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Moult migrant Tennessee Warblers undergo extensive stopover in peri-urban forests of southern Quebec

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Abstract

Stopovers are the most energy- and time-consuming events during avian migration, yet individuals of certain species make long stopovers to moult ("moult migration"). Requiring abundant energy and a prolonged stay, moult migrants should occupy small stopover home ranges in resource-rich habitats. Understanding migrant behaviour at their stopovers is critical for implementing conservation efforts for declining Neotropical passerines. To examine the stopover timing and habitat use of one such moult migrating passerine, we radio-tagged 18 moulting and 4 post-moult Tennessee Warblers (*Leiothlypis peregrina* (A. Wilson, 1811)) at an autumn stopover site. Although our data were biased towards one sampling year, moult migrants generally arrived at the stopover site earlier (average = 2 August) than post-moult migrants (average = 12 September). Moult migrants also stayed longer (46 ± 5 days) than post-moult migrants (8 ± 6 days) and had large overlapping stopover home ranges (∼15 ha) that were dependent on high abundance of forest (%) and forest edge (m). We conclude that Tennessee Warblers occupied forested stopover sites within a peri-urban landscape where they successfully moulted before continuing migration. This study illustrates the importance of including stopover sites in conservation plans, particularly in cities where quality habitats are scarce.

Key words: moult migration, urban stopover, habitat use, forest, Tennessee Warbler, *Leiothlypis peregrina* (A. Wilson, 1811)

Résumé

Les escales sont les événements les plus longues et énergétiques durant la migration des oiseaux. Certains migrants s'arrêtent pendant de longues périodes durant une seule escale pour muer leurs plumes (« migration de mue »). Ayant besoin d'énergie abondante et d'une escale prolongée, les migrateurs en mue devraient occuper de petits domaines vitaux dans des forêts riches en ressources. Il est essentiel de comprendre le comportement des migrants lors de leurs escales pour la conservation des passereaux néotropicaux en déclin. Pour examiner leur comportement et leur usage d'habitat, nous avons marqué par radiotélémétrie 18 parulines obscure (*Leiothlypis peregrina* (A. Wilson, 1811)) en mue et 4 parulines en post-mue entre 2018 et 2022 sur un site d'escale automnale. Bien que nos données sont biaisées par rapport à une année d'échantillonnage, les migrants en mue sont généralement arrivés sur le site d'escale plus tôt (moyenne = 2 août) que les migrants post-mue (moyenne = 12 septembre). Les migrants en mue sont restés plus longtemps (46 ± 5 jours) que les migrants post-mue (8 ± 6 jours) et avaient des domaines vitaux étendus (∼15 ha) qui contenaient en grand parti des forêt (%) et des lisières de forêt (m). Nous concluons que les parulines obscures occupaient des sites forestiers dans un paysage périurbain où elles muent avant de poursuivre leur migration. Nos recherches illustrent l'importance d'es sites d'escale dans les plans de conservation, particulièrement dans les villes où les habitats de bonne qualité sont rares.

Introduction

Migration is a time-sensitive and energetically costly event, coinciding with up to 85% mortality in some species (Sillett and Holmes 2002; Klaassen et al. 2013). Animals across many taxa, from sea to land, undergo migration of various distances at various times during the year (Dingle 2014). At every stage, from stopover duration, habitat selection, and departure, migrants must decide the best course of action that will optimize their survival. For a migrant, this can entail a speedy migration and an early arrival to summer or winter grounds where they will have first pick of high-quality territories. Stopover duration is the biggest time and energy investment during migration, having an important contribution to overall migration speed (Schaub and Jenni 2001; Wikelski et al. 2003; Nilsson et al. 2013). Migrants seek food and safety at stopover sites but at times must choose habitats that cannot accommodate both (Pomeroy et al. 2008), a decision that can have important consequences for their survival and migration speed. For migrating birds who moult at stopover sites, their high energy requirements and limited mobility should urge them to seek out green spaces that offer food and shelter from predators (e.g., Tietz and Johnson 2007; Fox et al. 2014) while they maintain small stopover home ranges and spend more time at their stopover site than post-moult migrants (e.g., Morales et al. 2022).

Quality stopover habitats are particularly limited in urban areas. Nocturnal migrants are drawn to cities by the artificial lights they emit and proceed to undergo their stopover in urban habitats (La Sorte et al. 2014; Araújo et al. 2019). Cities are dangerous places for birds as fatal collisions with buildings and vehicles are quite common (Loss et al. 2014). In addition, cities offer unfamiliar food sources (Matthews and Rodewald 2010) and habitat loss, fragmentation, and homogenization diminish the quality of urban green spaces (Seto et al. 2012; Piano et al. 2020). Nonetheless, forest fragments can be a refuge for birds who must replenish their fat reserves (Callaghan et al. 2019; Buron et al. 2022; Guo et al. 2023), an activity that requires twice as much energy as migratory flight (Wikelski et al. 2003), making it a period where resource abundance is very important. Given that habitat quality of stopover sites can profoundly affect the refueling rate of migrating birds (Lindström 2003), the presence of high-quality habitats in cities is critical. Despite the importance of stopover sites for migrants, they are often neglected in conservation plans.

Some individuals of certain species spend significant amounts of time at stopover sites, not only to refuel, but to moult their flight feathers too (“moult migration”; Rohwer et al. 2005; Pyle et al. 2009, 2018; Tonra and Reudink 2018). Many Neotropical passerines undergo moult migration (Pyle et al. 2018). For example, Kirtland’s Warblers (*Setophaga kirtlandii* (S.F. Baird, 1852)) have an extended autumnal stopover east of Georgian Bay, Ontario, during a period when they are presumably moulting (Cooper et al. 2017). Similarly, at a stopover site in southeastern Quebec, more than half of individuals of 11 songbird species are undergoing moult (Junda et al. 2020). At this same site, moult migrant Swainson’s Thrushes (*Catharus ustulatus* (T. Nuttall, 1840)) stay for ∼6 times as long as post-moult migrants, a significant amount of time to spend at a single stopover (Morales et al. 2022). Birds typically moult at their breeding grounds in late summer while some perform moult migration seemingly because resource shortages at breeding grounds “push” them towards better habitats, while simultaneously, they are “pulled” towards resource-abundant sites (i.e., the “push–pull” hypothesis proposed by Rohwer et al. 2005 and observed in Barta et al. 2008; Pyle et al. 2018; Pageau et al. 2020). For full-life cycle conservation of migratory birds, we need a better understanding of their habitat needs during migration stopover, particularly for moult migrants undergoing significant stopover (up to 13% of their full annual cycle during a single fall stopover event; Mehlman et al. 2005; Morales et al. 2022).

A large urban park in southeastern Quebec that hosts a banding station, the McGill Bird Observatory (MBO), is a moulting stopover site for many Neotropical migrants. The park is a matrix of forest and agricultural land within an urban migratory corridor called the “Montreal Gap” stretching 600 km from Lake Ontario and the Saint Lawrence Gulf (Gahbauer et al. 2016). Tennessee Warblers (*Leiothlypis peregrina* (A. Wilson, 1811), taxon concept last reviewed in Chesser et al. 2019) are a frequent moult migrant at the MBO where ∼57% of individuals are moulting upon capture (Junda et al. 2020). Previous research has been conducted at this site on the stopover duration and behaviour of Swainson’s Thrushes (*C. ustulatus*), another frequent moult migrant (Morales et al. 2022). Both Swainson’s Thrushes and Tennessee Warblers migrate long distances from their breeding grounds in the North American boreal forests to their overwintering grounds in Mexico and northern South America (Mack and Yong 2020; Rimmer and McFarland 2020). While both passerines have a similar migration route, differences in diet may cause different patterns of moult rate, stopover use, and migration timing. Tennessee Warblers being arboreal insectivores (Rimmer and McFarland 2020), for example, migrate earlier than Swainson’s Thrushes (Junda et al. 2020) as insects become less abundant in the North later in the season (Newton 2007). Moulting Swainson’s Thrushes spent significantly more time at their stopover site than post-moult birds and were more selective of weather conditions upon departure (Morales et al. 2022). Our study aims to describe the stopover duration, habitat use, and departure decisions of moult migrating Tennessee Warblers at the same autumnal stopover site.

