Vireos consistently ended their daily activity earlier than the other species, with activity ending before sunset while most species continued until just after sunset (4–11 minutes after sunset; Table S2), with Song Sparrows remaining active latest into the evening (17 minutes after sunset; Table S2). Activity differences among species are likely related to the variation in availability of food resources (frugivores vs. insectivores) and site-specific stopover timing [52]. Earlier activity could be related to locating and securing a foraging patch [53], which may be a stronger driver for birds consuming non-mobile food resources such as fruit or seeds. We see evidence of this in our study, with Hermit Thrush (frugivore) and Song Sparrow (granivore) being the two species with the earliest diel activity onset. Insect activity especially for aerial insects increases with warmer temperatures [25, 26], which may occur later in the morning during the fall. This may explain later starts by insectivorous species, such as the two warbler species and the Blue-headed Vireo, seen in our study. Compared to the more active foraging gleaning warbler species [54, 55], the Blue-headed Vireo foraging is slow and methodical and often includes aerial flight to capture prey [56]. This additional constraint of visual acuity needed for foraging may explain the species shorter diel activity.

While species-specific differences were the strongest factor influencing temporal niche width during migratory bird stopovers in our study, activity onset (Hermit Thrush) and cessation (Blue-headed Vireo) were earlier as departure approached. This pattern may indicate increasing foraging effort prior to migratory departure, as individuals attempt to maximize fuel stores before resuming migration or engaging in short pre-migratory flights aloft to assess suitability for departure [52]. However, species may vary in their changes in diel activity in proximity to departure, with some species ending earlier and others later than normal [38]. While the functional significance of the behaviour change is impossible to determine from the telemetry-derived activity data, it does suggest individuals may engage in preparatory behaviour prior to migratory flight and departure from a stopover site [38]

Migratory birds fine-scale habitat use of intermediate forest cover and structural heterogeneity during fall stopover

Migratory passerines selected habitat at smallest spatial scale considered (25 m) during fall stopover. Birds appear to use a hierarchical approach to habitat use during stopover, responding to landscape-level features to locate stopover areas but using finer-scale habitat decisions for foraging opportunities or to reduce predation risk [2, 6, 7]. Within this shared fine-scale context, species differed in their responses to canopy height, structural heterogeneity, and forest cover, suggesting that stopover habitats may be partitioned according to species-specific ecological traits. Ground-feeding or cover-dependent species such as the Hermit Thrush showed strong and generally positive associations with structural heterogeneity, consistent with the species' importance for heterogenous structures for foraging and concealment [57, 58]. Most species also showed selective response to intermediate forest cover (50–75%), with rapid declines of preference at very high or very low forest cover.

In contrast, our findings for intermediate level of forest cover use and higher structural diversity for the remaining species (thrush and warblers) match both our field observations and findings of non-breeding habitat use from other studies. While edge-dominated forests are not generally considered high-quality breeding habitat for forest-breeding species due to possible negative edge effects [59], there is evidence that forest-edge/shrubby habitat may be heavily used in spring [23] and fall migration (Rodewald and Brittingham 2004). For example, on a barrier island off the northern coast of the Gulf of Mexico, while shrubby habitat only accounted for 14% of available habitat, it has the highest species richness, diversity, and individual abundance for spring migrants [60]. Similarly, forest-area and shrubby habitat may be critical during other times during the annual cycle, such as the critical post-breeding molt period [27, 61]. Our findings add to the evidence that suggests that given the totality of time in forest-edge/shrubby habitat across the full annual cycle, greater conservation effort and recognition should be given to this under-recognized habitat for migratory birds. This includes efforts specifically where forest edges are more permanent than transient, such as woodlots in agricultural or urban/suburban landscapes [23]. Unless habitat requirements for migratory birds during the non-breeding period (e.g., migration stopovers) are met, conservation efforts focused on the breeding will be compromised [62].

