

Peri-urban forest margins are important stopover sites for moult-migrating songbirds

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ABSTRACT

Cities are significant barriers for migrating birds, but providing suitable greenspaces for stopovers can mitigate urban impacts. City planning for greenspaces often focusses on forests as parks, yet brushy edges and other successional habitats may be equally important especially for songbirds who spend weeks at stopovers in cities to moult their feathers ('moult migrants'). To investigate the role of *peri*-urban landscapes on moult migrants, we captured 48 moulting and 41 post-moult migrating Swainson's thrushes (*Catharus ustulatus*) within a large (3000 ha) urban park in Montreal, Canada. Each bird was randomly translocated to one of eight sites of varying habitat type and tracked using radiotelemetry. We compared the time spent at each translocation site with habitat characteristics, expecting birds to spend more time in areas with high food availability and concealment from predators. Migrating thrushes spent ~4 times as much time in dense forest margins than in fields and mature forests. Berry-producing shrubs that we identified as food for thrushes (by DNA-barcoding of their feces) best characterized those margins. Stopover home ranges were much smaller than the size of the park (50% core range: 10.6 ± 17.2 ha). This highlights the importance of urban greenspaces with dense forest margins during a vulnerable time for Swainson's Thrushes, and the conservation implications of maintaining these lower-valued greenspaces. Given that city parks are often lacking understory growth, we recommend keeping shrubby patches for migrating birds.

1. Introduction

Urban landscapes are rapidly expanding as our increasing human populations move toward cities (Seto et al., 2012). Urbanization causes cross-taxa declines due to habitat loss, fragmentation, and homogenization (McKinney, 2008; Piano et al., 2020; Seto et al., 2012). In response, the Kunming-Montreal Global biodiversity framework specifies, in Target 12, that cities should work on increasing the quality of urban green spaces (United Nations, 2022). Habitat alterations pose a particular problem for migratory birds who are an important component of temperate city biodiversity (Thompson et al., 2022). Many birds stop in urbanized areas with minimal green spaces to restore their fat reserves during migration (Rodewald and Matthews 2005; Matthews and Rodewald 2010a,2010b; Seewagen et al., 2010,2011). Nocturnal migrants are particularly drawn to cities as bright artificial lights attract migrating passerines flying at night (La Sorte et al., 2014; McLaren et al.,

2018; Van Doren et al., 2017). The ecological traps created by cities are particularly problematic as stopover sites in urban areas are limited in size (often < 4.5 ha), host invasive food sources that are unfamiliar to many species and provide many novel dangers (Matthews and Rodewald 2010a; Loss et al., 2014; Piontek et al., 2020). Thus, it is critical that urban forest patches be developed so as to create refuges for migratory birds (Matthews and Rodewald 2010a).

There is mounting evidence that migratory birds, stopping in cities, select spatially heterogeneous forest patches (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023). These green spaces in *peri*-urban areas hold higher bird biodiversity than in city centers or even natural forests with less habitat heterogeneity (Callaghan et al., 2019). Migratory landbirds occur in higher densities in deciduous and riparian forest patches in otherwise weakly-vegetated regions (i.e. low density urban landscapes; Cohen et al., 2022; Guo et al., 2023). Buron et al. (2022) found that migratory birds prefer to use urban forest fragments during

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stopover rather than residential areas.

Despite the importance of heterogeneous forest patches for birds (Estevo et al., 2017; Zuñiga-Palacios et al., 2020), we generally consider them an eyesore (Rega-Brodsky et al., 2018). Spontaneous (i.e. non-planted) vegetation in cities is perceived as being ‘unkempt’ and is not as ‘beautiful’ as human-designed gardens (Bonthoux et al., 2019). Spontaneous vegetation generally occurs in vacant or neglected lots which is a cause for its poor perception (Rega-Brodsky et al., 2018) but these plants contribute substantially to urban biodiversity (Phillips and Lindquist, 2021). Neglected spaces have the potential to develop into early successional landscapes which offer a mix of understory vegetation and taller trees (i.e. vertical spatial complexity; Swanson et al., 2011) that increase biodiversity (Hwang, 2016). While small forest patches may not be visually appealing, to meet Target 12, cities need to conserve these fragments that host a high abundance of migratory birds.

A large portion of migratory birds in North America breed in the boreal forest and many pass through large expanses of urban areas twice per year to reach their non-breeding grounds (Cohen et al., 2022; Wells, 2011). Indeed, for billions of songbirds that migrate from the boreal forest, cities in southern Canada are the first major human barrier that they encounter, many of which are funneled through the “Montreal Gap” between the Great Lakes and Gulf of St Lawrence (Gahbauer et al., 2016). Some individuals of certain passerine species spend a significant amount of time (~13% of their annual life cycle) at urban stopover sites to moult their flight feathers (Morales et al., 2022). While birds traditionally moult prior to migrating, some birds are ‘pushed’ by arid conditions at their breeding grounds and search for more suitable habitat to moult along their migration route (‘moult migration’; Barta et al., 2008; Cherry 1985; Pageau et al., 2020; Rohwer et al., 2005). These discrete moulting grounds exist in southern Quebec where banders have observed a high proportion (>50%) of migrants moulting at their site (Junda et al., 2020). Swainson’s Thrush (*Catharus ustulatus*; hereafter “thrushes”) is one such songbird species with frequent moult migrants (Junda et al., 2020; Pyle et al., 2018). Increasingly drier conditions in the boreal forests due to climate change (Price et al., 2013) could potentially push more birds towards these separate moulting grounds in cities.

