Foraging habitat drives the distribution of an endangered bat in an urbanizing boreal landscape

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Abstract. The boreal forest is the largest intact forest in the world, and a refuge for species experiencing range retractions as a consequence of climate and landscape change. Yet, large tracts of the boreal forest are threatened by the cumulative impacts of climate change, natural resource extraction, agriculture, and urbanization, perhaps warranting a shift in focus from biodiversity conservation in intact wilderness to that in anthropologically modiﬁed landscapes. We investigated landscape features that influence the distribution of the endangered little brown bat (Myotis lucifugus) in an urbanizing boreal landscape at two spatial scales. We hypothesized that little brown bat activity would be inﬂuenced by proximity to available building roosts, because roosts are a potential limiting factor for boreal bats. Secondarily, we predicted that bats would use potential foraging habitat, such as waterbodies, and would avoid young, cluttered forests at the landscape scale. We conducted acoustic surveys of bat activity at 210 sites distributed across the study area in Yukon, Canada, within 1-km grid cells. We tested a priori hypotheses with a set of candidate regression models, accounting for spatial autocorrelation. Our hypothesis about the relative importance of anthropogenic roosts was not supported. Little brown bats were equally active in urban areas (high building density) and rural areas (low building density), perhaps because roosts were adequately available throughout the region. Instead, habitat use was driven by the distribution of potential foraging habitat, particularly waterbodies, which are important sources of aerial insect prey. Little brown bats also avoided young (≤100-yr-old) forest at the landscape scale (including areas regenerating after fire), which may have been poor foraging or roosting habitat, and used areas with a smaller agricultural and industrial footprint. Our results suggest that waterbodies and mature forest are important little brown bat habitats that should be protected from urban encroachment. Proactive conservation of important habitat for species at risk is still possible throughout much of the boreal forest, where human densities are comparatively low and the urban footprint is currently small.

Key words: bats; boreal forest; endangered species; habitat models; Myotis lucifugus; urbanization.

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INTRODUCTION

The boreal biome comprises 36% of the world’s remaining intact forest (Potapov et al. 2017). In North America, the boreal forest has become a refuge for wildlife species experiencing habitat loss and population declines in more developed parts of their distributional range (Schaefer 2003, Laliberte and Ripple 2004, Berteaux et al. 2018). This vast biome is increasingly threatened by climate change, natural resource extraction, and agricultural development, all of which result in habitat loss and fragmentation (Brandt et al. 2013, Venier et al. 2014). Less attention has been given to urbanization as an agent of landscape change in the boreal forest. Compared with much of the rest of the world, human density in the boreal forest is currently low (Venter et al. 2016), but like elsewhere, residential development and urban settlements are expanding rapidly (Nitoslawsky et al. 2019). A warming climate coupled with the growing human population may amplify this trend, as immigration to the boreal region is bolstered by a northward shift in the agricultural climate zone (King et al. 2018, Hannah et al. 2020) and a booming resource development industry (Brandt et al. 2013). The growing urban footprint is a pressing conservation issue (Güneralp and Seto 2013); yet, in much of the boreal forest, opportunity remains to identify and protect areas of high biodiversity.

Bats are one of the most threatened vertebrate taxa, with approximately 31% of all North American species considered at risk (Hammerson et al. 2017). Many species have broad geographic ranges, but the major threats (e.g., disease, wind energy, and habitat loss) are currently concentrated in temperate parts of their ranges (Hammerson et al. 2017), whereas the boreal forest remains a comparatively stable refuge (Jung et al. 2014). Parts of the boreal biome may remain isolated from white nose syndrome—a fungal disease that has devastated some bat species (Frick et al. 2010)—because of limited inter-regional gene flow (Wilder et al. 2015, Davy et al. 2017) and a cold dry climate that may slow the spread of the fungus (Knudsen et al. 2013). As such, the boreal forest should be a priority region for bat conservation, but knowledge about bat habitat requirements in this biome lags far behind that in others (Jung et al. 2014).

Although urbanization is detrimental to many species of bats (Russo and Ancillotto 2014, Jung and Threlfall 2016), the endangered little brown bat (*Myotis lucifugus*) is a synurbic species often found at higher densities near human settlements (Coleman and Barclay 2012, Thomas and Jung 2019). Their synurbic tendencies are a consequence of their ability to exploit anthropogenic roosts (e.g., buildings, bridges), and in some high-elevation or high-latitude regions, they may depend on them (Johnson et al. 2019, Thomas and Jung 2019). Buildings provide a thermoregulatory advantage for reproductive female bats (Lausen and Barclay 2006, Johnson et al. 2019), particularly in the north where the climate is cool and natural roosting habitat is scarce (Slough and Jung 2008, Olson and Barclay 2013, Randall et al. 2014). However, there may be limits to their tolerance for urban density, similar to that seen for other bat species (Caryl et al. 2016). Developed areas alone may not meet all habitat requirements. For instance, little brown bats require adequate foraging habitat, which may include waterbodies, forests, and forest edges (Broders et al. 2006). Mature forests may provide better habitat than regenerating forests because of their open and uncluttered structure (Crampton and Barclay 1998, Jung et al. 1999, Luszcz and Barclay 2016), but mature forests decline with increasing urban footprint (Ren et al. 2012). Despite higher activity in urban areas (Coleman and Barclay 2012), little brown bats may suffer reduced fitness, perhaps due to stress, noise, or competition for limited insect prey (Coleman and Barclay 2011).