Conclusion

Migratory songbirds across different foraging guilds and migration strategies shared broadly similar movements at the same fall stopover site, while having markedly different diel activity patterns and fine-scale habitat associations. Across species, movements were highly localized, typical of centralized foraging during stopover, with some evidence of higher refueling pressure/movement distance associated with longer migration distances. Species varied in daily activity onset and cessation during migration stopover based on foraging guild. Lastly, habitat use during stopover was driven by microhabitat and suggests that maintaining heterogeneous forest structure within migratory bird stopover hotspots may be critical for supporting diverse species assemblages during this energetically demanding period of the annual cycle.

Declarations

Ethics declaration: Birds were banded under Animal Use Protocol 2007-5447 from McGill University, radio-tagged under Animal Use Protocol 22BF01 and 23BF01 from Environment and Climate Change Canada, and federal banding permits 10743B and 10743T issued by the Canadian Wildlife Service.

Consent for publication: Not applicable.

Availability of data and materials: Upon acceptance, all data and code will be uploaded and stored to OSF or another open data repository as specified by the journal.

Competing interests: The authors declare that they have no competing interests

Funding: Funding through the Environmental Damages Fund (KHE) and through Environment and Climate Change Canada (BF).

Authors' contributions: BF, ACM, MAG, and KHE conceived the ideas and designed the methodology, BF and ACM collected the data, BF and ACM analyzed the data and BF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Acknowledgement: This work was possible due to the generous support of the staff and volunteers at the McGill Bird Observatory, including Simon Duval, Shawna Sevigny, and Cindy Bouchard. Additional tracking of radio-tagged birds was accomplished through the hard work of student technicians including Elena Tranze-Drabinia, Ana Blanc-Benigeri, Nathanya Goudreau, Mackenzie Guest, and Mathilde Lefvert.

References

1. Schmaljohann H, Eikenaar C, Sapir N. Understanding the ecological and evolutionary function of stopover in migrating birds. Biol Rev. 2022;97:1231–52. https://doi.org/10.1111/brv.12839.
2. Moore FR, Kerlinger JGSA, Simons P. TR. Stopover habitat: management implications and guidelines. In: Finch, Deborah M; Stangel, Peter W, editorsMar Status and management of neotropical migratory birds: September 21–25, 1992, Estes Park, Colorado Gen Tech Rep RM-229 Fort Collins, Colo: Rocky Mountain Forest and Range Experiment Station, US Dept of Agriculture, Forest Service: 58–69 [Internet]. 1993 [cited 2026 Mar 5];229. https://research.fs.usda.gov/treesearch/22889. Accessed 5 2026.
3. Alerstam T, Hedenström A. The Development of Bird Migration Theory. J Avian Biol. 1998;29:343–69.
4. Alerstam T. Optimal bird migration revisited. J Ornithol. 2011;152:5–23. https://doi.org/10.1007/s10336-011-0694-1.
5. Moore F. Biology of landbird migrants: a stopover perspective. The Wilson Journal of Ornithology [Internet]. 2018 [cited 2026 Mar 5];130. https://doi.org/10.1676/1559-4491-130.1.1
6. Buler J, Moore FR, Woltmann S, A MULTI-SCALE EXAMINATION. OF STOPOVER HABITAT USE BY BIRDS. Ecology. 2007;88:1789–802.

