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The best watering hole in town: Characteristics of ponds used by an endangered bat in an urbanizing boreal landscape

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ABSTRACT

Small waterbodies, or 'ponds', have an important role in maintaining biodiversity and ecosystem services, particularly where freshwater sources are limited, such as arid or some urban environments. However, studies that examine the use of ponds by terrestrial wildlife are limited. In the boreal forest, aquatic habitats are important drinking and feeding habitat for endangered little brown bats (*Myotis lucifugus*), and their relative value likely varies based on their characteristics, such as size, adjacent land cover type, anthropogenic disturbance, and proximity to other water bodies. We examined the characteristics of ponds used by little brown bats along an urban-rural gradient in Yukon, Canada. We used ultrasonic detectors to sample 99 ponds and generalized linear mixed models to determine whether ponds with certain characteristics received more bat activity than others. Ponds were important habitat for little brown bats, as 98% of the ponds we sampled were used. Bats selected ponds based on local rather than landscape level factors, and there was less bat activity at ponds surrounded by additional open water/wetland habitat, which was contrary to our prediction. Ponds that were surrounded by additional open water/wetland habitat may have been too exposed for bats at high latitudes, where nights are short and not completely dark. Isolated ponds that are darker, such as those surrounded by mature forest, may be particularly valuable for little brown bats at high latitudes that exhibit risk-sensitive foraging. We suggest that ponds of comparatively high value for endangered little brown bats be further identified and that these ponds be protected from development, draining, and degradation, and the surrounding mature forest remains intact. More broadly, recognition and conservation of ponds and their surroundings as key habitat for species of bats requires further attention. Understanding the characteristics of ponds selected by threatened bats can help inform conservation priorities and measures that ensure the aquatic habitats they require are maintained in developing landscapes.

1. Introduction

Small waterbodies, or 'ponds' are increasingly recognized for their role in maintaining biodiversity and providing ecosystem

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services, particularly where freshwater environments are limited (e.g., arid landscapes) or may be degraded (e.g., urban and industrial landscapes; Hill et al., 2017, Ancillotto et al., 2019, Zamora-Marin et al., 2021). Ponds may substantially enhance local biodiversity and provide critical ecosystem services (Biggs et al., 2017). Because of their small size, ponds are particularly sensitive to human disturbance and impacts of climate change relative to larger water bodies; however, they are often overlooked in land use planning processes (Hill et al., 2018). Their contribution to local biodiversity and landscape-level processes remains less known than other types of water bodies, particularly in North America (Biggs et al., 2017). Yet, the value of including small scale landscape features that are associated with diverse taxa, such as ponds, in conservation planning processes has been recognized (Crous et al., 2013).

The use of ponds by terrestrial wildlife is not well understood, particularly outside Europe. While ponds may provide a source of water, food, and shelter for numerous species of wildlife, the relative importance of individual ponds likely varies based on characteristics such as size, adjacent land cover type, anthropogenic disturbance, and proximity to other water bodies (Bonifait and Villard, 2010). Additionally, beaver (*Castor canadensis*) activity may also have an influence on local biodiversity, through ecological engineering activities that increase habitat heterogeneity, such as the creation or maintenance of ponds (Grover and Baldassarre, 1995, McCall et al., 1996, Rosell et al., 2005, Hood and Larson, 2014, Nummi et al., 2019).

Aquatic habitats are important for insectivorous bats (e.g., Seibold et al., 2013, Salvarina, 2016, Clare et al., 2011, Gaulke et al., 2023) as drinking habitat. They also provide key foraging habitat for many species, given that they typically support higher abundances of aerial arthropods than terrestrial habitats (Fukui et al., 2006, Metcalfe et al., 2023). Correspondingly, ponds are likely important habitat features for many species of bats, particularly in landscapes where freshwater habitat is limited (Francl, 2008, Razgour et al., 2010, Stahlschmidt et al., 2012, Lison and Calvo, 2014, Ancillotto et al., 2019, Nelson and Gillam, 2020, Lehrer et al., 2021). Yet, aquatic habitats used by bats are threatened globally by anthropogenic development (Korine et al., 2016).