A previous study revealed that little brown bats in the boreal forest are more abundant near rural villages, likely because they are isolated islands of anthropogenic roosting habitat within a forest matrix (Thomas and Jung 2019). That study focused on small towns with human populations <1000, but the principles are untested in larger urban centers in the boreal forest. In rural settings, potential roosting habitat (buildings) and foraging habitat (forests and waterbodies) may be in relatively close proximity, but urbanization often creates spatial separation between these critical resources through forest and wetland loss (Ren et al. 2012, McCauley et al. 2013). Reproductive female bats are central-place foragers that disperse from maternal roosting sites,
which they must return to after nightly foraging bouts (Henry et al. 2002, Daniel et al. 2008, Rainho and Palmeirim 2011). This may impose trade-offs between the selection of roosting and foraging habitat in urban areas.

Our objective was to identify mechanisms that explained the distribution of little brown bat activity in an urbanizing boreal landscape. Our study area in Yukon, Canada, is a region with a gradient from urban (near city center) to rural. We evaluated multiple spatial scales of habitat use by little brown bats relative to local and landscape features that may influence potential roosting and foraging habitat, and travel between them. We hypothesized that availability of potential roosting habitat would be the most important determinant of bat activity, as roosts are likely a limiting resource for North American bats (Humphrey 1975, Fenton 1997). Human population density is quite low in this region, compared with other studies on bat responses to urbanization (Threlfall et al. 2011, Caryl et al. 2016), and we predicted that bat activity would be greatest where buildings were more available as potential roosts, near the urban center. We hypothesized that landscape features representing foraging habitat would be of secondary importance and predicted that bats would use areas with nearby water bodies and mature forest, particularly in proximity to potential building roosts. Little brown bats may use minor linear features (e.g., transmission lines) as travel corridors to commute to foraging areas, but preliminary work in the boreal forest suggests that they avoid roads (Jung 2020). As such, we predicted that bat activity would be positively associated with the density of minor linear features and negatively associated with the density of roads. Improved knowledge of how bat activity is distributed across anthropogenic landscapes is key to identifying and protecting important habitat from further development.

METHODS

Study area and species
Our study was conducted in the northern boreal forest, within a 50-km radius of Whitehorse, Yukon, Canada. This region is predominantly wilderness but contains the largest concentration of people and human development for >1000 km, most of which occurs in the city (2019 population = 32,395 people). The footprint of the urban core is ~35 km², with a human density of 622 people/km², although development and infrastructure extend to varying degrees through the surrounding wilderness. We selected this region for study because it represents an area of rapid and sprawling development.

Whitehorse and environs are located in the Boreal Cordillera Ecozone, which is characterized by rugged mountains of elevations ≥1000 m above sea level, and deeply incised river valleys that are largely forested. The study area contains numerous wetlands and lakes, and is bisected by two large rivers (Fig. 1). Much of the forest in the study area (~14%) is regenerating after a large and severe wildfire that occurred in 1958 (Strong et al. 2013). Common tree species include white spruce (Picea mariana), lodgepole pine (Pinus contorta), and trembling aspen (Populus tremuloides). Residential and industrial development, agriculture, and roads are the primary agents of anthropogenic landscape change. The climate is subarctic and semi-arid, with snow typically persisting in valley bottoms from mid-October to late-March and lakes remaining frozen until May. Mean daily temperatures in Whitehorse (1981–2010) for June, July, and August were 12.3°C, 14.3°C, and 12.6°C, respectively, while mean monthly precipitation was 32.4, 38.1, and 35.8 mm (Government of Canada 2019, unpublished data).

Several acoustic studies in southern Yukon reported that little brown bats were the most common bat species by far, albeit at low densities (Slough and Jung 2008, Thomas et al. 2019, Thomas and Jung 2019, Jung 2020). Other bat species are likely present but rarely detected (Jung et al. 2006, Slough et al. 2014). Little brown bats arrive in the study region in mid-April and adult females form maternity colonies throughout May, to which they exhibit roost-site fidelity (Slough and Jung 2020). In the boreal forest, these colonies are often in anthropogenic structures and may include hundreds of adults, although natural roosts (e.g., trees, rock crevices) are also used (Crampton and Barclay 1998, Slough and Jung 2008, 2020, Olson and Barclay 2013, Randall et al. 2014). Births occur in late June to early July, and maternal colonies tend to dissipate by late July once juveniles are volant.
Males in coniferous forests typically roost alone throughout the summer (Jung et al. 2004, Broders et al. 2006). Little brown bats are insectivorous, and typically capture their prey by aerial hawking over waterbodies or at forest openings or edges (Grindal and Brigham 1999, Broders et al. 2006). However, at high latitudes they may also glean insects and spiders from within forests.