7. Simons TR, Pearson SM, Moore FR. Application of Spatial Models to the Stopover Ecology of Trans-gulf Migrants. Stud Avian Biology. 2000;20.
8. Horton KG, Buler JJ, Anderson SJ, Burt CS, Collins AC, Dokter AM, et al. Artificial light at night is a top predictor of bird migration stopover density. Nat Commun Nat Publishing Group. 2023;14:7446. https://doi.org/10.1038/s41467-023-43046-z.
9. McLaren JD, Buler JJ, Schreckengost T, Smolinsky JA, Boone M, van Emiel E, et al. Artificial light at night confounds broad-scale habitat use by migrating birds. Ecol Lett. 2018;21:356–64. https://doi.org/10.1111/ele.12902.
10. Zuckerberg B, Fink D, La Sorte FA, Hochachka WM, Kelling S. Novel seasonal land cover associations for eastern North American forest birds identified through dynamic species distribution modelling. Bradley B, editor. Diversity and Distributions. 2016;22:717–30. https://doi.org/10.1111/ddi.12428
11. Tietz JR, Johnson MD. Stopover Ecology and Habitat Selection of Juvenile Swainson's Thrushes During Fall Migration Along the Northern California Coast. Condor. 2007;109:795–807. https://doi.org/10.1093/condor/109.4.795.
12. Loria DE, Moore FR. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. Behav Ecol. 1990;1:24–35. https://doi.org/10.1093/beheco/1.1.24.
13. Wang Y, Moore FR. Long–distance bird migrants adjust their foraging behavior in relation to energy store. Dong Wu Xue Bao. 2005;51:12–23.
14. Cohen EB, Lafleur JM, Moore FR. Density Dependent Refueling of Migratory Songbirds During Stopover Within an Urbanizing Coastal Landscape. Frontiers in Ecology and Evolution [Internet]. 2022 [cited 2022 Apr 8];10. https://www.frontiersin.org/article/10.3389/fevo.2022.837790. Accessed 8 Apr 2022.
15. Zimin SV, Zimin A, Burns DJ, Livne R, Paz R, Zvik Y, et al. Competition is a major limiting factor of refueling in migratory passerines during stopover. J Avian Biol. 2023;2023:e03137. https://doi.org/10.1111/jav.03137.
16. MacArthur RH. Population Ecology of Some Warblers of Northeastern Coniferous Forests. Ecology. 1958;39:599–619. https://doi.org/10.2307/1931600.
17. Cotton PA. Temporal partitioning of a floral resource by territorial hummingbirds. Ibis. 1998;140:647–53. https://doi.org/10.1111/j.1474-919X.1998.tb04710.x.
18. Pearman PB, Guisan A, Broennimann O, Randin CF. Niche dynamics in space and time. Trends Ecol Evol. 2008;23:149–58. https://doi.org/10.1016/j.tree.2007.11.005.
19. Dymit EM, Twining JP, Garcia-Anleu R, Allen JM, Levi T. Niche partitioning among neotropical felids. J Anim Ecol. 2026;95:115–30. https://doi.org/10.1111/1365-2656.70173.
20. Bellefontaine SC, Hamilton DJ. Shorebirds exhibit niche partitioning on multiple dimensions at a small staging site on the Northumberland Strait, New Brunswick, Canada. FACETS. Can Sci Publishing. 2023;8:1–12. https://doi.org/10.1139/facets-2022-0230.
21. Martin TE, Karr JR. Behavioral Plasticity of Foraging Maneuvers of Migratory Warblers: Multiple Selection Periods for Niches. Stud Avian Biology. 1990;13:353–9.