Little brown bats (*Myotis lucifugus*) were once one of the most common bat species in temperate and boreal biomes of North America. However, in recent years their populations have declined dramatically in the eastern half of their range largely due to white nose syndrome, as disease caused by the fungus (*Pseudogymnoacus destructans*; Frick, 2010, Cheng et al., 2021), and they are legally listed as endangered in Canada (ECCC, 2018). Consequentially, identifying and ensuring critical habitat for roosting and foraging remains on the landscape is key for remnant and recovering populations of little brown bats (ECCC, 2018).

Previous work on endangered little brown bats in the boreal forest has shown that habitat use is primarily driven by putative foraging habitat, (i.e., water bodies; Thomas et al., 2021). However, the types and characteristics of water bodies that are preferred by little brown bats in the boreal forest remain unknown. Understanding the characteristics of ponds selected by little brown bats can help inform conservation priorities and measures that ensure the aquatic habitats they prefer are maintained in developing landscapes. To aid in this regard, we conducted surveys using ultrasonic detectors to assess the characteristics of ponds selected by little brown bats in an urbanizing boreal landscape. Ponds sampled occurred along an urban-rural gradient and included those ranging from human-made (e.g., quarries, dug-outs, etc.) to those with minimal to no human influence or disturbance.

We hypothesized that the characteristics of ponds, such as size, shape, or beaver activity, would influence their use by little brown bats. We predicted that larger ponds with more complex shorelines and beaver activity would be selected by bats because insect

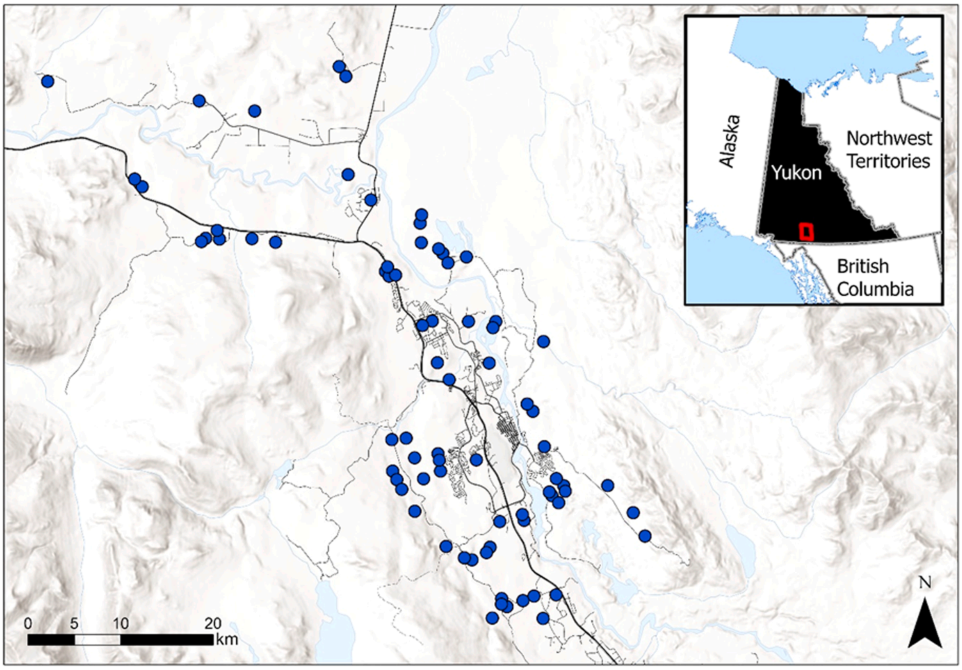

Fig. 1. Location of 99 ponds sampled for little brown bat (*Myotis lucifugus*) activity near Whitehorse, Yukon, Canada, during June to September 2020.

activity is likely increased in ponds that have more diverse aquatic microhabitat due to increased edge habitat or beaver modifications (Ciechanowski et al., 2011, Nummi et al., 2011). We also predicted that adjacent land cover may additionally influence bat activity at ponds. Specifically, we anticipated that ponds surrounded by mature forest (potential roosting habitat) would be more used by bats, and ponds that are adjacent to other ponds or wetlands, may also be attractive to bats because of increased foraging opportunities (Straka et al., 2016, Vasko et al., 2020). Finally, we predicted that increased human disturbance would reduce their use by little brown bats, due to light and noise pollution reducing foraging efficiency, and reduced insect abundance due to wind exposure and pollution (Stone et al., 2015, Straka et al., 2016).