Given that moulting takes no fewer than 35–40 days for passerines (Haukioja 1971; Francis et al. 1991), we expect Tennessee Warblers to spend similarly long stopovers as observed in Swainson’s Thrushes by Morales et al. (2022). According to the push–pull hypothesis, we should observe more moult migrants in years where conditions at the breeding grounds are poor. Tennessee Warblers are known to be dependent on spruce budworm outbreaks during breeding (Venier et al. 2009), and poor outbreak years may lead to low breeding success and a possible increase of moult migrants. The number of moult migrants should therefore be negatively correlated with the number of hatch-year individuals (as a proxy for productivity at the breeding grounds) for any given year. In addition, we expect moult migrants with limited mobility and reduced diurnal activity (Leu and Thompson 2002; Morales et al. 2022) to occupy small stopover home ranges. As moult migrants already spend significantly more time at their stopover site than post-moult migrants, we expect them to have the opportunity to align their departure with favourable weather conditions (similar to Morales et al. 2022 and Tsvey et al. 2007). Understanding the timing and distribution of a species (i.e., what habitats they are using) is critical to properly conserving them, particularly in a peri-urban area where habitat loss is high (Kosma et al. 2023).

Materials and methods

Study site

The MBO is located at the western tip of the island of Montreal (45.43°N, 73.94°W) in Quebec, Canada. Enclosed by agricultural fields belonging to McGill University and two nature reserves: the Morgan Arboretum and the Bois-de-la-Roche

Park, the habitat is characterized by a mix of wetland, shrubland, and mature deciduous forests (Bardo et al. 2003).The MBO has captured many moult migrating songbirds during their fall migration; Tennessee Warblers being the second most abundant (Junda et al. 2020). Junda et al. (2020) recently determined that approximately 57% of Tennessee Warblers are in the early stages of moult upon their capture at the MBO and presumably perform their entire moult on the MBO grounds each year. Since 2013, excluding 2014 and 2020, banders recorded the stage of moult for each adult individual. During these eight sampling years, the MBO collected data on 107 fall moult migrating Tennessee Warblers.

Radio-tagging and tracking

Tennessee Warblers were captured and radio-tagged at the MBO during their 2018, 2019, 2021, and 2022 fall migrations (between 30 July and 15 October). The radio-tags used were Lotek VHF NanoTags and were registered with the Motus Wildlife Tracking System. After-hatch year (AHY) individuals were captured using 30 mm mist nets and banded with numbered aluminum leg bands. Standard banding measurements were taken: sex, age based on plumage and skull ossification, mass, fat, and wing chord length. Birds were identified by experienced banders using the identification guide by Pyle et al. (1997). Due to the lack of dimorphism in Tennessee Warblers to visually distinguish between sexes, 100 μL blood samples were taken to perform DNA sexing following methods in (Griffiths et al. 1998). Sex was only analyzed for individuals captured in 2021 and 2022 and oftentimes inconclusive which did not garner a large sample size nor was it representative of the data (as most birds were captured in 2018). We therefore did not use sex in our analyzes. We also recorded individuals' moult status using methodologies described in Newton (1966) where each primary and secondary flight feather is given a score from 0 to 1, in 0.1 increments. A score of zero indicates that the old feather has not yet fallen, while a score of one means that the new feather has grown completely. These scores were cumulated to give a percent of moult completed. Birds who had completed 100% of their moult before capture were considered post-moult migrants, and we assumed they moulted at a separate location besides the MBO (following methods in Morales et al. 2022). Before release, we attached 0.26 g coded radio-transmitters (model NTQB2-1) using legloop harnesses to 42 moulting and 6 post-moult AHY Tennessee Warblers over three sampling years (see Table 1 in Results section). Birds were banded and radio-tagged under animal use protocol 2007-5446 from McGill University and federal banding permits 10743AE and 10743T issued by the Canadian Wildlife Service.

Tags had a burst rate of ~13 s and were detected by a Motus tower stationed at the MBO (45.4307°N, −73.9385°W) and at the McGill Macdonald Campus (45.4079°N, −73.939°W). As the tower's detection ranges are dependent on the density of vegetation surrounding them, we supplemented the detections by manually tracking individuals for the first 4 days after tagging and subsequently every 3 days. Trackers recorded a GPS point when signal strength was at least 130 dB at a gain (precision) between 9 and 40 dB.

Stopover home ranges

We then calculated 95% stopover home ranges for 17 individuals that had a minimum of 5 GPS points (4 moult migrants from 2019, and 8 moult migrants and 1 post-moult migrant from 2021, and 4 moult migrants from 2022) using the continuous-time movement modeling (*ctmm*) package in R 3.2. Due to the distribution of points, the package recommended the independent and identically distributed isotropic model for the best estimation of stopover home range, which confirmed the existence of a stopover home range (i.e., an asymptote in semivariance of points) rather than continuous movement. Stopover home ranges were overlaid on a 30 m resolution land cover map from data collected in 2019 (from *Partenariat Données Québec*). We extracted the proportions of landscape cover type and forest edge present within the stopover home ranges using the *raster* and *landscapemetrics* packages in R 3.2, respectively. Lastly, after scaling the variables, we performed a linear correlation comparing stopover duration and proportion of forested area within the stopover home ranges to determine whether habitat type and size might have influenced stopover length.

Moult rate and stopover duration

Rate of moult was calculated using annual data of percent moult completed. Data were collected from 107 individuals over 8 years, from 2013 to 2022 (excluding 2014 and 2020). Moult scores of <5% or >95% were excluded from moult rate calculations as moult intensity is often reduced at the beginning and end of moult (Mumme et al. 2021). With the average moult rate, we estimated the arrival date of each individual, assuming that they arrived at the MBO with 0% moult complete and began moulting the same day of arrival. We used the following equation to estimate arrival date: *arrival date* = *capture date* − (*moult completed* (%)/*moult rate* (%/day). While for post-moult migrants, we assumed they arrived the same day as their first capture.

We compared median arrival dates for both moult and post-moult migrants between years using a Kruskal–Wallis test. We also compared median arrival dates between moult and post-moult migrants across years using Mann–Whitney *U* tests. The number of hatch-year individuals caught in any given year was used as a proxy for productivity at the breeding grounds, assuming that good habitat conditions would lead to more chicks hatched. We investigated whether the number of hatch-year individuals was related to (1) the number of moult migrants captured and (2) the median arrival dates of moult migrants for each year using two separate linear regressions. Birds who were nearly finished moulting (i.e., having a moult score between 95% and 98%) upon capture were not included in arrival date and stopover duration calculations as it was ambiguous whether the individual had moulted at the MBO or had just arrived from another moulting site.