22. Parrish JD. Behavioral Energetic and Conservation Implications of Foraging Plasticity during Migration. Stud Avian Biology. 2000;20:53–70.
23. Rodewald PG, Brittingham MC. Stopover Habitat use by Spring Migrant Landbirds: The Roles of Habitat Structure, Leaf Development, and Food Availability. Auk. 2007;124:1063–74. https://doi.org/10.1093/auk/124.3.1063.
24. Linscott JA, Senner NR. Beyond refueling: Investigating the diversity of functions of migratory stopover events. Ornithological Appl. 2021;123:duaa074. https://doi.org/10.1093/ornithapp/duaa074.
25. Lemoine NP, Burkepile DE, Parker JD. Variable effects of temperature on insect herbivory. PeerJ. 2014;2:e376. https://doi.org/10.7717/peerj.376.
26. Maggini I, Hama F, Robson D, Rguibi-Idrissi H, Barlein F, Gargallo G. Foraging behavior of three species of songbirds during stopover in southeastern Morocco during spring migration. Journal of Field Ornithology [Internet]. 2015 [cited 2026 Mar 11];86. https://www.jstor.org/stable/24617956?seq=1. Accessed 11 Mar 2026.
27. Poirier V, Elliott KH, Frei B. Peri-urban forest margins are important stopover sites for moult-migrating songbirds. J Nat Conserv. 2023;126539. https://doi.org/10.1016/j.jnc.2023.126539.
28. Rodewald PG, Brittingham MC. Stopover Habitats of Landbirds During Fall: Use of Edge-Dominated and Early-Successional Forests. Auk. 2004;121:1040–55. https://doi.org/10.1093/auk/121.4.1040.
29. Bardo L, Goulet L, Hibbert A, Lukasik V, Poitras K. Ecological assessment of the Stoneycroft Wildlife Area. Internal Report. Department of Natural Resource Sciences, McGill University; 2003.
30. Jarjour C, Frei B, Elliott KH. Associations between sex, age and species-specific climate sensitivity in migration. Anim Migration De Gruyter. 2017;4:23–36. https://doi.org/https://doi.org/10.1515/ami-2017-0004.
31. Junda JH, Duval S, Gahbauer MA. Use of discrete molting grounds by migrant passerines undergoing prebasic molt in southern Quebec. Wilson J Ornithol. 2020;132:72. https://doi.org/10.1676/1559-4491-132.1.72.
32. Morales A, Frei B, Mitchell GW, Bégin-Marchand C, Elliott KH. Reduced diurnal activity and increased stopover duration by molting Swainson's Thrushes. Ornithology. 2022;139:ukab083. https://doi.org/10.1093/ornithology/ukab083.
33. Poirier V, Frei B, Lefvert M, Morales A, Elliott KH. Moult migrant Tennessee Warblers undergo extensive stopover in peri-urban forests of southern Quebec. Can J Zool [Internet]. NRC Research Press; 2023 [cited 2024 Feb 1]; https://doi.org/10.1139/cjz-2023-0109
34. Rappole J, Tipton A. New harness design for attachment of radio transmitters to small passerines. J Field Ornithol. 1991;62:335–7.
35. Pyle P, Howell S, Ruck S. Identification guide to North American birds: a compendium of information on identifying, ageing, and sexing near-passerines and. passerines in the hand. Institute for Bird Populations, and Point Reyes Bird Observatory. Bolinas, CA.: Slate Creek; 1997.

36. Almeida PJAL, Vieira MV, Kajin M, Forero-Medina G, Cerqueira R. Indices of movement behaviour: conceptual background, effects of scale and location errors. Zoologia (Curitiba). Sociedade Brasileira de Zoologia. 2010;27:674–80. https://doi.org/https://doi.org/10.1590/S1984-46702010000500002.
37. Fullman TJ, Person BT, Prichard AK, Parrett LS. Variation in winter site fidelity within and among individuals influences movement behavior in a partially migratory ungulate. PLOS ONE Public Libr Sci. 2021;16:e0258128. https://doi.org/10.1371/journal.pone.0258128.
38. Morbey YE, Beauchamp AT, Bonner SJ, Mitchell GW. Evening locomotor activity during stopover differs on pre-departure and departure days in free-living songbirds. J Avian Biology [Internet]. 2020. https://doi.org/10.1111/jav.02448. [cited 2024 Jan 17];51.
39. Killick R, Eckley IA. changepoint: an R package for changepoint analysis. J Stat Softw. 2014;58:1–19. https://doi.org/10.18637/jss.v058.i03.
40. Thieurmel B, Elmarhraoui A, suncalc. Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase [Internet]. 2022. https://CRAN.R-project.org/package=suncalc
41. Hartig F, DHARMa. Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models [Internet]. 2026 [cited 2026 Mar 12]. https://github.com/florianhartig/dharma. Accessed 12 Mar 2026.
42. Lele SR, Keim JL, Solymos P. ResourceSelection: Resource Selection (Probability) Functions for Use-Availability Data [Internet]. 2023 [cited 2026 Feb 9]. https://cran.r-project.org/web/packages/ResourceSelection/index.html. Accessed 9 Feb 2026.
43. Lenth RV, Piaskowski J, Banfai B, Bolker B, Buerkner P, Giné-Vázquez I et al. Mar. emmeans: Estimated Marginal Means, aka Least-Squares Means [Internet]. 2026 [cited 2026 Mar 12]. https://cran.r-project.org/web/packages/emmeans/index.html. Accessed 12 2026.
44. Gouvernement du Québec. ForetOuverte [Internet]. Ministère des Ressources naturelles et des Forêts. 2024. https://www.foretouverte.gouv.qc.ca/
45. Observatoire du Grand Montréal. Données géoréférencées [Internet]. 2023. https://observatoire.cmm.qc.ca/produits/donnees-georeferencees
46. Martin AE, Fahrig L. Measuring and selecting scales of effect for landscape predictors in species–habitat models. Ecol Appl. 2012;22:2277–92. https://doi.org/10.1890/11-2224.1.
47. Alerstam T, Lindström Å. Optimal Bird Migration: The Relative Importance of Time, Energy, and Safety. In: Gwinner E, editor. Bird Migration. Berlin, Heidelberg: Springer; 1990. pp. 331–51. https://doi.org/10.1007/978-3-642-74542-3_22.
48. Chernetsov N. Spatial behavior of medium and long-distance migrants at stopovers studied by radio tracking. Ann N Y Acad Sci. 2005;1046:242–52. https://doi.org/10.1196/annals.1343.021.
49. Seewagen CL, Slayton EJ, Guglielmo CG. Passerine migrant stopover duration and spatial behaviour at an urban stopover site. Acta Oecol. 2010;36:484–92. https://doi.org/10.1016/j.actao.2010.06.005.