To better understand what urban landscapes should be conserved for moult-migrating songbirds during this critical period of their annual cycle, we examine migrants’ occupancy decisions among several different habitat types within the Grand Parc de l’Ouest in Montreal, Canada’s largest municipal park. We tracked the movements of adult thrushes following their experimental translocation to three different habitat types (i.e. mature forests with low understory growth, immature forests with dense forest margins and understory growth, and open grassy fields) during their fall stopover. This study had four objectives: (i) to quantify migrants’ occupancy of each habitat type (i.e. translocation site), (ii) to analyze migrants’ resource selection by comparing used habitat types to available habitat types, (iii) quantify the distance the migrants travelled when leaving unfavourable translocation sites, (iv) describe migrants’ stopover home range sizes and habitat compositions. We used Swainson’s Thrushes as our subject species as they are the most frequent moult migrant (64% of individuals are moulting upon capture in autumn) at our study site (Junda et al., 2020).

We predicted that moult migrants with high energy requirements (Hoye and Buttemer, 2011) and a general need for high food availability (e.g. thrushes commonly eat native berries during migration, Parrish 1997) and protection from predators (i.e. concealment; Leu and Thompson, 2002; Pomeroy et al., 2018) will leave open field and mature forest habitats with sparse understory growth and move to immature forests with abundant berry-producing shrubs. In addition, based on their observed preference for heterogeneous forest patches (Buron et al., 2022; Callaghan et al., 2019; Guo et al., 2023), we expect migrants to select areas associated with forest edge and densely vegetated landscapes, like forest and wetlands, as opposed to open agricultural fields and anthropogenic areas. Finally, given their long stopovers, moult

migrants should form home ranges within habitats they prefer, which may be relatively small given the restricted size of urban forest patches.

2. Materials and methods

2.1. Radio-tagging and translocation

Thrushes were captured at the McGill Bird Observatory (“MBO”, 45.4307°N, 73.9385°W) during their 2021 and 2022 fall migration (between 1 August and October 21) using 30 mm mist nets. After hatch-year individuals were banded with numbered aluminum leg bands and aged based on their plumage and skull ossification. We recorded the percentage of moult completed where each primary and secondary flight feather was given a score from 0 (i.e. old feather) to 1 (i.e. new feather), in 0.1 increments (Newton, 1966; Morales et al., 2022). We attached 1 g and 0.35 gr coded radio-transmitters to 48 (23 in 2021 and 25 in 2022) moulting and 41 (21 in 2021 and 20 in 2022) post-moult thrushes using leg-loop harnesses. The radio-tags were NTQB-6-1, NTQB2-1, and NTQB2-4-2 models manufactured by Lotek and registered as part of the Motus Wildlife Tracking System (Frei, 2021–2022). Bird banding and radio-tagging were performed under animal use protocol 2007–5446 from McGill University, and federal banding permits 10743AE and 10743 T issued by the Canadian Wildlife Service.

We translocated thrushes to different habitat types (see below) within ~1200 ha of the capture site. Though still located in a city, this area encompassed several nature parks, agricultural farms, and residential areas, we therefore found ‘peri-urban’ to be a better classifier for the study site than ‘urban’. We chose six translocation sites in 2021 and seven in 2022 (Fig. S1). Translocation sites were chosen by in-person observation of the dominant habitat type: mature forest with sparse understory growth (3 sites), immature forest with dense understory growth (3 sites), or open grassy field (1 site in 2021 and 2 sites in 2022). Note that translocation sites differ in number and location between sampling years as we strived for more evenly distributed sites (spatially and habitat type-wise) in 2022. Translocation sites were also required to be within the detection range of the four Motus towers (<1.1 km per Crewe et al., 2019 recommendations; see Fig. S1 for the site locations relative to the towers). The Motus towers, in turn, had to be installed in open areas, all of which had to be accessible by truck. The capture site (MBO) was treated as an immature forest translocation site in analyses. Site size had no effect on thrushes’ occupancy [see ‘Results: Occupancy’]. All birds were randomly assigned to a translocation site and transported to their site by car and foot. Birds assigned to the capture site were given a minimum of 10-minute car ride to standardize the birds’ treatments. See ‘Manual tracking of radio-tagged Swainson’s Thrushes’ in Supplementary materials for the detailed manual tracking schedule and methods.