2. Methods

2.1. Study area and species

Our study was conducted in the boreal forest, within a 30-km radius of the City of Whitehorse, Yukon, Canada (Fig. 1). The Yukon is largely undeveloped, and Whitehorse is the largest concentration of people (approx. 33,000 people; 79% of Yukon's population; Yukon Bureau of Statistics, 2020) and infrastructure in the region. Thus, our study area can be characterized as an urban island within a wilderness matrix (e.g., Thomas and Jung, 2019).

Our study area was within the Boreal Cordillera Ecozone, and located in a broad U-shaped valley. Common tree species included white spruce (*Picea mariana*), lodgepole pine (*Pinus contorta*) and trembling aspen (*Populus tremuloides*). Residential, agricultural, and industrial developments were the primary anthropogenic disturbances. The climate was sub-arctic and semi-arid, with snow typically persisting in valley bottoms from mid-October to mid-April, and lakes remaining frozen until May. Mean temperature and precipitation recorded at the Whitehorse weather station during our study (July 2020) was 13.8°C and 65 mm, respectively (Government of Canada; Whitehorse weather station; weather.gc.ca).

'Pond' is an ambiguous term with no universally accepted definition. In their extensive review on the importance of small waterbodies on biodiversity and ecosystem services, Biggs et al. (2017), defined small waterbodies based on their size. Ponds were defined as permanent or seasonal water bodies from 1 m^2 to 5 ha, but definitions up to 10 ha in size have also been used (Oertli et al., 2002, 2005). The Ramsar Convention adopted a threshold of 8 ha to demarcate between ponds and lakes (Ramsar Convention Secretariat, 2013). We defined a pond in our study area as being $\leq$6 ha.

Surveys using ultrasonic detectors in the Yukon reported that little brown bats were by far the most common bat species in the territory, with other species present but rarely detected (Slough and Jung, 2008, Jung et al., 2006, Slough et al., 2014, Thomas and Jung, 2019). 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, maternity colonies are often reported in anthropogenic structures and may include hundreds of adults, although natural roosts in dead trees or rock crevices are also used (Crampton and Barclay, 1998, Olson and Barclay, 2013, Randall et al., 2014, Slough and Jung, 2020). Births occur in early July, and maternal colonies tend to dissipate by late July once juveniles are volant. Males typically roost alone or in small groups in forest throughout the summer (Jung et al., 2004, Broders et al., 2006). Little brown bats are obligate insectivores, and typically capture their prey by aerial hawking over waterbodies or at forest openings or edges (Grindal and Brigham, 1999, Broders et al., 2006), but they also glean spiders from tree branches within high latitude boreal forest when aerial arthropods are not available (Shively et al., 2018).

2.2. Acoustic surveys

We limited our study area to $\leq$30 km of the city centre to focus our effort specifically at an urban-rural gradient. We applied a second filter to limit our study area to $\leq$900 m above sea level, because little brown bats in our study area are not known above this elevation outside of migration (Slough and Jung, 2008). Within these sampling constraints, we identified all ponds between 0.2 and 6.0 ha (n = 146) in GoogleEarth in our study area and randomly selected a subset of 110 ponds as our sample.

We conducted passive acoustic surveys for little brown bats from 3 June to 1 September 2020, using nine ultrasonic detectors (D500X; Pettersson Elektronik AB, Uppsala, Sweden) with external microphones mounted on 3 m tall poles. A single detector programmed to record continuously from 30 min before sunset to 15 min after sunrise was set at each pond. We aimed to sample each pond for five consecutive nights, however logistical constraints and equipment failures resulted in our sampling varying from 3 to 7 nights (see Results). To reduce spatial autocorrelation (i.e., the same individual bat being detected at multiple ponds on the same night), ponds <2 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, and maximize detections, we placed ultrasonic detectors along the shoreline and oriented microphones towards the centre of each pond. Temperature loggers (MicroLite 5008 L, Fourtec Technologies, Rosh Ha'ayin, Israel) recorded ambient temperatures at 30-min intervals, and we later extracted the temperature at sunset. If a temperature logger failed, we used the average sunset temperature calculated from the ponds within an 8 km radius that were monitored on the same nights.