Departure dates and time were collected using two Motus wildlife tracking towers described above. We considered a migratory departure to occur when a rapid increase in signal strength from all antennas at the MBO tower was followed by a decrease in signal strength until it disappeared (Packmor

Table 1. Sample sizes for moult and post-moult after-hatch year (AHY) Tennessee Warblers over eight sampling years (2013–2022, excluding 2014 and 2020).

	Sample sizes							*Arrival dates*		
Year	Total HY	Total AHY	# moult	% moult	Tagged	Tagged moult	Tagged post-moult	Moult arrival *median (range)*	Post-moult arrival *median (range)*	Comparison of median arrival
2022	26	13	8	62%	5	5	0	3 August (21 July–18 August)	31 August (21 August–18 September)	$W = 54$ $p < 0.001$
2021	63	17	14	82%	9	6	3	4 August (21 July–3 September)	28 August (14 August–22 September)	$W = 87$ $p = 0.013$
2019	105	14	7	50%	9	7	2	11 August (3 August–20 August)	21 September (8 September–22 September)	$W = 63$ $p < 0.001$
2018	59	29	27	93%	25	24	1	3 August (8 July–23 August)	12 September (26 August–20 September)	$W = 128$ $p = 0.001$
2017	31	17	11	65%	0	0	0	5 August (20 July–12 August)	27 September (5 September–30 September)	$W = 65$ $p = 0.002$
2016	17	12	11	92%	0	0	0	7 August (21 July–30 August)	26 September (26 September–26 September)	NA ($n = 1$ for post-moult)
2015	46	23	11	48%	0	0	0	8 August (17 July–4 September)	14 September (8 September–25 September)	$W = 169$ $p < 0.001$
2013	229	20	18	90%	0	0	0	17 August (25 July–4 September)	22 September (1 September–3 October)	$W = 99$ $p = 0.002$

Note: Moult migrant arrival dates were estimated based on the calculated moult rate (2.5%/day), assuming individuals arrived at 0% moult and began moulting immediately. Post-moult (identified as birds having 100% completed moult upon capture) arrival dates are the dates of first capture. Median arrival dates for both groups include all banded birds. The comparisons of median arrival dates were performed using Wilcoxon rank sum tests. Note that values from 2013 differ slightly from numbers reported in Junda et al. (2020) as they classified moult migrants as birds having moult scores of >0% and <100% upon capture, whereas we included birds with moult scores of 0%.

et al. 2020). In most cases, we were able to detect a similar change in signal at the Macdonald campus tower as the bird migrated southwest. In addition, individuals who departed before 19:00 hours were excluded from analyses as nocturnal migrants generally depart after sunset (Schmaljohann and Naef-Daenzer 2011; Muller et al. 2016; Cooper et al. 2023).

Stopover duration was described as the difference between the arrival and departure dates in days. Since we could not confirm departure times for all radio-tagged birds due to inconsistent detections, stopover length could only be calculated for 4 post-moult migrating individuals (3 from 2019 and 1 from 2021) and 18 moult migrants (10 from 2018, 2 from 2019, 2 from 2021, and 3 from 2022). We then used a Mann–Whitney U test to determine whether moult and post-moult migrants spent significantly more or less time at their stopover site. Similarly, we performed additional Mann–Whitney U tests to determine whether arrival and departure dates changed significantly between moult and post-moult migrants. We also used Kruskal–Wallis tests to determine whether average arrival and departure dates changed significantly between years, keeping moult and post-moult migrant values separate for these calculations.

Use–availability analysis: migrants' resource selection

We compared "used" to "available" habitat to determine migrating Tennessee Warblers' resource selection in regards to landscape composition (i.e., anthropogenic, forest, and agriculture,) during their stopover. We also included forest edge (in meters) as a landscape measurement due to its appeal for migrating birds in urban and peri-urban spaces (Terraube et al. 2016; Stanley et al. 2021). The GPS coordinates obtained through manual tracking (see radio-tagging and tracking section) were our "used" points. Two "available" points were created for every "used" point by placing it the same distance away from where the bird was released at a random angle from that release point. We only included migrants with more than one "used" point ($N = 17$ moult and 1 post-moult migrant). All points were overlaid on a 30 m resolution landscape cover map from 2019 (obtained from *Partenariat Données Québec*). We constructed buffers of 50, 100, and 200 m radii around these points, and extracted landscape composition and forest edge measurements from each buffer. We performed a scale of effect analysis by comparing full models of each buffer size using Akaike information criterion values corrected (AIC_c) model selection. The 100 m radius buffer had the strongest scale of effect for habitat use (see Results sections) and thus we used this buffer size in our subsequent analyses. Available points that were composed of 100% water were discarded, as Tennessee Warblers are not aquatic birds and would not realistically be occupying those spaces.

We constructed four binomially distributed generalized linear mixed-effect models: (i) a global model including proportions of forest and anthropogenic land, and the length of forest edge, (ii) a human disturbance model including proportion of anthropogenic land, (iii) a forest model including proportion of forest and length of forest edge, and (iv) a null model (Table 2). All models also included the bird's identification (ID) number as a random effect. All variables were tested for collinearity, and we found that the proportion of forest and agriculture were highly correlated (Pearson's $r > 0.7$), and so proportion of agricultural land was excluded from the models. Finally, all four models were ranked using AIC$_c$ for small sample sizes and analyzed for goodness of fit using the area under the curve (AUC) method for discrimination and the Hosmer–Lemeshow goodness of fit test for calibration.

Departure decisions

We used time-dependent Cox proportional hazards models to determine departure decision of the moult migrating Tennessee Warblers (following examples in Packmor et al. 2020; Morales et al. 2022). Every day, starting from the time an individual had presumably completed 75% of its moult and thus regained most of its feathers and mobility (or from their capture date if the individual already had >75% moult complete upon capture; see similar methods in Morales et al. 2022) until their departure, was considered a potential departure day where individuals were actively deciding to "stay" or "leave" the site. All weather variables (i.e., temperature, wind conditions, and change in atmospheric pressure) were included as time-dependent covariates and obtained from Environment and Climate Change Canada (weather.gc.ca, see Supplementary material for a description of the weather stations used). Wind speed and direction were also combined into one measurement of wind support (following Morales et al. 2022; see Supplementary material). We also included residual mass as a relative measurement of body size for each bird as an endogenous factor that may influence departure (note that the ordinary least-squares regression used to calculate residual mass had a weak predictability, $R^2 = 0.052$, see Supplementary material for detailed methods). We assume that, as the season draws on, individuals will feel greater pressure to leave regardless of weather conditions and thus calendar date (of every given night where a bird decided to stay or leave the stopover site) was included as a random covariate in all models.

We created four Cox models: an endogenous model (including residual mass), an exogenous model (including temperature, wind support, and change in atmospheric pressure), a global model (including residual mass, temperature, wind support, and change in atmospheric pressure), and a null model. Year, calendar date (i.e., number of days since 1 January of its respective year), and moult status (i.e., moult or post-moult) were also included as random covariates in each model. We then used AIC$_c$ model selection to rank the models.