2.2. Habitat characteristics within and across translocation habitat types

Habitat surveys were completed from July through September 2021 and June through July 2022. We established randomized 10 m-diameter circular quadrats within each site, totaling approximately 10 ± 2.5 surveys per site (range of 4 to 14; see Table S1 in Supplementary materials). The measurements taken in each plot included diameter at breast height (DBH) of trees > 3 cm in diameter, stand density, shrub cover, canopy cover, concealment, and density of berry-producing plants where we counted the number of shrubs by their stems and identified them by species. Shrub cover was measured using line transects in 2021 following methods in Higgins et al. (1994) and Tietz and Johnson (2007) and a cover pole in 2022 following methods in Griffith and Youtie (1988). Canopy cover was measured as the percent of canopy to open sky using ImageJ, a Java-based image processing program, as validated for use in Smith and Ramsay (2018). Concealment was measured based on methodologies in Tietz and Johnson (2007) whereby we observed the viability (%) of a 1 m by 1 m checkerboard sheet placed

on the ground. See ‘Detailed methods: Habitat characteristics’ in the [Supplementary materials](#) for a detailed explanation of the how these habitat characteristics were measured.

For the measurements of berry-producing shrub density, we only considered shrub species that we had confirmed were consumed by thrushes during the fall period using DNA barcoding analysis of fecal samples collected in 2021 [see ‘Results: Habitat characteristics within and across translocation habitat types’]. Swainson’s Thrushes were placed in paper bags for ~5 min or until they defecated. Their feces were stored in ethanol before being sent to the Canadian Center for DNA Barcoding (CCDB) where DNA was extracted using plant-specific primers (ITS-S2F_t1/ITS4_t1) and amplified through polymerase chain reactions (PCR), producing > 100 bp sequences. Results were compared to a comprehensive BOLD reference library (see the Barcode of Life Data System) and assigned an identity using the Basic Local Alignment Search Tool (BLAST) algorithm.

We performed a non-parametric multivariate analysis of variance (PERMANOVA) to compare the mean and standard deviation of all habitat variables (i.e. DBH, stand density, shrub cover, canopy cover, concealment, and density of berry-producing shrubs) between habitat types (i.e. immature forest, mature forest, and field) using the Wilks’ Lambda type statistic with the *npmv* package in R.3.2. Statistically significant results ($\alpha = 0.05$) were followed with Kruskal-Wallis tests and pairwise comparisons using the Dunn method and incorporating the Benjamini-Hochberg procedure to minimize false positives. We also performed a principle component analysis comparing habitat characteristics between each translocation habitat type (see ‘Detailed methods: Habitat characteristics’ in [Supplementary materials](#)). Note that data was homoscedastic but not normally distributed.

2.3. Occupancy of the translocation sites

We analyzed occupancy (i.e. how long a bird stayed at their translocation site) based on manual tracking data. We calculated ‘length of stay’ as the percent of days each bird spent in their respective translocation site (known through manual tracking), out of their total stopover duration. Stopover duration (in days) was calculated as the difference between the capture (i.e. translocation) date and the departure date. Departure dates were recorded as the last date an individual was detected by one of the three Motus towers located in the study site.

For one moulting individual in 2022, tower detections were too weak to determine departure date. Instead, we calculated the number of days it would take that individual to completely moult (following a moult rate of 2.0 ± 0.6 % per day, calculated using data from 2013 to present from this site) as a proxy for departure date. In all, length of stay was calculated for 69 individuals (41 moult and 28 post-moult migrants; see [Table S2 in Supplementary materials](#) for details) and logit-transformed before all analyses.

We constructed generalized linear mixed models (GLMMs) comparing length of stay with concealment and berry-producing shrub density. We built four GLMMs (with Gaussian error distributions): a global model (including concealment and density of berry-producing shrubs), an intercept-only model, a concealment-only model, and a berry-producing shrub density model. Moult status was included as a random effect in each model. No other habitat variables were included in these models because they were all highly correlated (see [Fig. S2 in the Supplementary materials](#)). Predictor and response variables were scaled and centered prior to modeling. We finally ranked the four models using the Akaike information criterion method for model selection adjusted for small sample sizes (AICc).

2.4. Resource selection: Comparing used and available habitats

We conducted a use-availability analysis to investigate migrating thrushes’ resource selection during their stopover. The GPS coordinates collected through manual tracking were the ‘used’ points in our analysis.

We only included birds that had >1 associated GPS points ($N = 64$ different birds totaling 481 GPS points). We produced two available points for every used point and placed them at equivalent distances (to their paired used point, ranging from 1 m to 3500 m) from the bird’s release site at a randomly selected angle from that site. All points were overlaid on a 30 m-resolution landscape cover map from 2019 (obtained from *Partenariat Données Québec*). We extracted the proportion of landscape cover type (note that these are broader categories from the translocation habitat types: i.e. agriculture, anthropogenic, forest, and wetland) and length of forest edge (in meters) within 50 m, 100 m, and 200 m-radius buffers around each used and available point. Any available points that were 100% surrounded by water were removed as thrushes are not aquatic birds and would not realistically be using these areas. Data was centered and scaled before modeling.