We used Sonobat (ver. 4.3.0 for North American bats; Arcata, CA, USA) to process acoustic data using the same protocols as Thomas et al. (2021). We first removed noise files with a frequency-based filter mechanism, then 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 for Sonobat), and manually vetted all files to ensure accurate separation of *Myotis* bat calls from non-*Myotis* calls. Because detection of species other than little brown bats in our region is exceedingly rare (Slough et al., 2014), and because the calls of *Myotis* bats are difficult to identify to species with certainty (e.g., Jung et al., 1999, Thomas and Jung, 2019), we assumed all *Myotis*-type calls were from little brown bats. As it was not central to our objectives, we did not differentiate calls of different types (e.g., feeding, traveling, social). We used the number of acoustic files (3-second duration) containing bat calls per night as our metric of bat activity, which represents an index of relative abundance (Howard et al., 2014, Law et al., 2015).

2.3. Habitat covariates

We derived a small suite of covariates that we expected to be meaningful biological determinants of pond use by little brown bats (Table 1). We used forest inventory data (scale 1:5000; Government of Yukon 2015) to determine land cover classes and forest age structure in our study area and calculated the percent of mature forest (≥90 years old), open water/wetlands, and human footprint (e.g., roads, buildings, industrial and agricultural clearings). We extracted land cover covariates at two scales: a 1000 m buffer around pond perimeters, because previous work on little brown bats in the study area showed it had a strong predictive power to explain landscape level activity of bats (Thomas et al., 2021), and a 100 m buffer to examine if finer scale habitat around the pond shoreline affected bat activity. In addition to land cover covariates, we obtained elevation from a Digital Elevation Model (DEM) for each pond and calculated the pond area (ha) and perimeter length (m). We calculated the Shoreline Development Index (SDI; Hutchinson, 1957) for each pond as a measure of the tortuosity of the shoreline of ponds. Shorelines with greater tortuosity provide more edge habitat per area, and edges are preferred foraging habitats for bats, especially on windy nights. The SDI is the ratio of shoreline length to the length of the circumference of a circle of area equal to the area of the pond (Hutchinson, 1957). An SDI of zero represents a pond that is perfectly round, and SDI increases as the shoreline becomes more indented. We used ArcGIS to obtain all spatial covariates. We also determined the influence of beavers at each pond, based on field observations when setting up or retrieving ultrasonic detectors, as well as from an aerial survey conducted at the end of our sampling period (Jung et al., unpublished data). We classified a pond as influenced by beaver if we observed that the pond environment had been altered (e.g., flooded) due to beaver activities.

2.4. Analyses

We developed *a priori* hypotheses to determine which characteristics influenced little brown bat activity at sampled ponds (Table 2) and used generalized liner mixed models (GLMM) to compare candidate models. Specifically, we focused on how pond characteristics in combination with the surrounding landscape composition may affect bat activity at two spatial scales: local (100 m) and landscape (1000 m). To account for multiple recording nights at each site, pond ID was included as a random effect in all GLMMs. A temporal covariate of survey period was also included as a random effect in our models to account for reproductive phenology, given that phenology has previously explained significant variation in bat activity in or near our study area (Randall et al., 2011, Thomas et al., 2021). We split our study period into early (21 May to 20 July) and late (21 July to 12 September) periods, based on previously identified dates for our region (Slough and Jung, 2008). The early period was when females were in late gestation or rearing non-volant pups, and the late period was when pups became volant and both pups and females spent less time in their roost and were more active on landscape. Temperature at sunset was included in all models to account for the temporal effect it may have on bat activity each night. We used GLMMs and a model selection framework to evaluate 23 candidate models, including global models at 100 m and

Table 1
Description of covariates expected to influence activity of little brown bats (*Myotis lucifugus*) at ponds, with ecological mechanisms, and the predicted effect of each covariate.