Results

Moult migrating Tennessee Warblers at the MBO

From 2013 to 2022 (excluding 2014 and 2020), the MBO captured 107 actively moulting Tennessee Warblers during their fall migration. The years 2019 and 2022 recorded the lowest numbers of moult migrants (only seven and eight individuals, respectively), while 2018 was the highest, having captured 27 moult migrants (Table 1). Note that we found two radio-tagged moult migrants deceased in the wild. The average proportion of AHY individuals that were moulting upon capture was 73% ± 19% ($n = 145$, Table 1). The number of HY individuals caught per year (as a proxy for productivity at the breeding grounds) was not significantly correlated with the number of moult migrants (Pearson's $r = 0.277$, $p = 0.506$) but was positively correlated with moult migrants' median arrival date (Pearson's $r = 0.844$, $p = 0.008$). Finally, years with high numbers of AHY individuals had higher numbers of moult migrants as they were strongly correlated (Pearson's $r = 0.831$, $p = 0.010$). Note that a similar table including data from 2013 to 2022 (excluding 2014 and 2020) can be found in the Supplementary material (see Table S1).

Moult rate and stopover duration

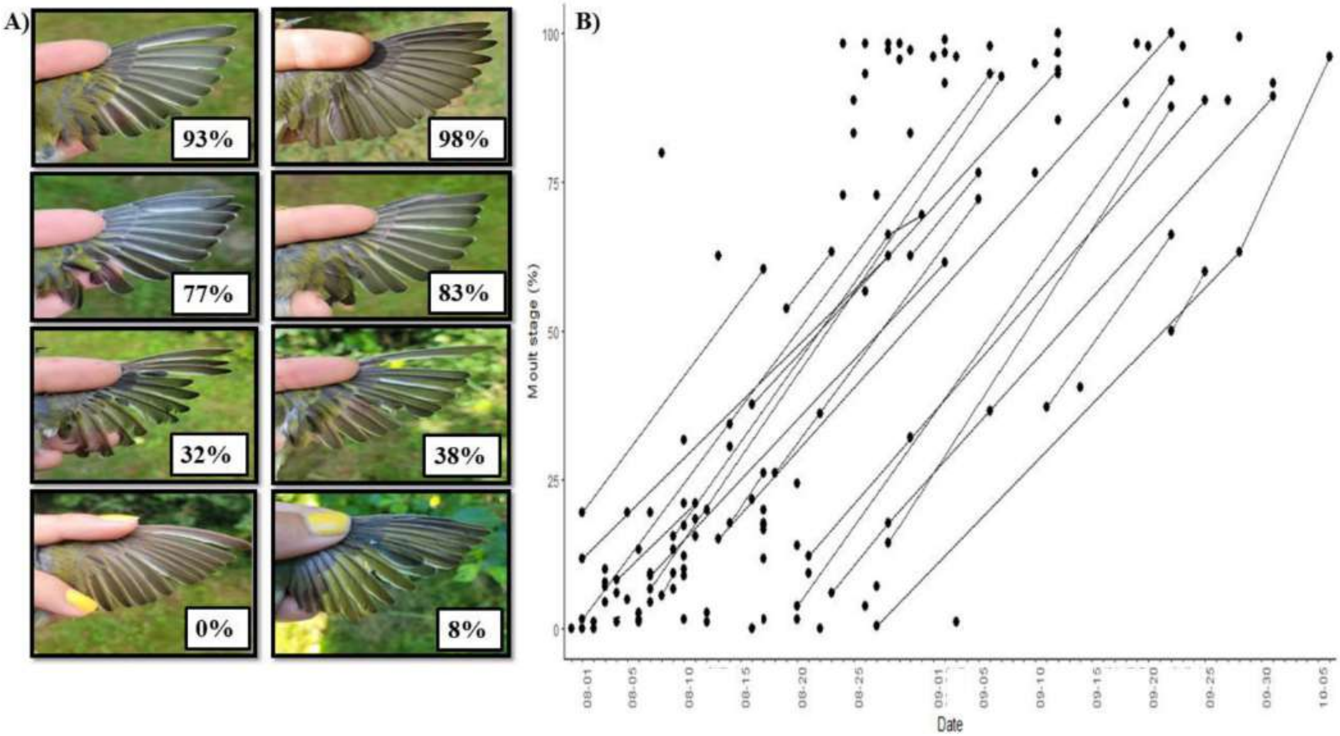
Across all years (2013–2022), moult migrants were most frequently captured in early August (mode: 10 August; median: 17 August, $n = 107$). Upon capture, the average individual had completed 39% ± 38% of their moult. The average moult rate for Tennessee Warblers was 2.5% ± 0.6% per day ($n = 72$, Fig. 1). Based on this estimation, the median arrival date for moult migrants across all sampling years (from 2013 to 2022) was 6 August (mode: 4 August, $n = 107$). The median arrival date for moult migrants did not differ significantly between years (Kruskal–Wallis test, including data from 2013 to 2022; $p = 0.068$, $\chi^2_{[7]} = 13.2$, $n = 107$) nor did it differ for post-moult migrants ($p = 0.076$, $\chi^2_{[6]} = 11.4$, $n = 38$). Median arrival date between moult and post-moult migrants, however, was significantly different ($p < 0.001$, $W_{[1]} = 5980$, $n = 145$). While moult migrants arrived in early August, post-moult migrants arrived more than a month later in September (median: 14 September, $n = 38$; see Table 1).

Departure dates were statistically similar between moult and post-moult migrants ($p = 0.89$, $W_{[1]} = 36$, $n = 22$). Note that departure date calculations are biased as moult migrants were much more numerous (18 compared to 4 post-moult migrants) and most were tagged in 2018 ($n = 14$), whereas post-moult migrants were more evenly distributed between years (see Fig. 2). The median and mode departure date for moult migrants was 16 September ($n = 18$), while the median departure date for post-moult migrants was 20 September ($n = 4$, with no mode; Fig. 2). Among both moult and post-moult migrants, year had no effect on departure dates (Kruskal–Wallis test: $p = 0.158$, $\chi^2_{[3]} = 5.19$, $n = 22$).

Table 2. Akaike information criterion values corrected (AIC_c) of four generalized linear mixed-effect models comparing presence/absence coordinates (with 50 m buffer zones) of migrating after-hatch year Tennessee Warblers ($n = 18$) during their stopover at the McGill Bird Observatory in southern Quebec.

Model	Variables	−LL	ΔAIC_c	Wt
Forest	Forest (%) + forest edge (m) + bird ID	−235	0.00	0.65
Global	Anthropogenic (%) + forest (%) + forest edge (m) + bird ID	−234	1.25	0.35
Human disturbance	Anthropogenic (%) + bird ID	−485	497	0.00
Null	Bird ID	−487	500	0.00

Fig. 1. Tennessee Warblers' stage of moult (i.e., percent of moult completed) over time during their fall migration stopover at the McGill Bird Observatory (MBO). (A) Visual representation of Tennessee Warblers' flight feather moult stages (photos taken during 2021 and 2022 fall migration). (B) Graph showing the moult stage of individuals upon capture. Each point represents a date when an individual was captured at the MBO and their moult stage was recorded. This figure represents 72 individuals across 8 years (from 2013 to 2022).