We constructed four binomially distributed GLMMs. First, we built separate global models for each buffer size and compared them through AICc model selection to determine the scale of effect. The resulting best model’s buffer size (i.e. 50 m-radius, see ‘Results: Use-availability analysis: peri-urban resource selection’) was then used to construct the following four candidate models: a ‘landscape composition’ model including the proportion of different landscape types (i.e. agriculture, anthropogenic, forest, wetland) in the available/used area, a ‘forest edge’ model including only the length of forest edge (in meters), and a global model including both landscape composition variables and forest edge, and an intercept-only model. All four models also included the habitat type of the translocation site (see [Fig. S1 in the Supplementary materials](#)) and the bird’s identification number (ID) as random effects. We also tested for multicollinearity between all the predictor variables before constructing our models and found no correlation (Pearson’s $r < 0.7$). The four candidate models were ranked using AICc model selection and analyzed for goodness of fit using the Hosmer and Lemeshow test.

2.5. Distance thrushes travelled from translocation sites

We calculated the distance between chronologically consecutive GPS points (i.e. displacements) for 74 thrushes (44 moult migrants and 30 post-moult migrants). Distances were calculated using the *move* package in the R.3.2 and are presented in meters. We considered individuals translocated to immature forests, mature forests, and fields separately and compared the average first displacement between habitat types using a Kruskal Wallis and subsequent Dunn’s test with the Bonferroni method.

2.6. Stopover home range size and habitat composition

We constructed stopover home ranges from the GPS locations of the thrushes obtained through manual tracking. We determined 95% and 50% stopover home ranges using independent and identically distributed (IID) isotropic models as suggested by the AICc model selection in the *ctmm* package in the R.3.2, confirming the existence of a stopover home range rather than continuous movement. The IID isotropic model indicates that the bird’s presence is distributed independent of all other GPS points and direction. These stopover home ranges were then overlaid on a 30 m-resolution landscape cover map from 2019 (obtained from *Partenariat Données Québec*). Calculations included data from 42 individuals across both sampling years (21 moult and 7 post-moult migrants from 2022, and 14 moult migrants from 2021) since these individuals had at least five GPS points to successfully build their stopover home range.

3. Results

3.1. Habitat characteristics within and across translocation habitat types

All translocation habitat types were significantly different from one another ($p < 0.05$) across all habitat measurements ($p < 0.001$).

Concealment (i.e. concealment, shrub cover, and canopy cover) and tree-related measurements (i.e. stand density and DBH) were consistently highest in mature forest sites whereas most shrub density-related measurements (i.e. shrub and berry-producing shrub density) were highest in immature forest sites (Fig. S3). All habitat variables were consistently low in field sites. For sites sharing the same habitat type, only immature forest sites were statistically similar for all habitat measurements ($p > 0.05$), while there were slight differences within mature forest and field sites (Table S4).

We detected plant DNA in 82% of thrushes' fecal samples ($N = 38$), however, only 44% of detections could be identified to genus. The plant genera present were *Rubus* (13.0%), *Juglans* (13.0%), *Ambrosia* (13.0%), *Rhamnus* (8.7%), *Frangula* (8.7%), and *Boehmeria* (8.7%), of which *Rhamnus*, *Rubus*, and *Frangula* were berry-producing shrubs present on site.

3.2. Occupancy of the translocation sites

Average length of stay was highest in the immature forest sites ($25 \pm 16\%$ of their stay or 12 ± 7 days), followed by the mature forest sites ($7 \pm 20\%$ or 3 ± 9 days) and was nearly negligible in the field sites ($0.15 \pm 0.56\%$ or 1 ± 3 days). Length of stay was significantly different among all habitat types ($p < 0.001$) except between mature forest and field sites ($p > 0.05$). There was no relationship between length of stay and site size (adjusted $R^2 = -0.10$ and $p = 0.66$). Average stopover duration (see 'Methods: Occupancy of the translocation sites') for moult migrants was 46 days versus 8 days for post-moult migrants.

The best model to predict length of stay only included berry-producing shrub density (>2.0 $\Delta AICc$ values between all other models except the global model; Table 1). This berry model had a pseudo- R^2 (1-null deviance/ residual deviance) of 0.700. Berry-producing shrub density in this model had an estimated coefficient of 0.11 ± 0.01 ($p < 0.001$). The global model was second best, followed by the intercept-only model, and finally the concealment-only model (Table 1). The global model had a similar goodness of fit value (0.705) and estimated coefficient for berry-producing shrub density (0.11 ± 0.01 ; $p < 0.001$). In both the global and concealment models, concealment had no significant effect on length of stay ($p > 0.05$).

3.3. Resource selection: Comparing used and available habitats

The global model which extracted habitat measurements from a 50 m-radius around the used and available points was significantly better than the models of buffer sizes 100 m and 200 m (>2.0 ΔAIC). The global model including the proportion of landscape types (i.e. agriculture, anthropogenic, forest, and wetland) and the length of forest edge was the best (>2.0 ΔAIC difference between all other models, see Table 2a) for predicting used versus available areas (i.e. thrushes' presence). Three of the global model's five fixed variables significantly affected thrush presence: proportion of agricultural land ($p = 0.004$),

Table 1

AICc of four generalized linear mixed models comparing migrating Swainson's Thrushes' occupancy decisions (i.e. proportion of their stopover duration that they spent at their translocation site) to the sites' berry-producing shrub density and concealment. The moult status of the birds (i.e. moult or post-moult) was considered a random effect in these models.