Fig. 1. Acoustic sampling locations near Whitehorse, Yukon, Canada, surveyed from May to September 2019. Recorded little brown bat (*Myotis lucifugus*) activity levels are indicated by color. The 900 m elevation cutoff (thick black lines) and roads (thin black lines) are also shown. Low and high activity equals 1–9 and ≥10 bat files per session, respectively.
Study design and acoustic surveys

Our study was designed to systematically sample the study area, covering a broad range of land cover types over a large landscape. We divided the study area into 1 × 1-km grid cells but excluded those that were >900 m above sea level, because little brown bats in our study area are not found above this elevation outside of migration (Slough and Jung 2008). We further reduced the study area to ≤1 km from maintained roads for sampling efficiency, although this biased our sampling toward developed areas and away from more remote parts of the study area. This yielded 621 grid cells, of which 210 were randomly selected for acoustic surveys. We generated three random sites within each grid cell using ArcGIS (ver. 10.4; ESRI, Redlands, California, USA). One site was selected for surveys; however, if the first random site could not be surveyed because of access constraints (i.e., physical barriers or lack of land owner permission), we selected the second or third site as needed. Sites in adjacent grid cells were ≥250 m apart.

We conducted acoustic surveys from 21 May to 12 September 2019, using 14 ultrasonic detectors (D500X; Pettersson Elektronik AB, Uppsala, Sweden) with external microphones mounted on 3-m poles. We passively monitored each site (n = 210) for three consecutive nights using a single detector programmed to record continuously from 30 min before sunset to 15 min after sunrise. For efficiency, we focused our survey effort on one part of the study area (north, east, south, or west) during each 3-night session, selecting a subset of grid cells to survey. To reduce spatial dependence (i.e., the same individual bats being detected at multiple sites on the same night), sites <3 km apart were not surveyed simultaneously.

For some species of bats, echolocation detection rates may be reduced by vegetative clutter (Patriquin et al. 2003), although little brown bat calls may be less affected due to their moderate frequency (>40 kHz) and high intensity (≥100 db; Jung et al. 1999, Patriquin et al. 2003). To minimize acoustic interference, we used two ultrasonic detectors in the most open habitat available within 100 m of the survey site (e.g., small forest clearings, open forest stands, waterbodies, or trails). We oriented microphones toward the direction of least clutter. Despite our precautions, acoustic data have inherent bias caused by imperfect detection and the inability to distinguish between individuals (Gibb et al. 2019). Regardless, bat activity is a metric of relative rather than absolute abundance, and it is useful for inferring habitat use (Hayes 2000, Law et al. 2015). Temperature loggers (MicroLite 5008L; Fourtec Technologies, Rosh Ha‘ayin, Israel) at a subset of 11 sites per night recorded ambient temperatures at 30-min intervals; sunset temperatures were later extracted. For sites without temperature loggers (n = 53), we took average sunset temperatures from sites monitored during the same 3-night period and within 10 km of the site with missing data.

We used Sonobat (ver. 4.3.0 for North American bats; Arcata, California, USA) to process the acoustic data. We first removed noise files with a frequency-based filter mechanism, and files were manually reviewed to check for screening errors. Next, we ran an autoclassification algorithm to identify bat calls to species or genus level (using the northeast British Columbia regional classifier) and manually vetted all files to ensure accurate separation of Myotis bat calls from non-Myotis calls. Because detection of other bat species in Yukon is rare (Slough et al. 2014), and because the calls of Myotis bats are difficult to identify to species with certainty, we assumed all Myotis-type calls were little brown bats. We used the number of acoustic files (3-s duration) containing bat calls as our metric of bat activity. We selected bat activity as our response variable because, as an index of relative abundance, it contains more detailed information than presence/absence data and may yield more accurate predictions about species distributions (Howard et al. 2014, Law et al. 2015).

Habitat covariates

We derived a number of spatial covariates that were hypothesized to be meaningful predictors of little brown bat activity (Table 1) using ArcGIS and R (ver. 3.6.3; R Core Team, Vienna, Austria). We used a combination of land cover data from the NASA Arctic-Boreal Vulnerability Experiment and R (ver. 3.6.3; R Core Team, Vienna, Austria).
Table 1. Description, mechanism, and predicted effect (positive or negative) of covariates hypothesized to influence the distribution of little brown bat (*Myotis lucifugus*) activity across an urbanizing boreal landscape near Whitehorse, Yukon, Canada.