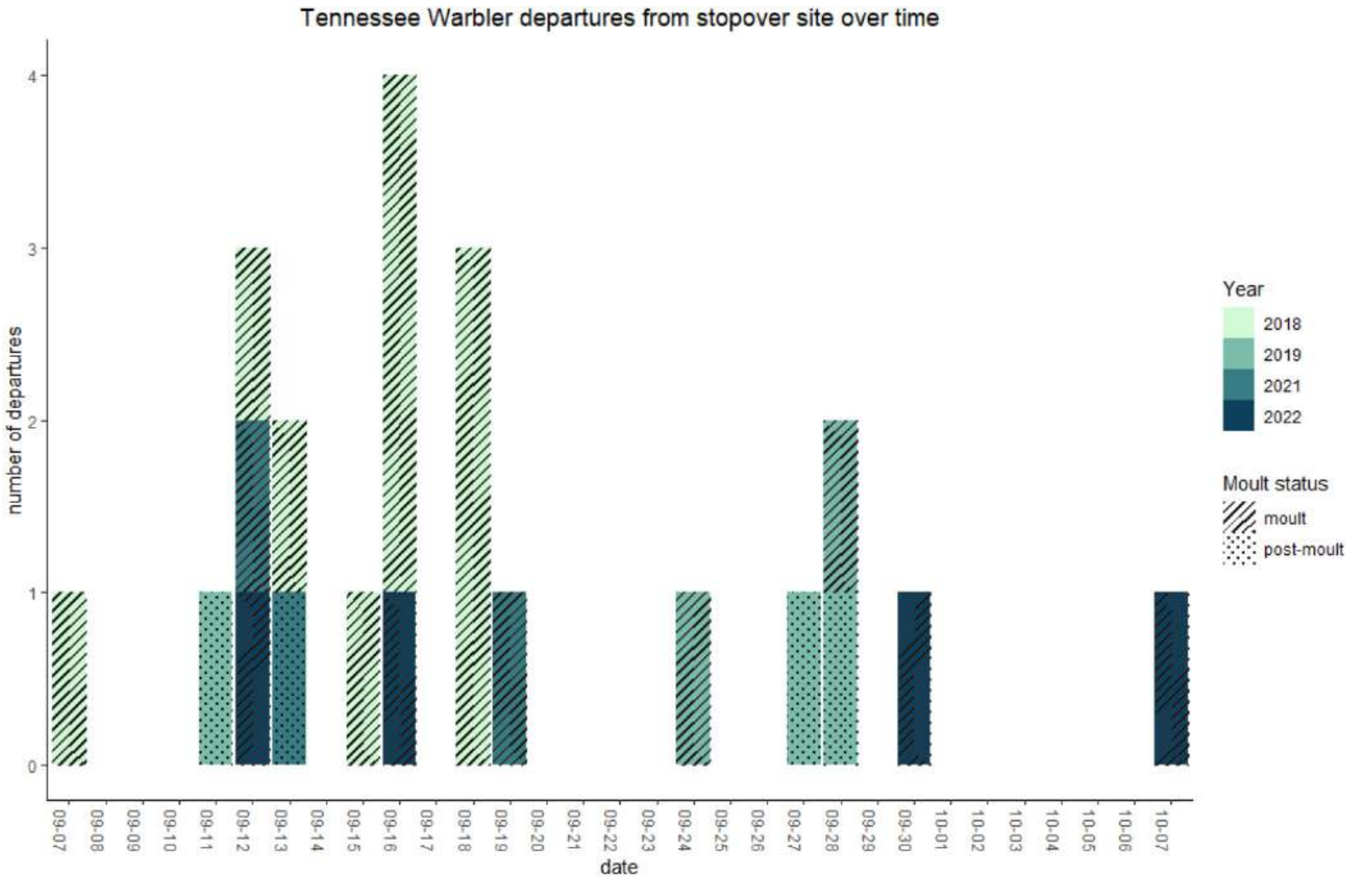
Assuming individuals arrived at the start of their moult and maintained a constant 2.5% moult rate throughout their stay, moult migrants spent 46 ± 5 days ($n = 18$) at their stopover, while post-moult migrants stayed for 8 ± 6 days ($n = 4$, see Fig. 3). The minimum stay was 39 days (in 2018), while the maximum was 56 days (in 2022). According to the estimated moult rate (2.5%/day), it would take a bird 40 days to moult their feathers, which was near the average stay of moult migrants.

Stopover home ranges

The one post-moult migrant had an estimated 95% stopover home range of 5.79 ha (with 95% confidence intervals extending from 1.58 to 12.70 ha), while the moult migrants ($n = 16$) had an average 95% stopover home range size of 14.6 ha (with standard error of ± 4.4 ha). The largest stopover home range across all tagged Tennessee Warblers was 58.8 ha and the smallest was 1.33 ha, both obtained from moult migrants in 2022 and 2021, respectively (see Table S2 in the Supplemental material). Figure. 4B shows a map of the stopover home ranges.

Almost half (48.83% ± 21.43%) of the Tennessee Warblers' stopover home ranges were composed of forests (Fig. 4B). More than a third (33.03% ± 25.25%, $n = 17$) of the area spanned agricultural land. Water and wetland types covered 10.12% ± 11.20% and 7.31% ± 5.46% of the total area of the stopover home ranges, respectively. The least prevalent land cover type over which the stopover home ranges were found was anthropogenically modified habitat (excluding agriculture), which represented 0.71% ± 1.99% of the total area. See Table S3 in the Supplementary material for a summary of the land types present in each bird's stopover home range. We found no correlation between the proportion of forested stopover home range and stopover duration ($p = 1$, $W_{[16]} =$

Fig. 2. Barplot showing the number of radio-tagged Tennessee Warblers making migratory departures from the McGill Bird Observatory stopover on any given night during the fall season. Data are color-coded by year, and moult versus post-moult migrants are differentiated by pattern as seen in the legend.



32, $R^2 = 0.164$, $n = 8$) nor between stopover duration and stopover home range size ($p = 0.959$, $W_{[16]} = 31$, $R^2 = 0.095$, $n = 8$).

Use–availability analysis: migrants' resource selection

A comparison of the global models at different buffer sizes (50, 100, and 200 m) revealed that the 100 m radius buffer was the best (>2.0 ΔAIC_c between all other models). The models discussed in this section therefore include landscape measurements obtained from a 100 m radius buffer around the used and available points.

The forest model (including the proportion of forest and length of forest edge (m)) and the global model (including the same variables plus percent anthropogenic land) were the two best models (>2.0 ΔAIC_c between all other models) to predict resource selection of migrating Tennessee Warblers (Table 2). In both models, the proportion of forest and length of forest edge had a significantly positive influence on Tennessee Warbler presence ($p < 0.001$, see Table 3 and Fig. 5). The conditional version of the forest model including bird ID as a random effect had a higher theoretical R^2 (=0.82) than the marginal model excluding bird ID ($R^2 = 0.69$). These two best models also had high scores following the AUC goodness of fit test for discrimination (AUC = 0.942). Both the forest and global models, however, failed the Hosmer–Lemeshow goodness of fit test for calibration ($\chi^2_{[8]} = 36500$ and 37100, $n = 702$ GPS points from 18 individuals, and $p < 0.001$, respectively).