Model	Variables	-LL	Δ AICc	Wt
Berry	berry-producing shrub density + moult	-57.07	0.00	0.75
Global	concealment + berry-producing shrub density + moult	-56.66	1.51	0.25
Intercept-only	moult	-89.01	61.62	0.00
Concealment	concealment + moult	-88.86	63.57	0.00

Table 2a

AICc of four resource selection (i.e. binomial generalized linear mixed-effects) models comparing 64 migrating Swainson's Thrushes' used versus available (50 m-radius) locations based on their landscape composition and the length of forest edge (in meters). Habitat type of the area and the individual's identification (ID) are included as random effects in each model.

Model	Variables	-LL	Δ AICc	Wt
Global	agriculture + anthropogenic + forest + wetland + forest edge + habitat type + bird ID	-816	0.00	0.99
Landscape composition	agriculture + anthropogenic + forest + wetland + habitat type + bird ID	-822	9.66	0.01
Forest edge	forest edge + habitat type + bird ID	-856	72.83	0.00
Intercept-only	habitat type + bird ID	-899	156.58	0.00

proportion of forest ($p = 0.006$), and the amount of forest edge ($p < 0.001$; see Fig. 1 and Table 2b). The second-best model, the landscape composition model, had similarly significant predictor variables: proportion of agricultural ($p < 0.001$) and anthropogenic land ($p = 0.002$; see Table 2b). We found very similar pseudo- R^2 values between the marginal and conditional global models (R^2 conditional = 0.2 and R^2 marginal = 0.18, calculated using the *r.squaredGLMM* function in the R programming software; Nakagawa and Schielzeth, 2013). A Hosmer and Lemeshow goodness of fit test showed that the global model poorly fit the data ($\chi^2 = 1396$, $df = 8$, $p < 0.001$).

3.4. Distance thrushes travelled from translocation sites

Thrushes generally made one large movement before settling in their stopover home range for the rest of their stopover (Fig. S5). This first displacement was significantly shorter for individuals translocated to immature forest sites (195 ± 425 m) than those from mature forest sites (419 ± 633 m, $p = 0.013$). Meanwhile, first displacements made from field sites (266 ± 377 m) were neither significantly longer nor shorter than those from immature forests or mature forests, respectively ($p > 0.05$).

4. Stopover home range size and habitat composition

According to independent and identically distributed (IID) isotropic models we determined that the average (95%) stopover home range size of thrushes across both years was 56.74 ± 106.9 ha. The average 95% stopover home range size was approximately two times larger for moult migrants (62.97 ± 116.3 ha) than post-moult migrants (27.39 ± 30.23 ha; Fig. S6, Table S5). Core (50%) stopover home ranges averaged 10.55 ± 17.16 ha across both years (Fig. 2). Moult migrants still had ~2 times larger core stopover home ranges (11.68 ± 18.85 ha) than post-moult migrants (5.92 ± 5.33 ha; Table S6).

On average, the 50% core stopover home ranges were composed of $56.65 \pm 28.34\%$ forest, $25.44 \pm 25.24\%$ agricultural land, $10.41 \pm 14.62\%$ wetlands, and a small percentage of water bodies ($5.76 \pm 16.94\%$) and anthropogenic areas ($1.74 \pm 4.55\%$). Similarly, the 95% stopover home ranges were mainly composed of forests ($50.75 \pm 20.95\%$), followed by agricultural land ($30.02 \pm 19.41\%$), wetlands ($10.55 \pm 12.44\%$) and a small percentage of anthropogenic areas ($4.06 \pm 6.96\%$) and water sources ($4.62 \pm 10.25\%$; Table S3 in Supplementary materials for more detail).

5. Discussion

Neotropical songbirds encounter many urban and peri-urban landscapes along their migration route and use them to refuel during migration (Rodewald and Matthews 2005; Matthews and Rodewald 2010a, 2010b). While some birds spend ~7 days at these stopover sites to rest and refuel before their next migratory flight, others spend ~48