| Covariate                        | Description                              | Mechanism                                                                 | Predicted effect | References                                      |
|----------------------------------|------------------------------------------|---------------------------------------------------------------------------|------------------|-------------------------------------------------|
| Forest                           | % cover woody vegetation >3 m tall       | Bats avoid cluttered forest, use residential/urban areas (more roosts)    | –                | Pauli et al. (2017), Thomas et al. (2019)       |
| Young forest                     | % cover forest <100 yr old               | Bats avoid young forest which is dense and cluttered, poor foraging habitat | –                | Crampton and Barclay (1998), Luszcz and Barclay (2016) |
| Urban                            | % cover urban, residential, and commercial areas with buildings | Buildings provide roosting habitat, particularly for maternity colonies | +                | Thomas and Jung (2019), Coleman and Barclay (2012) |
| Human footprint                  | % cover agriculture, mining, other industrial clearings | Human footprint increases habitat heterogeneity in homogenous forest landscape | +                | Yates and Muzika (2006), Pauli et al. (2017)    |
| Linear density                   | Density (km/km²) of cutlines and unpaved roads | Bats use small linear features as travel corridors | +                | Morris et al. (2010), Thomas and Jung (2019)    |
| Road density                     | Density (km/km²) of paved roads          | Bats avoid major roads because of wide openings, lights, and sound         | –                | Claireau et al. (2019), Jung (2020)             |
| City distance                    | Distance to Whitehorse urban core        | The city has abundant roosts; bats have energetic flight constraints      | –                | Coleman and Barclay (2012), Thomas and Jung (2019) |
| Still water                      | Distance to nearest lake, pond, or wetland | Open (still) water provides foraging and drinking habitat                 | –                | Broders et al. (2006), Rainho and Palmeirim (2011) |
| Watercourse                      | Distance to nearest river or stream      | Riparian areas are foraging habitat (abundant insects), travel corridors  | –                | Ford et al. (2005)                              |
| Building distance                | Distance to nearest building             | Buildings provide roosts; bats have limited dispersal from roosts         | –                | Rainho and Palmeirim (2011), Randall et al. (2014) |
| Canopy                           | Average % canopy openness                | Closed canopies are associated with clutter, reduced foraging efficiency  | +                | Ford et al. (2005), Thomas et al. (2019)        |
| Elevation                        | Elevation (m)                            | Sites at higher elevation are colder and have fewer insects               | –                | Slough and Jung (2008)                          |
| Temperature                      | Average sunset temp across three survey nights | Bat activity increases with ambient temperature                           | +                | Broders et al. (2006)                           |
| Survey period                    | Early: 21 May–20 July; Late: 21 July–12 September | Pups become volant during late period, which increases activity          | + Early – Late  | Talerico (2008), Thomas et al. (2019)           |
| Week                             | Chronological survey week (1–16)         | Accounts for weather, night length, and reproductive phenology            | N/A              | Slough and Jung (2008)                          |

(http://above.nasa.gov/) and anthropogenic disturbance mapping and hydrological data from Government of Yukon to develop a 9-class land cover raster (coniferous forest, deciduous forest, shrub, herbaceous, wetland, barren ground, water, urban/residential, and human footprint) with 30-m resolution. To assess the accuracy of land cover data, we compared the predicted land cover class at 156 random points with the true land cover class, derived from recent satellite imagery (Google Earth Pro, ver. 7.3.3; Google, Mountain View, California, USA); accuracy varied from 90% to 96% among classes. We used the landscapemetrics package in R to calculate percent cover of forests, urban/residential areas, and human footprint within a 100- and 1000-m radius of each acoustic survey site. We used datasets from the Government of Yukon to map and calculate the density of
linear disturbances (road, pipeline, transmission line, and railway) at each spatial scale. We determined the locations of the nearest buildings from satellite imagery, including houses, barns, cabins, and commercial structures. We used forest inventory data (Government of Yukon 2020, unpublished data) and forest fire history to determine forest age structure in our study area and calculated the percent young forest (≤100 yr old) at both spatial scales.

We used hemispherical photography (a fisheye lens coupled to a smartphone) to measure canopy openness at each site (Bianchi et al. 2017). Photographs were taken at each of the four cardinal locations, 10 m from the bat detector. We estimated canopy openness from a single cropped hemispheric image, with the caveat that canopy openness was likely overestimated (<5%) but that relative values were unbiased (Bianchi et al. 2017). We used Gap Light Analyzer (ver. 2.0;Frazer et al. 1999) to convert images to black-and-white, representing canopy and visible sky, and calculated the black-and-white pixel ratios to represent canopy openness.

**Data analysis**

We developed nine a priori hypotheses to test factors that potentially influence the distribution of little brown bat activity (Table 2). Specifically, we focused on how human development and natural landscape composition may affect potential roosting, foraging, and commuting habitat across two scales: local (100 m) and landscape (1000 m). We included a temporal covariate—survey period—to account for reproductive phenology. During the early period (21 May–20 July), female little brown bats give birth and rear pups, but during the late period (21 July–12 September) bat activity increases as juvenile bats become volant (Slough and Jung 2008). Temperature and survey period were included in all candidate models, as they previously explained a significant amount of variation in bat activity (Randall et al. 2011, Thomas et al. 2019).