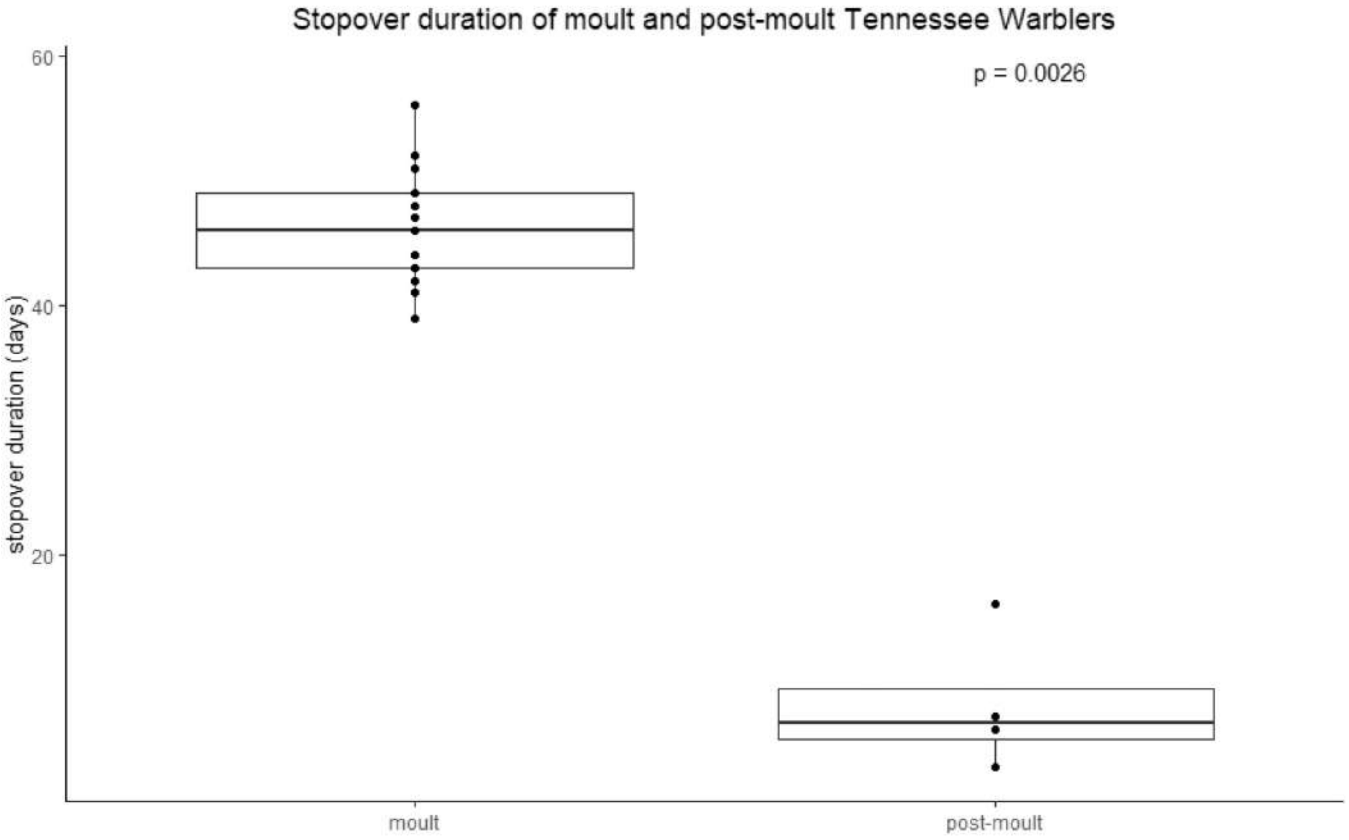
Departure decisions

The null model, which included only calendar date, year, and moult status as random effects, was the highest ranked model for predicting a migrant's departure (Table 4). Although the exogenous model was ranked second-best (within <2.0 AIC_c of the null model), it explained little variability in the data. None of the predictor variables in any of the models was significant ($p > 0.05$), and the goodness of fit measurement of concordance for all models was similar to the null model ($C = 0.5$).

Discussion

Moult migrant Tennessee Warblers in a peri-urban green space spent significantly more time at their stopover site than post-moult migrants. Specifically, moult migrants spent around 46 days at their stopover site, which is just slightly more than the number of days needed to complete moult (i.e., 40 days). Meanwhile, post-moult migrants only occupied the site an average of 8 days (although this did not account

Fig. 3. A boxplot illustrating the difference in stopover duration between moult and post-moult migrating Tennessee Warblers at the McGill Bird Observatory in southern Quebec. Stopover duration for post-moult migrants is defined as the number of days between their first capture and departure dates, while for moult migrants, it is their estimated arrival (based on their moult stage and an estimated moult rate (2.5%/day), assuming migrants arrived at the start of their moult) and their departure dates.



for days prior to first capture). This stopover duration is very similar to Swainson's Thrushes that stayed for an average of 47 (moult migrant) versus seven (post-moult migrants) days at the same stopover site (Morales et al. 2022). This single stopover period (47 days) consists of 13% of a Tennessee Warbler's annual life cycle, making the moult migration a significant event, longer than breeding (∼24 days for incubation + chick-rearing; Rimmer and McFarland 2020) or fall migration itself. This is also far longer than the 6–13 days recorded via banding data (Junda et al. 2020) or for post-moult individuals of other passerine species (2.9 days for Ovenbirds (*Seiurus aurocapilla* (Linnaeus, 1766)) observed in Seewagen et al. 2010 or <4 days for assorted songbirds in Morris et al. 1996). Since moult takes at least 35–40 days for passerines (Haukioja 1971; Francis et al. 1991), we presume that these migrants spent most of their stopover moulting (an assumption often confirmed through recaptures) and reserved their remaining few days to refuel for migratory flight.

The departure decisions of both moult and post-moult migrants were independent of initial body condition (i.e., residual mass) and weather (i.e., residual temperature, wind support, and change in atmospheric pressure). We suspect the reason we did not detect a relationship between endogenous/exogenous factors and departure decisions was because the sample size was too small (moult migrant $n = 18$, post-moult migrant $n = 4$) and biased towards 1 year (i.e., the majority of moult migrants were radio-tagged in 2018). Indeed, many other studies have recorded the influence of fat reserves (see Deppe et al. 2015; DeSimone et al. 2022) and weather (see Richardson 1990; Gill et al. 2014; Beauchamp et al. 2020; Morales et al. 2022) on departure decisions.

We speculate that migrants were "pushed" away from poor conditions at the breeding grounds (as part of the push–pull hypothesis proposed by Rohwer et al. 2005) in favour of moulting at better habitats along their migration route. In years that we observed an abundance of hatch-year birds, presumably caused by a productive breeding site, we observed later arrival dates for moult migrants. Likewise, in years of poor conditions at the breeding grounds (i.e., less hatch-year birds), moult migrants arrived at the stopover site earlier presumably because they were "pushed" from their breeding grounds. Still, there are several instances of Tennessee Warblers moulting at sites away from their breeding territory (e.g., Craves 2009; Junda et al. 2020), and it may not always be influenced by habitat quality. Tennessee Warblers may also be migrating earlier after a failed breeding attempt, which may be caused by insufficient resources in and around the breeding territory. A push away from poor breeding grounds has

Fig. 4. (A) Map of the West Island of Montreal showcasing the McGill Bird Observatory (MBO) and Motus tower locations. In the bottom left corner shows where the West Island of Montreal is located in northeastern North America. The blue circle indicates the area represented in map "B". (B) Map of the 95% stopover home ranges (and their associated GPS points) of moult and post-moult migrating Tennessee Warblers at the MBO. Individuals were radio-tagged and tracked in 2018, 2019, 2021, and 2022. Both maps use a 30 m resolution landscape cover layer from 2019 (obtained from *Partenariat Données Québec*). Map projection is WGS84, and the coordinate system used is UTM zone 11. Inset map data provided by Google © 2023, INEGI.