50. Paxton KL, Van Riper C, O'Brien C. Movement patterns and stopover ecology of Wilson's Warblers during spring migration on the lower Colorado River in southwestern Arizona. Condor. 2008;110:672–81. https://doi.org/10.1525/cond.2008.8602.
51. Smith AD, McWilliams SR. What to do when stopping over: behavioral decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions. Behav Ecol. 2014;25:1423–35. https://doi.org/10.1093/beheco/aru148.
52. Schofield LN, Deppe JL, Zenzal TJ, Ward MP, Diehl RH, Bolus RT, et al. Using automated radio telemetry to quantify activity patterns of songbirds during stopover. Auk. 2018;135:949–63. https://doi.org/10.1642/AUK-17-229.1.
53. Beauchamp AT, Guglielmo CG, Morbey YE. Stopover refuelling, movement and departure decisions in the white-throated sparrow: The influence of intrinsic and extrinsic factors during spring migration. J Anim Ecol. 2020;89:2553–66. https://doi.org/10.1111/1365-2656.13315.
54. Hunt PD, Flaspohler DJ. Yellow-rumped Warbler (Setophaga coronata), version 1.0. Birds of the World [Internet]. Cornell Lab of Ornithology, Ithaca, NY, USA; 2020 [cited 2025 Apr 4]; https://doi.org/10.2173/bow.yerwar.01
55. Dunn EH, Hall GA. Mar. Magnolia Warbler - Setophaga magnolia. Birds of the World [Internet]. Ithaca, NY, USA: Cornell Lab of Ornithology; 2020 [cited 2026 Mar 11]; https://birdsoftheworld.org/bow/species/magwar/cur/introduction. Accessed 11 2026.
56. Morton ES, James RD. Blue-headed Vireo (Vireo solitarius), version 1.0. Birds of the World [Internet]. Cornell Lab of Ornithology, Ithaca, NY, USA; 2020 [cited 2026 Mar 11]; https://doi.org/10.2173/bow.buhvir.01
57. Arcese P, Sogge MK, Marr AB, Patten MA. Song Sparrow (Melospiza melodia). Birds of the World [Internet]. Cornell Lab of Ornithology, Ithaca, NY, USA; 2020 [cited 2026 Mar 11]; https://doi.org/10.2173/bow.sonspa.01
58. Dellinger R, Bohall Wood P, Jones PW, Donovan TM. Mar. Hermit Thrush - Catharus guttatus. Birds of the World [Internet]. Ithaca, NY, USA: Cornell Lab of Ornithology; 2020 [cited 2026 Mar 11]; https://birdsoftheworld.org/bow/species/herthr/cur/introduction. Accessed 11 2026.
59. Askins RA, Philbrick MJ, Sugeno DS. Relationship between the regional abundance of forest and the composition of forest bird communities. Biol Conserv. 1987;39:129–52. https://doi.org/10.1016/0006-3207(87)90030-9.
60. Moore FR, Kerlinger P, Simons TR. Stopover on a Gulf Coast Barrier Island by Spring Trans-gulf Migrants. Wilson Bull. 1990;102.
61. Rivera JHV, McShea WJ, Rappole JH, Haas CA. Postbreeding Movements and Habitat Use of Adult Wood Thrushes in Northern Virginia. Auk. 1999;116:458–66. https://doi.org/10.2307/4089379.
62. Buler JJ, Moore FR. Migrant–habitat relationships during stopover along an ecological barrier: extrinsic constraints and conservation implications. J Ornithol. 2011;152:101–12. https://doi.org/10.1007/s10336-010-0640-7.