We used ordinal logistic regression (proportional odds) models to evaluate our hypotheses (rms package in R). The ordinal response variable consisted of the summed bat activity at a site over the three survey nights, which was binned into three categories: zero activity, low activity (1–9 bat files), and high activity (≥10 files). We used an ordinal approach because bat activity data may be more informative than presence/absence data (Howard et al. 2014, Law et al. 2015), while simultaneously addressing issues caused by zero-inflated counts. We averaged temperature across the

**Table 2. Candidate ordinal regression models designed to test a range of factors hypothesized to influence the distribution of little brown bat (Myotis lucifugus) activity near Whitehorse, Yukon, Canada.**

| Mode name     | Hypothesis                                         | Model structure                         |
|---------------|----------------------------------------------------|-----------------------------------------|
| Urban         | Buildings provide artificial roosting habitat     | Building distance + City distance + City distance + Urban† + Temperature + Survey period Human footprint† + Temperature + Survey period |
| Human footprint | Development alters habitat through land cover change | Linear density† + Road density† + Temperature + Survey period Forest† + Young forest† + Canopy + Temperature + Survey period |
| Linear density | Linear disturbance creates travel corridors and/or fragments habitat | Still water + Watercourse + Temperature + Survey period |
| Forest        | Forest cover and composition affects potential commuting /foraging/roosting habitat | Survey period + Week                      |
| Water         | Waterbodies are potential foraging and drinking habitat |                                           |
| Phenology     | Bat reproductive phenology affects activity levels |                                          |
| Environment   | Environmental conditions affect activity levels    |                                          |
| Global model  | All covariates are important                      |                                          |
| Null model    | No covariates are important                       |                                          |

*Note: Covariates are described in Table 1.*  
† These covariates were evaluated at two spatial scales (100 and 1000 m).
three nights, because preliminary analysis showed little variation in nightly sunset temperatures during a given survey week. All continuous covariates were centered and scaled (i.e., converted to z scores). We tested ordinal regression assumptions (ordinality and proportional odds) using visual diagnostics (Guisan and Harrel 2000, Liu and Zhang 2018). To address potential multicollinearity, we calculated variance inflation factors (VIFs) for each candidate model (Dormann et al. 2013) and sequentially removed predictors with high VIFs (>3; Zuur et al. 2010). Thus, we removed forest (%) and urban (%) from models at the 1000-m scale.

We compared candidate models (Table 2) using an information-theoretic approach, with Akaike’s information criterion (AIC) adjusted for small sample size and overdispersion (QAICc, Burnham and Anderson 2002). We added interactive model terms when there was a biological rationale; for example, we tested the interaction between survey period and building distance because bats in maternal colonies disperse during the late survey period (Henry et al. 2002). Quadratic terms were also considered if we anticipated non-linear effects, and only retained if they reduced QAICc. We calculated model weights (wi) to aid interpretation. We included models with ΔQAICc ≤6 in the confidence set of models (Richards 2005), using only those models for inference. We evaluated effect sizes based on regression coefficients and 95% confidence intervals; covariates had a significant effect on bat activity if their confidence intervals did not overlap zero. We tested for spatial autocorrelation in the top models by plotting Moran’s I spatial correlograms of ordinal regression residuals (Liu and Zhang 2018; spdep package). When spatial autocorrelation was detected, we included a residual autocovariate term (Crase et al. 2012) using a distance-weighting scheme proposed by Bardos et al. (2015; spdep package in R). We used autologistic models for subsequent inference, if they reduced autocorrelation and improved model fit. Lastly, we evaluated the predictive capacity of our top (and global) models using leave-one-out cross validation, calculating Somer’s Dxy (Guisan and Harrel 2000) and area under the receiver operating characteristic curve (AUC). A model with an AUC of >0.7 was considered to have good predictive accuracy (Manel et al. 2002).

**RESULTS**

We recorded a total of 3070 acoustic files containing bat calls during 670 detector nights (survey nights by number of bat detectors). Our detectors malfunctioned at four sites, reducing our sample size to 206 sites. Only five (0.2%) bat files were attributed to non-*Myotis* bats and were omitted from the dataset. Bat activity in our study area was generally low, with substantial variation among sites. The number of little brown bat files recorded per site ranged from zero to 537 files (mean = 14.9 ± 55.2 SD). Zero bat calls were recorded at 83 sites (40%), while 87 sites (42%) were classified as low activity (1–9 bat calls) and 36 sites (18%) as high activity (≥10 bat calls; Fig. 1). Broad-scale spatial patterns in bat activity were apparent; sites with zero activity were concentrated in the northern half of the study area, whereas the central Whitehorse and southeast regions had the most high-activity sites (Fig. 1).