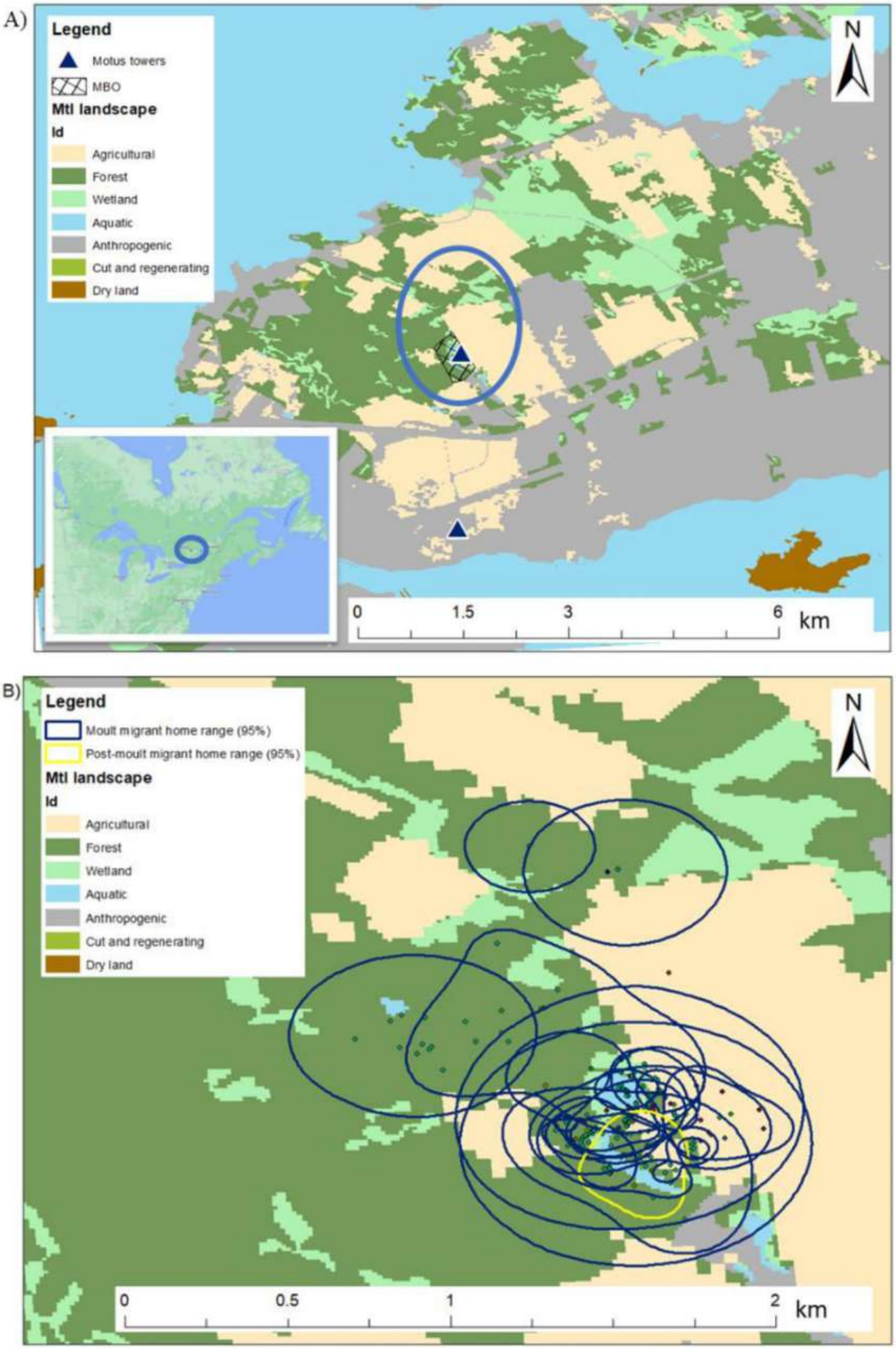
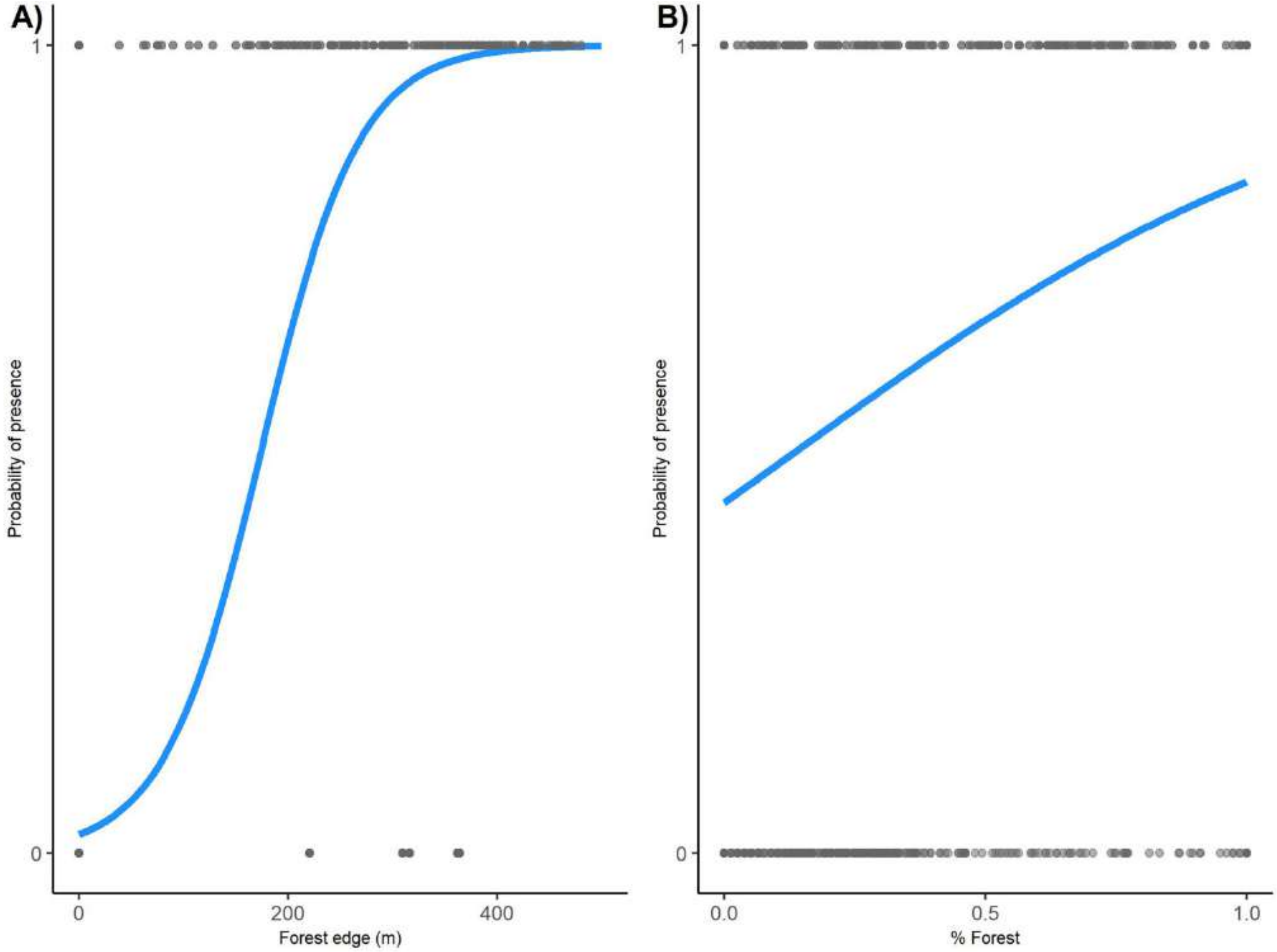


Table 3. Summary of the parameter estimates of the top two resource selection models (the landscape composition and global models) predicting presence of migrating Tennessee Warblers ($n = 18$) during their stopover at the McGill Bird Observatory in southern Quebec.