Figures

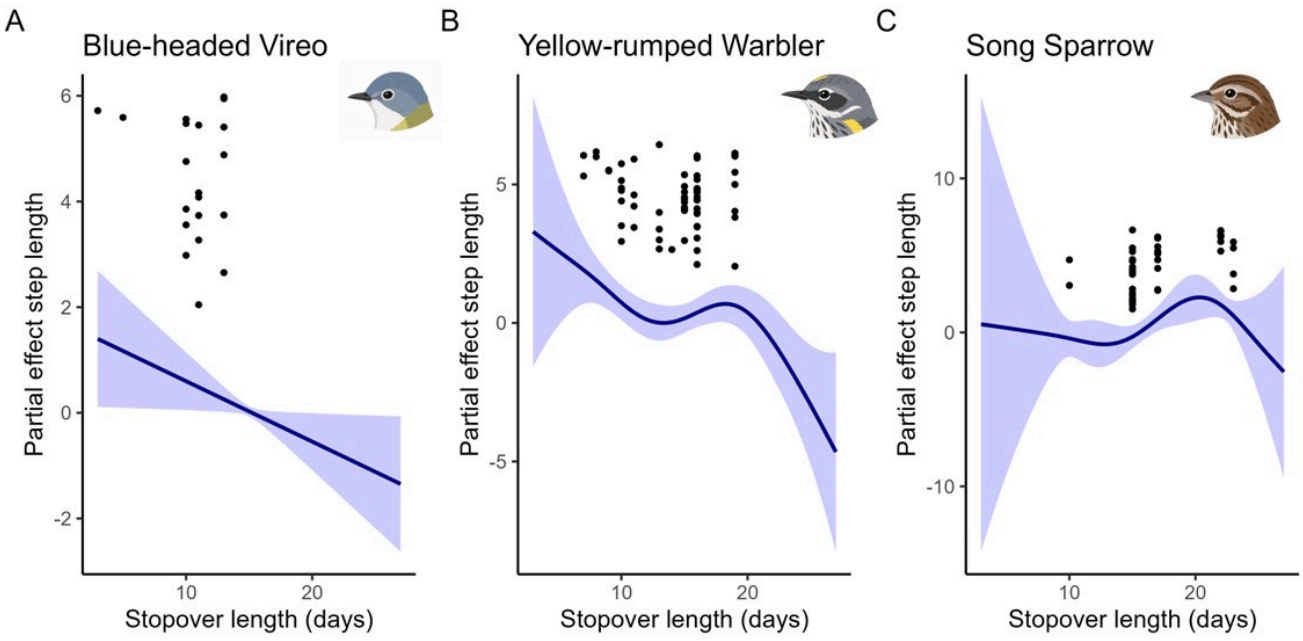


Figure 1

Predicted step length of daily movements during fall stopover for (A) Blue-headed Vireo (B) Yellow-rumped Warbler, (C) Magnolia Warbler based on the length of individual stopover of generative additive mixed models (GAMMs) of during the 2022-2023 fall migratory period in Montreal, Quebec, Canada. Blue lines and 95% confidence intervals show statistically significant relationships ($\alpha = 0.05$), with points showing distribution of raw data. Although species-specific prediction curves diverge, they are informed by the global dataset (including data from Hermit Thrush and Magnolia Warbler not included here) and shared variance structure in the model.