The confidence set included five models with QAICc ≤6, and the Water model, including covariates that represented foraging and drinking habitat, was the model best supported by the data (Table 3). Only additive models were used for inference; none of the interactive or quadratic model terms were retained, as they did not improve model fit. No single model had overwhelming support, although the top model received 41% weight, and the top three models (Water, Environment, and Forest; 1000-m scale) accounted for 86% of the total weight. Model selection suggested that 1000 m was the appropriate spatial scale for describing little brown bat distribution within the study area, although one model at the 100-m scale was included in the confidence set. Spatial autocorrelation was detected in the residuals of all confidence models and the global model at both spatial scales, with lag distances of 0.9–6.3 km (Appendix S1: Fig. S1). We added autocovariate terms, which reduced residual autocorrelation and improved fit (Appendix S1: Fig. S1). The top and global models had good predictive capacity (top model $D_{xy} = 0.46$, AUC = 0.74; global model, 1000 m, $D_{xy} = 0.51$, AUC = 0.76; Table 3).

Increasing distance from still water had a relatively strong negative effect on bat activity ($\beta = -0.66$, standard error [SE] = 0.17), such that sites further from water had lower activity...
(Figs. 2, 3). Elevation ($\beta = -0.29$, SE = 0.14), percent young forest (1000 m scale $\beta = -0.47$, SE = 0.13; 100 m scale $\beta = -0.37$, SE = 0.15), and human footprint (1000 m scale $\beta = -0.30$, SE = 0.14) also had significant negative influence on bat activity, while canopy openness had a positive effect ($\beta = 0.33$, SE = 0.14). Although included in the confidence set of models, distance to watercourse ($\beta = 0.08$, SE = 0.14), forest cover (100 m scale $\beta = -0.13$, SE = 0.18), and temperature (top model $\beta = 0.20$, SE = 0.14) had negligible and non-significant effects on bat activity. Survey period had a consistent positive effect across all models (top model $\beta = 0.79$, SE = 0.28; Fig. 2), indicating that bat activity levels were higher during the late survey period (Fig. 3).

To summarize, our results suggest that little brown bat activity was greatest in areas close to waterbodies, at low elevations, and with less young forest (≤100 yr old) and a smaller human footprint at the landscape scale (1000 m). At the local scale, bats used forest patches with open canopies.

**DISCUSSION**

The boreal forest is rapidly changing in response to climate change and human development (Brandt et al. 2013, Venier et al. 2014). Thus, there is a pressing need to identify and conserve the habitat of rare and threatened species within expanding anthropogenic landscapes. We sought to better understand the habitat requirements of the little brown bat, an endangered species in Canada, in an urbanizing region of the boreal forest. Our main finding was that the availability of anthropogenic roosts was not the driver of little brown bat distribution in our landscape, contrary to our hypothesis. Instead, landscape features that represented potential foraging habitat were the most important predictors of activity levels. Bats used areas near waterbodies, regardless of proximity to potential building roosts. Little brown bats also avoided young forest at the landscape scale—including regenerating burns—and used low-elevation areas with small agricultural and industrial footprints.

There was little evidence to support our hypothesis that bat activity would be driven by the distribution of buildings, which are associated with anthropogenic roosting habitat. Potential roost availability, represented by distance to nearest building, distance to urban core, and urban/residential footprint, had no perceptible influence on bat activity, in contrast with evidence from previous studies. Roosting habitat is thought to be a limiting factor for North American bats (Humphrey 1975, Fenton 1997), yet little brown bats are highly successful at exploiting

| Model                          | K  | Log likelihood | QAICc | $\Delta$QAICc | $\omega_0$ | AUC  | $D_{xy}$ |
|-------------------------------|----|----------------|-------|---------------|-----------|------|---------|
| Water                         | 7  | -197.05        | 224.15| 0             | 0.41      | 0.74 | 0.46    |
| Environment                   | 6  | -199.92        | 225.01| 0.86          | 0.27      | 0.71 | 0.41    |
| Forest (1000 m)               | 7  | -198.61        | 225.79| 1.64          | 0.18      | 0.71 | 0.41    |
| Human footprint (1000 m)      | 6  | -200.17        | 228.86| 4.71          | 0.04      | 0.68 | 0.36    |
| Forest (100 m)                | 8  | -200.17        | 229.62| 5.47          | 0.03      | 0.67 | 0.33    |
| Linear density (100 m)        | 7  | -202.99        | 230.40| 6.24          | 0.018     | 0.67 | 0.33    |
| Null model                    | 2  | -213.24        | 231.15| 6.99          | 0.015     | 0.50 | 0.00    |
| Linear density (1000 m)       | 7  | -204.05        | 231.52| 7.37          | 0.010     | 0.66 | 0.31    |
| Human footprint (100 m)       | 6  | -206.42        | 231.85| 7.70          | 0.009     | 0.65 | 0.30    |
| Global model (1000 m)         | 15 | -190.17        | 232.90| 7.75          | 0.009     | 0.76 | 0.51    |
| Urban (1000 m)                | 8  | -202.61        | 232.19| 8.04          | 0.007     | 0.65 | 0.30    |
| Urban (100 m)                 | 8  | -203.66        | 233.29| 9.14          | 0.004     | 0.64 | 0.28    |
| Global model (100 m)          | 17 | -190.89        | 237.43| 13.28         | 0.0005    | 0.70 | 0.40    |
| Phenology                     | 18 | -190.86        | 238.78| 14.62         | 0.0003    | 0.69 | 0.38    |