Model	Variables	Estimate	Standard error	z	p
Forest	Forest edge	3.27	0.284	11.5	<0.001
	% forest	0.550	0.138	3.99	<0.001
Global	Forest edge	3.28	0.286	11.5	<0.001
	% forest	0.532	0.139	3.82	<0.001
	% anthropogenic	−0.131	0.158	−0.825	0.409

Fig. 5. Probability of presence of migrating Tennessee Warblers within a 100 m radius area as predicted by a generalized linear mixed effects model. The model's predictors include the proportion of forest and wetland, and the length of forest edge (in meters), and individual (bird ID) as a random effect. (A) shows the positive relationship between migrants' presence and the amount of forest edge (coefficient = 3.27, $p < 0.001$) and (B) shows the positive relationship between migrants' presence and the proportion of forest (coefficient = 0.55, $p < 0.001$).



been recorded in western North America where arid conditions drove migrants to moult at stopover sites (Pageau et al. 2020). Should migrants be similarly pushed in eastern North America, it may be caused by food availability. Tennessee Warblers are known to benefit from outbreaks of spruce budworm (*Choristoneura fumiferana* (Clemens); Germain et al. 2021), but the resource may be quickly depleted locally and regionally. Tennessee Warblers may therefore perform moult migration as a result of a food shortage in the post-breeding season in the boreal forest following defoliation (Drever et al. 2018; Germain et al. 2021). Indeed, two abundant years for hatch year individuals was in 2019 (105 birds) and 2015 (46 birds) when nearby spruce budworm populations were high (Maine Forest Service 2021). In these same years, moult migrants arrived at the MBO later in the season presumably because they spent more time breeding in the boreal forest.

Table 4. Akaike information criterion values corrected (AIC_c) model selection performed on four models describing departure decisions for both moult ($n = 18$) and post-moult ($n = 4$) migrant Tennessee Warblers from their autumnal stopover in a large urban park.

Model	Variables	−LL	ΔAIC_c	Wt
Null	Calendar date + year + moult	−90.10	0.00	0.50
Exogenous	Temperature + wind support + Δ atmospheric pressure + calendar date + year + moult	−87.74	1.53	0.23
Endogenous	Residual mass + calendar date + year + moult	−90.09	2.04	0.18
Global	Temperature + wind support + Δ atmospheric pressure + residual mass + calendar date + year + moult	−87.70	3.58	0.08

Future research should investigate this relationship between resource abundance at the breeding ground and the prevalence of moult migration.

Migrating Tennessee Warblers moulted at 2.5% ± 0.7% per day. We assume a constant moult rate (excluding the stages before and after moult, i.e., at 0% and 100% completion), which emulates preferred models for calculating moult intensity (Terrill et al. 2021). As resources and weather conditions (like rainfall) change from day to day, so will a bird's ability to moult, presumably causing sudden drops and rises in moult rate (e.g., moult rate varied between captures for the same individuals). Most individuals were captured near the start and end of moult, presumably due to their increased mobility at these times. According to Rohwer et al. (2009), small birds weighing ~10 g, like the Tennessee Warbler, should take 21 days to simultaneously moult all their primary flight feathers, which is nearly half the time we estimated (i.e., 40 days). The longer moulting period at this stopover site could be because Tennessee Warblers were additionally moulting their secondary flight feathers and presumably spent time refueling for migration. The Tennessee Warblers' moult rate was faster than for some larger species at the stopover site. For example, the Swainson's Thrushes moulted their feathers at 1.9% per day at the same autumn stopover site as this study (Morales et al. 2022). Tennessee Warblers depart several weeks before Swainson's Thrushes, possibly resulting in this faster moult rate as, unlike Swainson's Thrushes, Tennessee Warblers are mainly insectivorous (Rimmer and McFarland 2020), which may make them more vulnerable to cold snaps and necessitate an earlier migration (Newton 2007).

Despite their limited mobility (Leu and Thompson 2002), moult migrants occupied overlapping and relatively large stopover home ranges (14.1 ± 17.2 ha), perhaps to search for the food and safety they require to successfully moult (Pomeroy et al. 2008). Larger stopover home ranges encompassing multiple forest patches may alleviate the effect of small forest fragments (<4.5 ha; Matthews and Rodewald 2010) that reduce a migrant's ability to refuel due to increased density of birds and thus higher competition (Cohen et al. 2022). Habitat variables like branch and stem densities seem to be good predictors of home range size (Anich et al. 2010) and may be why Tennessee Warblers established stopover home ranges with high percentages of forested area (~48%; Fig. 4). Indeed, according to our best model, migrating Tennessee Warblers chose to occupy habitats with abundant forests and forest edges and they made these decisions at a relatively small scale (within a 100 m radius or 0.785 ha). The model could not accurately predict what areas Tennessee Warblers might be using across the landscape but still informed what habitat characteristics, namely proportion of forest and forest edge, made for good stopover sites. Tennessee Warblers may choose to moult in habitats (i.e., forests) similar to their breeding grounds, a strategy observed in other moult migrants unless otherwise influenced by external factors (precipitation levels, competition, etc.; Chambers et al. 2011). Future research should compare habitat use in breeding and moulting sites and explore shifts in habitat requirements between these two life stages. Habitat selection also seemed to depend on the individual bird as our models performed considerably worse (theoretical $R^2 = 0.69$ compared to $R^2 = 0.82$) when we removed bird ID as a random effect. Individual-level variance in resource selection could be due to differences in orientation strategies and intraspecific competition (Alatalo 1981; Beardsworth et al. 2021), but such analyses are beyond the scope of this project. To conclude, the *Grand Parc de l'Ouest* in Montreal was capable of providing sufficient habitat (i.e., forest patches with high forest edge to interior ratios) to host migrating birds who require abundant resources to moult and refuel. Moulting sites during stopovers are often overlooked in conservation management despite their significant effect on species success. Our findings on stopover home range size of a Neotropical moult migrant suggests for cities to provide critical stopover habitat for moult migrants by retaining larger forested green spaces (e.g., of at least 15 ha in size).

Conclusion

Although once thought to be rare in Neotropical passerines, especially in eastern North America, a high proportion (~ 73%) of Tennessee Warblers observed at the MBO perform moult migration. Individuals stop for ~1.5 months, six times longer than their post-moult counterparts, and moult intensely (completing ~2.5% of their moult per day). Breeding success was lower in years when mean arrival date was later, implying they were "pushed" from breeding grounds due to low resources, and supporting the idea that migration timing is controlled by refueling rates. During their stay, Tennessee Warblers had relatively large and overlapping stopover home ranges (~15 ha), meaning that they moved around to take advantage of resources in the region for refueling. They selected habitats with high proportions of forest and high ratios of forest edge to interior. Forests compose 48% of their stopover home ranges, more than any other landscape cover type. Forests presumably offered sufficient food and protection from predators for migrants moulting and (or) refueling during their stopover. In conclusion, Tennessee Warblers were able to occupy forested stopover sites in a large urban park where they could successfully moult and refuel. This study demonstrates the value of urban green spaces as stopover sites for migrating species, and their importance for conservation.

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Data availability

The data collected for this project are available and can be supplied by the corresponding author upon request. Bird banding data are available through the NatureCount portal (naturecounts.ca).

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/cjz-2023-0109.

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