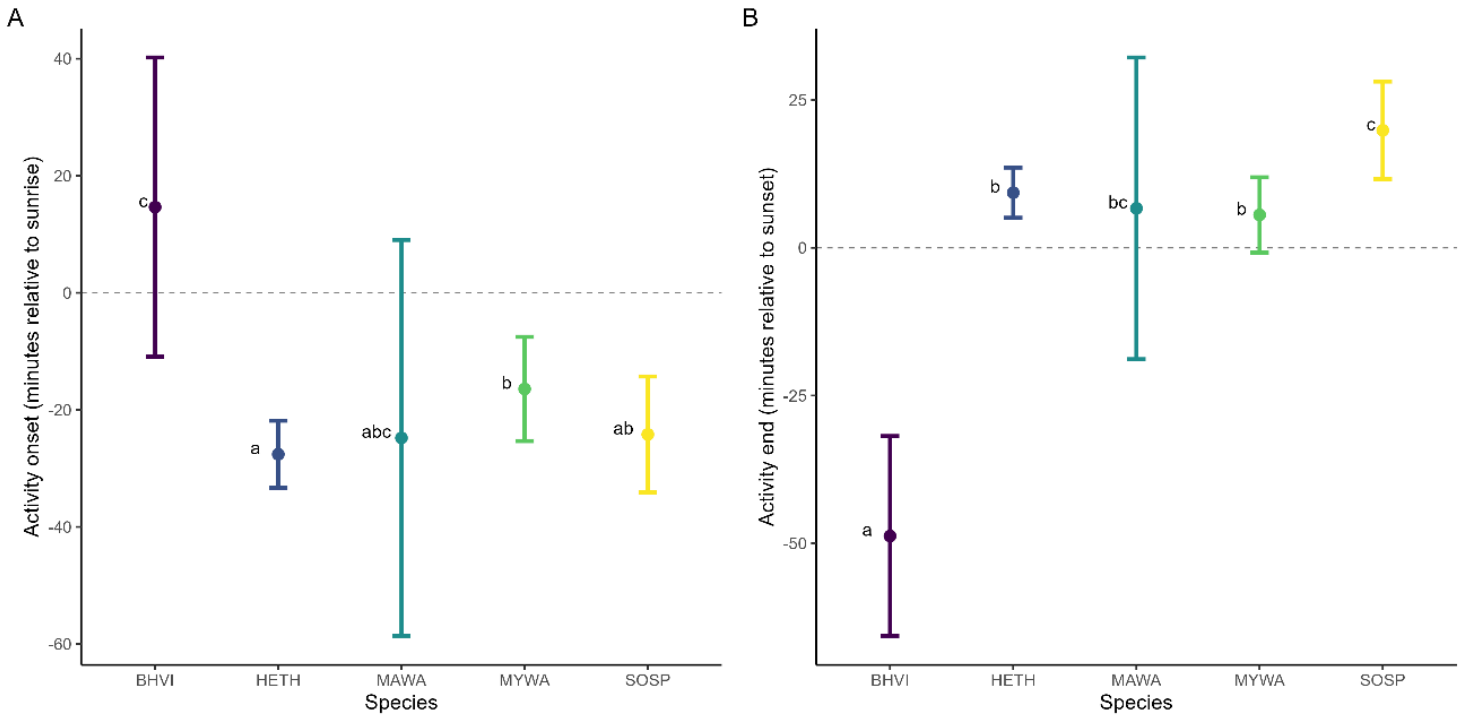


Figure 2

Comparison of (A) activity onset (minutes relative to sunrise) and (B) activity end (minutes relative to sunset) for Motus tagged migratory birds during the 2022-2023 fall stopover period in Montreal, Quebec, Canada. Letters used to demonstrate significant differences between estimated marginal means using Tukey-adjusted pairwise comparisons. (BHVI = Blue-headed Vireo; HETH = Hermit Thrush; MAWA = Magnolia Warbler; MYWA = Yellow-rumped (Myrtle) Warbler; SOSP = Song Sparrow).