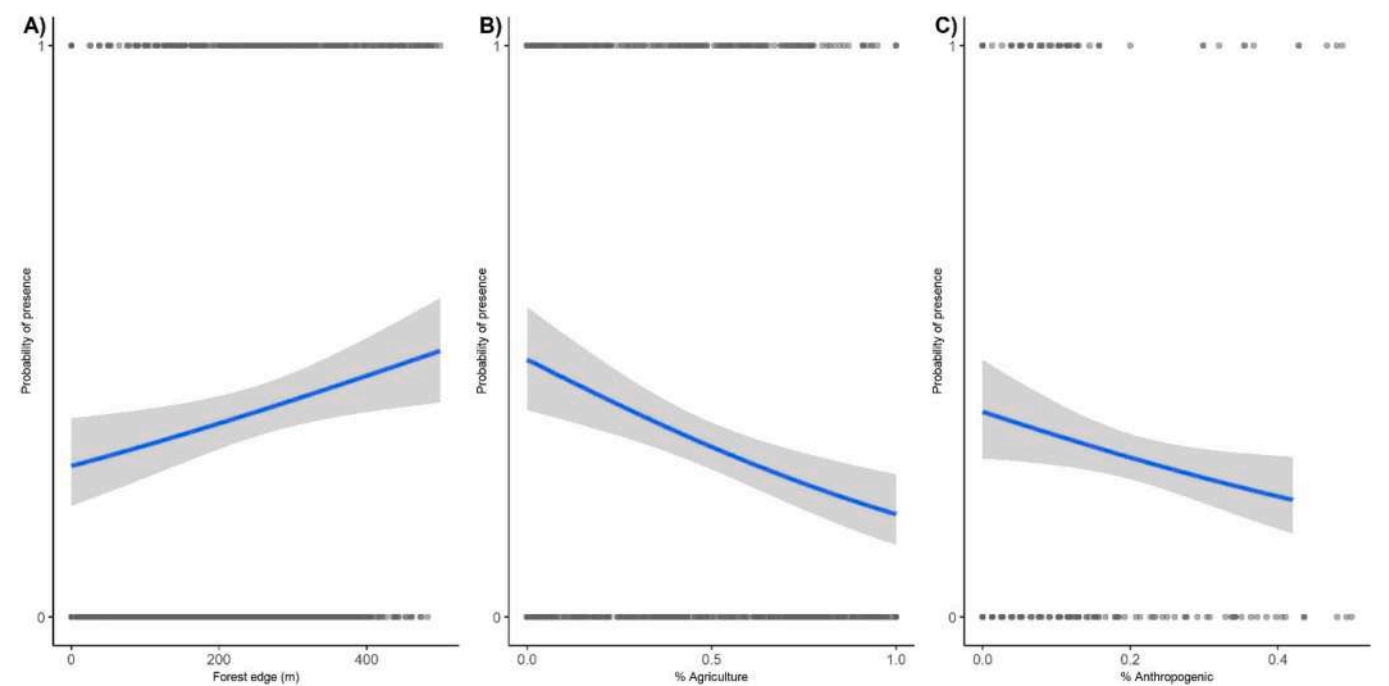


Fig. 1. Probability of presence of migrating Swainson's Thrushes in a given 50 m-radius area as predicted by a generalized linear mixed effects model. The model's fixed effect variables include the percentage of agricultural, anthropogenic, forested land, and wetland, and the length of forest edge (in meters). Random effects in the model were translocation site and bird ID. (A) Swainson's Thrush probability of presence as positively influenced by the amount of forest edge (coefficient = 0.26, $p < 0.001$). (B) Swainson's Thrush probability of presence as negatively influenced by the proportion of agricultural land (coefficient = -0.51 , $p = 0.004$), and (C) shows Swainson's Thrush probability of presence as negatively influenced by the proportion of anthropogenic land (coefficient = -0.3 , $p < 0.006$).

Table 2b
Model parameters of the two best resource selection models predicting the presence/absence of 64 migrating Swainson's Thrushes within (50 m-radius) areas based on their landscape composition and the length of forest edge (in meters). Habitat type of the area and the individual's identification (ID) are included as random effects in each model.

Variable	Coefficient estimate	Standard error	z	p
<i>Global model</i>				
Forest edge (length in meters)	0.256	0.076	3.392	<0.001
Agricultural land (%)	-0.514	0.180	-2.863	0.004
Anthropogenic land (%)	-0.296	0.108	-2.735	0.006
Forest (%)	0.144	0.157	0.916	0.360
Wetland (%)	0.019	0.105	0.180	0.857
<i>Landscape composition model</i>				
Agricultural land (%)	-0.595	0.176	-3.374	<0.001
Anthropogenic land (%)	0.336	0.106	-3.162	0.002
Forest (%)	0.161	0.156	1.034	0.301
Wetland (%)	0.081	0.102	0.802	0.423

days to moult their feathers (Morales et al., 2022). Both are significant periods in a bird's lifecycle where high quality habitats are critical for their physiological fitness (Leu and Thompson 2002). The lack of quality habitats in cities (Loss et al., 2014) and the equal lack of research on urban stopovers, for moulting birds especially, is therefore a point of concern. This study aimed to fill this knowledge gap by identifying moult and post-moult migrant habitat-occupancy trends (using Swainson's Thrushes as an example) within a peri-urban matrix.

5.1. Occupancy of translocation sites

Migrating thrushes in a peri-urban setting spent significantly more time in immature forest, primarily shrubby edges with dense understory

growth, rather than mature forests or fields. These immature forests were mainly characterized by dense understory (i.e. shrub density and density of berry producing shrubs), while mature forests were represented by higher stand density, canopy cover, tree diameter, shrub cover, and concealment.

Although berry-producing shrubs and concealment would both be critical factors in determining habitat quality for birds (Fox et al., 2014), in this study, density of berry-producing shrubs alone was the most influential factor when predicting occupancy. Indeed, the immature forest sites which migrants preferred had the highest density of berry-producing shrubs. Common buckthorn (*Rhamnus cathartica*), an invasive species in Canada (Canadensys 2022), was the most frequent berry-producing shrub across all sites and most abundant in immature forest sites. Other berry-producing plants found in the immature forest sites include glossy buckthorn (*Frangula alnus*), raspberry and blackberry (*Rubus spp.*), Virginia creeper (*Parthenocissus quinquefolia*), and river-bank grape (*Vitis riparia*). Thrushes are considered generalists and have been seen eating some of the berries mentioned here (Beal 1915).