Covariate	Description	Mechanism	Predicted Effect	References
Pond size	Open water area (ha)	Increased resources (drinking, prey, access)	Positive	Harrison (2021), Razgour et al. (2010)
Elevation	Elevation above sea level (m)	Ponds at higher elevation are less productive.	Negative	Slough and Jung, (2008)
Shoreline Development Index (SDI)	Shoreline shape complexity: 0 index is perfectly round pond.	Complex shoreline (tortuosity) increases edge habitat in feeding areas	Positive	Nelson and Gillam, (2017)
Mature forest	Forest ≥90 yrs old (%; 100 m & 1000 m buffer around pond)	Security and roosting habitat, less cluttered than young forest	Positive	Luszcz and Barclay, (2016), Thomas et al. (2021)
Open water/wetland	Water/wetland habitat (%; 100 m & 1000 m buffer)	Increased and connected resources (drinking, prey, reduced isolation)	Positive	Mas et al. (2021)
Human footprint	Anthropogenic disturbance (%; 100 m & 1000 m buffer)	Decreased habitat heterogeneity, environmental/light/sound pollution	Negative	Thomas et al. (2021) Barre et al. (2023) Seewagen et al. (2023)
Beaver Effect	Is the pond modified by beaver? (Y/N)	Increased habitat heterogeneity for prey, feeding	Positive	Nummi et al. (2019)
Survey period	Breeding phenology (early=prior to 20 July, late=after 20 July)	Bat population increase once juvenile bats are volant; increased bat activity	- Early + Late	Thomas and Jung, (2019); Thomas et al. (2021) Talerico, (2008)
Survey temp	Temperature at sunset during each survey night (°C)	Bats and insect prey more active when warmer	Positive	Broders et al. (2006)

Table 2
A priori hypotheses about the factors influencing bat activity at ponds, and the candidate models for comparing these hypotheses. Covariates are described in Table 1. Survey night temperature (T) is included in all models, except Null. Survey period and Pond ID are included in all models as random effects.

Model Name/Hypothesis	Model Structure
Pond Characteristics	Pond Size + SDI + Elevation + T
Beaver	Beaver +T
Forest	Mature Forest + T
Human	Human + T
Water	Water/Wetland + T
Temperature	T
Pond Characteristics and adjacent Water	Pond Size + SDI + Elevation + Water/Wetland + T
Pond Characteristics and adjacent Forest	Pond Size + SDI + Elevation + Mature Forest + T
Pond Characteristics and adjacent Human	Pond Size + SDI + Elevation + Human + T
Pond Characteristics and Beaver	Pond Size + SDI + Elevation + Beaver + T
Pond Characteristics, Beaver, and adjacent Water	Pond Size + SDI + Elevation + Water/Wetland + Beaver + T
Pond Characteristics, Beaver, and adjacent Forest	Pond Size + SDI + Elevation + Mature Forest + Beaver + T
Adjacent Water and Human	Water/Wetland + Human + T
Adjacent Water and Forest	Water/Wetland + Mature Forest +T
Beaver and adjacent Forest	Beaver + Mature Forest + T
Beaver and adjacent Water and Forest	Beaver + Water/Wetland + Mature Forest + T
Global Model	Pond Size + SDI + Elevation + Mature Forest + Water/Wetland + Human + Beaver + T

1000 m scales and a null model, which included only the intercept. Pond ID and survey period were random effects in all models. Because we were also interested in the influence of individual covariates related specifically to pond characteristics, we further used GLMMs to assess the relative importance of each pond covariate (pond size, SDI, elevation, and beaver activity) on nightly bat activity. We included pond ID and survey period as random effects.