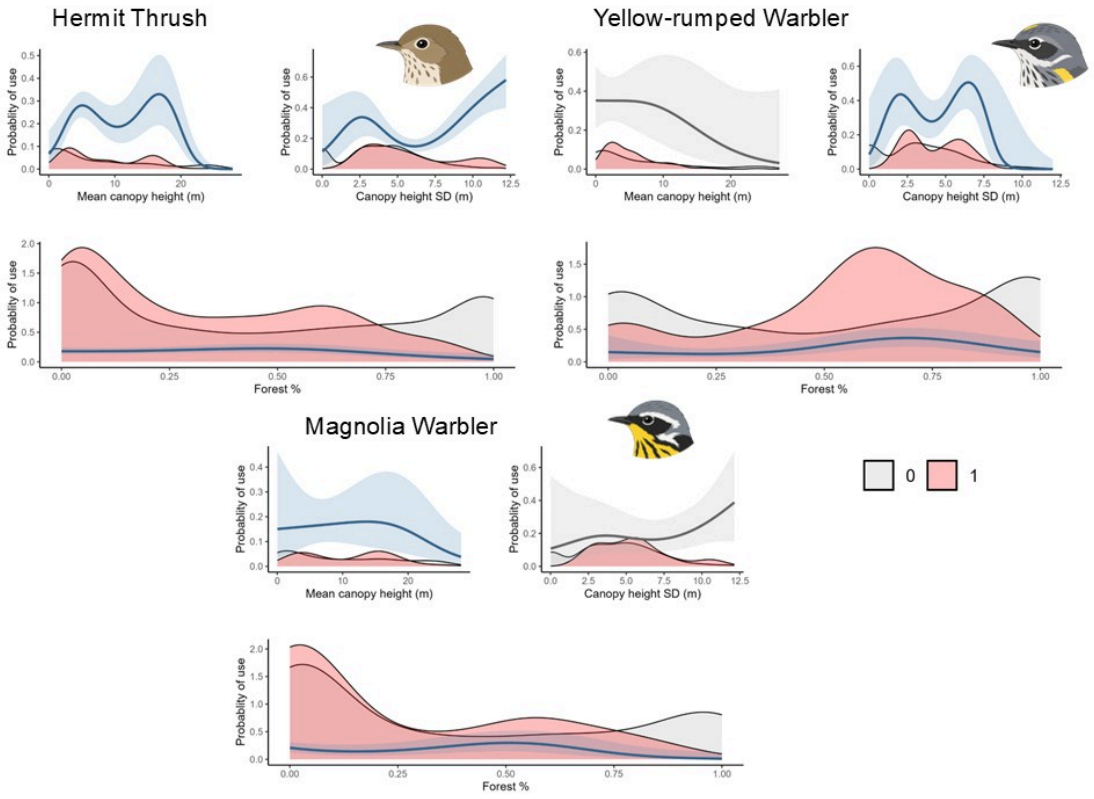


Figure 3

Predicted use probabilities of habitat covariates from general additive models (GAMs) of resource selection functions for four species of Motus tagged migratory birds during the 2022-2023 fall stopover period in Montreal, Quebec, Canada. Blue lines and 95% confidence intervals show statistically significant relationships (α = 0.05); grey lines and 95% confidence intervals show non-statistically significant relationships. Density distributions along the x-axis depict the distribution of used (1) locations in red and available (0) locations in grey, providing context for habitat availability and selection across the observed environmental gradients.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SI.docx