Based on fecal samples collected from our tagged birds in 2021, individuals were indeed consuming fruits present in the immature forest sites: *Rhamnus*, *Rubus*, and *Frangula*. The abundance of fruit in these habitats must be attractive to migrating birds who require abundant energy to successfully moult and refuel for migration (Leu and Thompson 2002; Ramirez et al., 2022). Non-native shrubs, however, tend to have less fat and be less energy-dense than native shrubs (Bolser et al., 2013; Smith et al., 2013; White and Stiles 1992) and therefore may not be as beneficial for migratory birds looking to bolster their fat reserves. Thrushes preferentially inhabit native shrubland during autumnal stopovers (Oguchi et al., 2018) and individuals in our study may be relying on exotic shrubs only due to their abundance in disturbed, urban habitats (Ricotta et al., 2017). City managers should therefore support the growth of berry-producing shrubs, especially those native, nutritious species.



Fig. 2. Maps and habitat composition of the 50% independent and identically distributed (IID) isotropic calculated stopover home ranges of moult migrating (in navy blue) and post-moult migrant (in yellow) Swainson's Thrushes during their autumnal stopover in the West Island of Montreal. (A) 14 moult and 2 post-moult migrants who were translocated to immature forest sites and (B) 17 moult and 5 post-moult migrants who were translocated to mature forests or field sites. Bar plot C) shows the habitat types (% average) within the stopover home ranges of the moult and post-moult migrants. Average stopover home range size for moult migrants was 11.68 ha (standard deviation = 18.85 ha) and 5.92 ha (standard deviation = 5.33 ha) for post-moult migrants. GPS points on the maps were taken through manually tracking using radio telemetry when signal strength was at least 130 dB at a gain (precision) between 9 dB and 40 dB. Points of the same color belong to the same bird. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

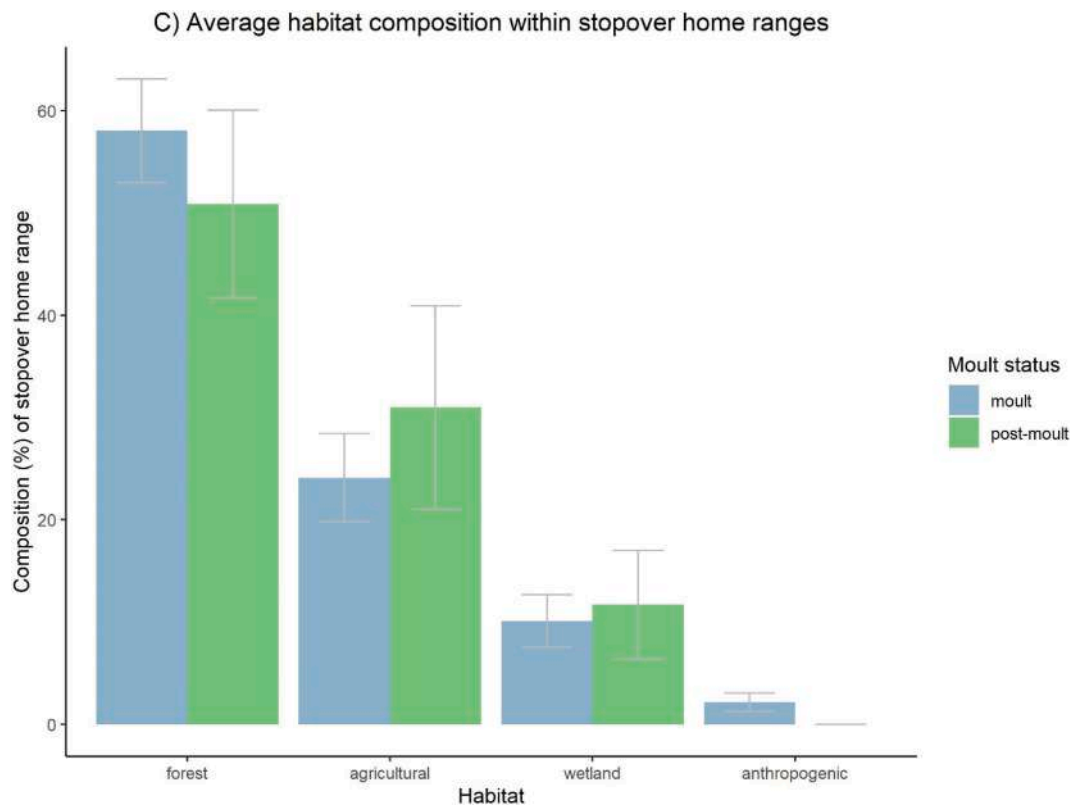


Fig. 2. (continued).