Continuous covariates were centered and scaled prior to modelling (Schielzeth, 2010). Models were fit using a zero-inflated generalized Poisson response with package 'glmmTMB' (Brooks et al., 2017) in R (ver. 4.2.1; R Core Team, 2022). We assessed collinearity between variables by calculating variance inflation factors (VIFs) for each candidate model (Lüdecke et al., 2021), ensuring there was minimal correlation between covariates included in the same model (VIF < 2). We used Akaike's information criterion corrected for small sample sizes (AIC_c) to select the best model from each candidate set, with models with $\Delta AIC_c \leq 2$ considered competitive (Burnham and Anderson, 2002). We calculated model weights (w_i) for the competitive models to aid in interpretation. We evaluated effect sizes based on model-averaged regression coefficients (β) and 95% confidence intervals (CI) calculated for all models with weights summing to 0.95 but eliminated any models with uninformative parameters (i.e., unnecessarily complex versions of simpler, nested models that receive a lower weight than the simpler model; Richards, 2008, Arnold, 2010). Model-averaged covariates were considered to have a significant effect on nightly bat activity if their confidence intervals did not overlap zero. We tested for spatial autocorrelation of the residuals (RAC; Crase et al., 2012, Bardos et al., 2015) in the top-supported models and global models by plotting Moran's I spatial correlograms (Dormann et al., 2013) using package 'spdep' (Pebesma and Bivand, 2023). We found no significant spatial autocorrelation of residuals in any of our models.

3. Results

We sampled 99 ponds with a mean of 5.3 ± 1.2 (SD) sampling nights at each pond and recorded 61664 bat files during 527 survey nights. Little brown bats were present at 98% of the ponds (n = 97). We recorded a mean of 142 ± 263 (SD) bat files per night at each pond (range = 0–2084). For analyses, we selected all ponds with ≥3 nights of data and removed nights when temperature dropped below 5°C (Thomas and Jung, 2019), which resulted in 516 effective survey nights at 96 ponds.

The best-fit model of nightly bat activity was an additive model including pond characteristics (pond size, SDI, elevation), adjacent open water/wetland cover, and beaver activity (Table 3). Three other models were within a ΔAIC_c of <2, including (1) an additive model of adjacent open water/wetland and mature forest cover, and beaver activity ($\Delta AIC_c = 1.20$), (2) an additive model of pond characteristics and adjacent open water/wetland ($\Delta AIC_c = 1.28$), and (3) a simple model of adjacent open water/wetland ($\Delta AIC_c =$

Table 3
Generalized linear mixed models describing the activity of little brown bats (*Myotis lucifugus*) relative to ponds and surrounding habitat in Yukon, Canada. Only those models that contributed to model weight are reported. The full candidate model set is available in Appendix S1.

Model	K	AICc	ΔAICc	w_i	Log likelihood
Pond Characteristics + Water + Beaver	11	5128.82	0.00	0.34	-2553.15
Water + Forest + Beaver	9	5130.02	1.20	0.18	-2555.83
Pond Characteristics + Water	10	5130.10	1.28	0.18	-2554.83
Water	7	5130.53	1.71	0.14	-2558.16
Water + Forest	8	5132.12	3.30	0.06	-2557.92
Water + Human	8	5132.55	3.73	0.05	-2558.13
Global	13	5132.96	4.14	0.04	-2553.12

1.71). No single model had significant support, although the top model received 34% weight, and the top four models combined accounted for 84% of the total weight. All top models were at the 100 m scale indicating that pond characteristics at the local scale were better at describing little brown bat activity at our ponds than those at a landscape level.

Bat activity increased at ponds with less open water/wetland land cover (β = −0.59, CI = −0.88 – −0.30), which is opposite to our predictions. Pond size had a marginal positive effect on bat activity (β = 0.17, CI = −0.06 – 0.40). Although included in the best-supported models, SDI (β = 0.04, CI = −0.25 – 0.33), elevation (β = 0.04, CI = −0.21 – 0.29), mature forest cover (β = 0.02, CI = −0.23 – 0.27), and beaver activity (β = 0.36, CI = −0.23 – 0.95) had negligible and non-significant effects on bat activity (Fig. 2). Survey temperature had a significant positive effect across all models (β = 0.13, CI = 0.05 – 0.21), as expected.

Our univariate analysis of specific physical pond characteristics showed that bat activity was best explained by pond size (β = 0.30, CI = 0.06 – 0.54), receiving 82% model weight. Elevation (β = 0.00, CI = 0.00 – 0.00), SDI (β = 0.06, CI = −0.65 – 0.77), and beaver activity (β = 0.03, CI = −0.56 – 0.62) had negligible effects on bat activity on their own (Fig. 3).