Notes: Confidence models (QAICc ≤ 6) are shown in bold. Columns are the number of model parameters (K), model log likelihood, QAICc, $\Delta$QAICc, $\omega_0$, area under the receiver operating curve (AUC), and Somer’s $D_{xy}$.
anthropogenic roosts, causing an increase in their abundance near urban or residential areas (Coleman and Barclay 2012, Johnson et al. 2019). In a previous study, we found evidence that little brown bats used rural villages as islands of roosting habitat, embedded in a matrix of wilderness where roosts were scarce (Thomas and Jung 2019). We expected a similar result in near Whitehorse, which comprises an urban to rural gradient, from the downtown core to the sparsely populated areas around the city periphery. Little brown bats used the full urban–rural gradient, evidently never reaching a point where urban development was prohibitive, nor where building roosts were too scarce at the other end of the spectrum.

We suspect that the urban island phenomenon was not observed because anthropogenic roosting habitat was adequately available throughout the urban–rural gradient of our study area. We did not sample any wilderness; even in the most rural areas, low-density residential developments were present, although sparse. By necessity, our site selection was biased toward areas near maintained roads, resulting in undersampling of remote areas. The maximum distance between an acoustic sampling site and a potential building roosts was 4.7 km, and little brown bats are known to travel >5 km from their roosts to reach foraging areas (Randall et al. 2014). A small number of buildings may be enough to support little brown bats on a landscape, if they are suitable for roosting (Shively and Barboza 2017, Johnson et al. 2019), as one building can host a maternity colony of hundreds of bats (Slough and Jung 2020).

Fig. 2. Regression coefficients (points) and 95% confidence intervals (error bars) from the confidence set of models ($\Delta$AIC$_C \leq 6$) predicting little brown bat (*Myotis lucifugus*) distribution near Whitehorse in Yukon, Canada. Different symbols are used for each model, which are described in Table 2. The size and direction of covariate effects are indicated by the coefficient value. Covariates with confidence intervals that do not overlap zero are considered to have a significant effect on bat distribution.
Alternatively, natural roosting structures may have supplemented anthropogenic roosts in the rural, peripheral parts of our study area, where buildings were less available. Little brown bats roost in trees and rock crevices in the boreal forest (Crampton and Barclay 1998, Jung et al. 2004, Olson and Barclay 2013, Randall et al. 2014), but observations of maternity colonies in natural structures are rare compared with anthropogenic roosts (Slough and Jung 2008). The absence of data on natural roosts is a limitation; however, we expect that roosting trees are scarce in our study area, given the prevalence of young forest and regenerating burn, where suitable large-
diameter trees and snags may be scarce (Crampston and Barclay 1998, Jung 2020). Interestingly, bat activity levels in this study were substantially lower than in rural villages with much smaller human populations and urban footprints (Thomas and Jung 2019). This may be attributed to the broad distribution of potential roosts in the Whitehorse area; conversely, anthropogenic roosts are confined to a comparatively small area within rural villages, perhaps resulting in higher concentrations of bat activity.

Little brown bat activity was strongly influenced by the distribution of waterbodies and mature patches of forest, which may have been important foraging habitats. Within the urban–rural gradient, proximity to lentic ecosystems (wetlands, ponds, and lakes) was the most important predictor of bat activity, consistent with other studies (Broders et al. 2006, Rainho and Palmeirim 2011, Straka et al. 2016, Ancillotto et al. 2019). Waterbodies are a source of aerial insect prey (Fukui et al. 2006, Salvarina 2016), which may be relatively scarce in urban environments, particularly where housing densities are high (Threlfall et al. 2012). Foraging habitat, such as waterbodies, is vital to the persistence of bat populations (Fenton 1997), yet it tends to be patchily distributed on the landscape, which in turn may influence patterns of bat distribution (Ekman and Jong 1996). Waterbodies also provide drinking habitat, another critical resource for bats that is important in arid climates (Seibold et al. 2013, Salvarina 2016, Russo et al. 2019) such as our study area, particularly for lactating female bats (Adams and Hayes 2008). We did not distinguish between drinking, foraging, and general activity, so drinking activity may have contributed to the strong association with waterbodies. Regardless, it is apparent that water is important on the landscape. Relatively pristine waterbodies are abundant in and around Whitehorse. While others have identified small patches of remnant foraging habitat in highly urbanized landscapes (Gehrt and Chelsvig 2004, Straka et al. 2016, Ancillotto et al. 2019), there is a unique opportunity to proactively identify and protect habitat from future development in the boreal forest, where the landscape is still relatively intact.