5.2. Resource selection: Comparing used and available habitats

Migrating thrushes actively avoided agricultural and anthropogenic landscapes, preferring to occupy forest patches with abundant forest edge. Thrushes' avoidance of both agricultural and anthropogenic landscapes is presumably due to a lack of food in these areas. As frugivorous ground-foraging birds (Mack and Yong 2020), migrating thrushes would find little food from the dry-fruit-producing herbaceous plants found in fields, nor would the managed lawns and grey infrastructure in cities provide many natural fruit sources (Loss et al., 2014). In addition, considering the dangers present in anthropogenic areas (Loss et al., 2014), it is logical that migrants would be averse to them as birds often prioritize safety (alongside food) during habitat selection (Pomeroy et al., 2018). An avoidance of anthropogenic areas in favor of urban forest patches has been equally observed for multiple migrating species (Burton et al., 2022). Similarly, a general avoidance of agricultural lands was observed in several species in Callaghan et al. (2019) and Buler and Dawson (2014), though they may be preferred sites for seed-eating birds (Zuckerberg et al., 2016). These results highlight the unsuitability of human-centric spaces for avian stopovers and thus the importance of conserving urban forest fragments.

Migrating thrushes were consistently found along the forested edges of their translocation sites. Indeed, our resource selection function comparing occupied and available habitats showed that Swainson's Thrushes presence was positively associated with forest edges. Other studies have highlighted the positive relationship between long-distance migrants and forest edges, particularly for insectivorous and understory-gleaning birds, and thus their importance for conservation (Stanley et al., 2021; Terraube et al., 2016). In cities where habitat fragmentation has created patches with higher ratios of forest edge to forest interior, migrants may find suitable habitat in these areas.

Contrary to previous studies indicating that thrushes are less selective of their stopover habitat and forest types during migration (Stanley et al., 2021; Tietz and Johnson 2007), we provide evidence that

Swainson's Thrushes select stopover habitats at a relatively small scale (within a 50 m radius or smaller). The resource selection exemplified by the Swainson's Thrushes in this study further supports studies such as Burton et al. (2022) and Guo et al. (2023) showing migrating birds' use of urban forest fragments as stopover sites. Our study suggests that migrants search for good-quality habitats in urban areas and that small forest fragments, despite their low value to humans, are important stopover sites. Given that songbirds are attracted to cities during migration where they must stop and refuel, cities have the responsibility of preserving these small forest fragments to meet conservation initiatives such as Target 12.

5.3. Distance thrushes travelled from translocation sites

Swainson's Thrushes made one long (a few hundred meters long) movement before settling in their stopover home range. Migrants translocated to immature forest sites made shorter initial displacements (~200 m) than those translocated to mature forest sites (~500 m), perhaps indicating a closer availability of suitable habitat in immature forest sites. The relatively short displacements indicate that migrants will not venture very far before settling on a stopover site. Researchers similarly followed Northern Wheatears after release at a stopover site and found that migrants travelled for only ~13 min before settling to forage (Delingat et al., 2006). Minimizing this search and settling phase seems to be a good strategy to reduce energy and time investments during an activity (i.e. migration) that is costly in both.

5.4. Stopover home range size and habitat composition

The small size of the forest fragments in this study was seemingly not an issue as migrating Swainson's Thrushes occupied similarly small stopover home ranges (50% IID isotropic distribution = 10.55 ± 17.16 ha). Though still relatively small, maintaining 10 ha-size forest patches for migrating birds may not be feasible in all cases, as not all urban green

spaces are this size. Vegetated patches born from vacant lots, for example, can be as small as 0.05 ha (Doroski et al., 2021). Matthews et al. (2010a), for example, found that Swainson's Thrushes moved away from urban forest patches <4.5 ha in size. Cities must therefore consider conserving forest fragments of at least 10 ha to maintain their ecological relevance for migrating birds.

6. Conclusions and conservation implications

Although our study is limited to one species, our results may be applied to all species with a similar foraging pattern (i.e. frugivorous ground-foragers) as they would presumably have similar habitat requirements. Considering the abundance of long-distance migrants stopping to refuel, and sometimes moult, in cities (McLaren et al., 2018), conserving urban forest patches would benefit many birds. This study supports growing, though limited, evidence that migrants preferentially occupy fragmented green spaces in otherwise poorly-vegetated urban areas (Burton et al., 2022; Callaghan et al., 2019; Guo et al., 2023).

Whether actively moulting or simply refueling for migration, migrants did not settle for unfavourable stopover sites (such as agricultural fields and residential areas) and instead searched for good quality habitats nearby despite the extra time it would take to find one in an anthropogenic landscape. According to these thrushes, areas characterized by dense vegetation are favourable for stopovers but are less common in cities (Jiao et al., 2021; Threlfall et al., 2016) as people often prefer to maintain managed parks and lawns and remove 'messy' vegetation. Although not necessarily used by humans, these areas carry high value for migrating songbirds during a particularly vulnerable stage in their life. Considering their broader ecological role, these areas can help cities achieve wildlife conservation goals in accordance with emerging initiatives such as the Kunming-Montreal Global biodiversity framework.

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CRediT authorship contribution statement

Vanessa Poirier: . **Kyle H. Elliott:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing. **Barbara Frei:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data is available at <https://doi.org/10.5061/dryad.vq83bk40s>.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jnc.2023.126539>.

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