Forests are also potential foraging habitat for little brown bats (Patriquin and Barclay 2003, Broders et al. 2006). In the northern boreal region, bats may feed on forest arthropods at times when aquatic aerial insects are scarce (Kaukas and Barclay 2018, Shively et al. 2018). Forest is the dominant land cover class in the study region, on average comprising 56% of the area around each site (within 1 km), but the quality of habitat likely varies with forest age. As we predicted, bats responded negatively to the amount of young (≤100-yr-old) forest at the landscape scale. In the northern portion of the study area, much of the forest is regenerating from a major wildfire in 1958, the footprint of which largely coincides with areas of zero or low bat activity. Regeneration of boreal forests after fire is exceedingly slow due to the cool and semi-arid climate (Hogg and Wein 2005), and forests ≤100 yr old maintain young forest characteristics such as small stem diameters, high stem densities, and lack of structural diversity. Young, dense forests tend to have more vegetative clutter (Jung et al. 1999, Luscz and Barclay 2016), which reduces flight efficiency and inhibits echolocation during foraging and navigation (Schnitzler and Kalko 2001). Little brown bats may have a tree density threshold below which occupancy declines (Thomas et al. 2019). Accordingly, bats in our study area used open canopies, which tended to occur in mature forests with low stem densities and natural gaps (Jung et al. 1999). Mature boreal forests also have more suitable roosting trees than young forests (i.e., larger-diameter live trees and snags with cavities or sloughing bark; Crampton and Barclay 1998, Olson and Barclay 2013, Fabianek et al. 2015). While our study was not able to distinguish between the relative importance of foraging and roosting activity in forests, evidence indicates that little brown bats in the boreal region tend to forage in forests (and over waterbodies) and roost in buildings (Talerico 2008, Randall et al. 2014, Thomas and Jung 2019, Slough and Jung 2020).

Little brown bats were affected by other types of human disturbance aside from urbanization (agriculture, mining, quarries, and other forest clearings) at the landscape scale; however, the direction of this effect was opposite to our prediction. We expected that artificial forest clearings would increase habitat heterogeneity and foraging opportunities across the forest-dominated landscape (Yates and Muzika 2006, Pauli
et al. 2017). We also thought bats would benefit from edge habitat created by forest clearings, which they may use for foraging and commuting between habitat patches (Grindal and Brigham 1999, Hein et al. 2009). In contrast, we found that bat activity decreased in areas with a large human footprint, which was predominantly agriculture. Little is known of how bats respond to agriculture in the boreal forest, where farming is less prevalent than in temperate biomes (although climate warming may change this; King et al. 2018, Hannah et al. 2020). At high latitudes, where summer nights are short and well illuminated (particularly around solstice), bats may avoid openings because they prefer the protective cover and relative darkness of forest, which may be safer from predators (Talerico 2008). This behavior might explain the observed avoidance of agricultural areas in our study region. Agricultural areas may also be associated with reduced abundance of insect prey (Williams-Guillen et al. 2016).

CONCLUSIONS

Our study helps to explain the distribution and habitat requirements of the endangered little brown bat in an urbanizing region of the boreal forest. This knowledge may facilitate habitat management and conservation if incorporated into future urban planning. We provided evidence that potential foraging habitat—such as waterbodies and mature forest—drives the spatial distribution of bats in urban and rural areas where anthropogenic roosting habitat is relatively abundant. Yet, despite intensive survey effort and a large sample size, our habitat models lacked some explanatory power, likely due to confounding factors, which are common in landscape-scale studies. In addition, bats are a taxonomic group with complex behaviors that are still poorly understood, including those species in the boreal forest (Jung et al. 2014). For example, lack of information about roosting habitat in our study area was a limitation. Better knowledge of both natural and anthropogenic roosts would likely have benefitted our interpretation of habitat models. A more detailed understanding of the type of waterbodies preferred by foraging bats would also be beneficial. Although our findings may be broadly applicable to other urbanizing landscapes in the boreal forest because of our mechanistic approach, our study is from a single urban area. Similar data from other urbanizing landscapes in the boreal forest area would be informative (Li et al. 2019). Our study suggests that waterbodies and mature forests should be secured through stewardship agreements with land owners and protected within urban and regional land-use plans. Fortunately, there remains substantial opportunity for proactive conservation of bat habitat across relatively intact boreal landscapes. This is in contrast to reactive and often costly conservation and management of small remnant patches of habitat that are characteristic of more developed temperate regions (Russo et al. 2016, Trubitt et al. 2019). Given the growing list of human-caused threats to bats, including climate change, natural resource development, disease, and urbanization (Voight and Kingston 2016), proactive management of their key habitats is more important than ever.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3457/full