To summarize, our results indicated that little brown bat activity was influenced more by the characteristics of ponds at a local rather than landscape scale. Bat activity was negatively affected by the open water/wetland habitat surrounding the pond, and larger ponds may be preferential to little brown bats than smaller ponds. Within this context, ponds that were surrounded by mature forest and where beaver were active may positively influence bat activity.

4. Discussion

We examined the importance of ponds for endangered little brown bats in an urbanizing, semi-arid region of the boreal forest. A key finding from our data was that ponds are important habitat for bats. Little brown bats were active at 98% of the ponds we sampled, whereas they were present at 60% of randomly-selected sites during a previous acoustic survey in our study area (Thomas et al., 2021). This difference indicates that ponds were hot spots of bat activity in the urbanizing boreal landscape where our surveys occurred. Ponds were likely used as both drinking and foraging habitat, although we did not explicitly differentiate between the two.

Another key finding from our study was that the relative value of specific ponds for little brown bats is determined by the characteristics of each pond and the immediate surroundings (100 m scale), rather than landscape-level factors. This result is contrary to our prediction and an earlier study that reported when sampled randomly across our study area, activity by little brown bats was influenced by covariates at the landscape level (1000 m scale; Thomas et al., 2021). In another acoustic study of boreal bats in our region (Thomas and Jung, 2019), little brown bats were concentrated near human settlements, likely due to the availability of buildings as roosting habitat, indicating that urban and peri-urban areas, in general, are likely attractive for bats. This finding has also been seen elsewhere at higher elevations at more southern latitudes where environmental conditions, other than the light regime, are similar to our study area (e.g., Johnson et al., 2019, Micalizzi et al., 2023). Thus, landscape-level habitat selection by little brown bats in our study area may have already occurred, and local bat populations choose ponds for feeding and drinking based on fine-scale characteristics (DeCesare et al., 2012), such as distance from the roost and pond-specific characteristics.

Considering the physical characteristics of the pond (size, shape, and elevation), only size had an influence on little brown bat activity, whereas elevation and pond shape (SDI) were insignificant. Other studies have reported larger pond size as important for bats (Downs and Racey, 2006, Razgour et al., 2010, Harrison, 2021). Larger ponds may have more wind which results in aerial arthropods (prey) congregating along pond edges, where it is easier for bats to locate them as they fly along the ecotone. Edge-biased distribution has been documented for many flying arthropods, and similarly, little brown bats have been shown to exhibit positive response to edges while feeding (Jantzen and Fenton, 2013, Nelson and Gillam, 2017, Nguyen and Nansen, 2018, Caitano et al., 2020). Pond shape did not explain bat activity patterns, which was surprising because we expected that shoreline complexity may increase the availability of sheltered shorelines for bats to hunt. However, invertebrate richness and diversity are generally related to waterbody size,

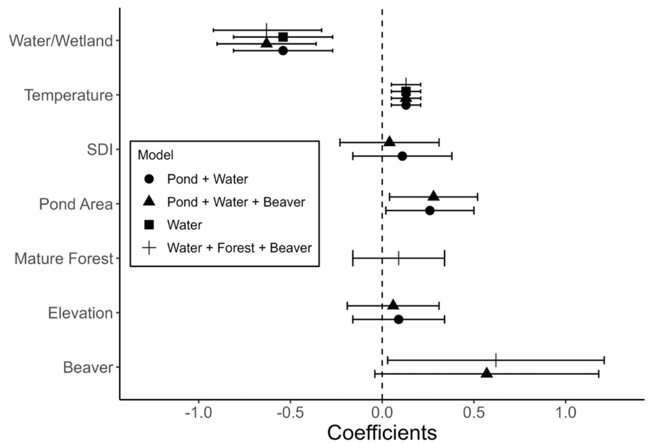

Fig. 2. Model-specific regression coefficients and 95% confidence intervals from the top-supported models ($\Delta AIC_c < 2$) predicting little brown bat (*Myotis lucifugus*) activity at ponds in Yukon, Canada.

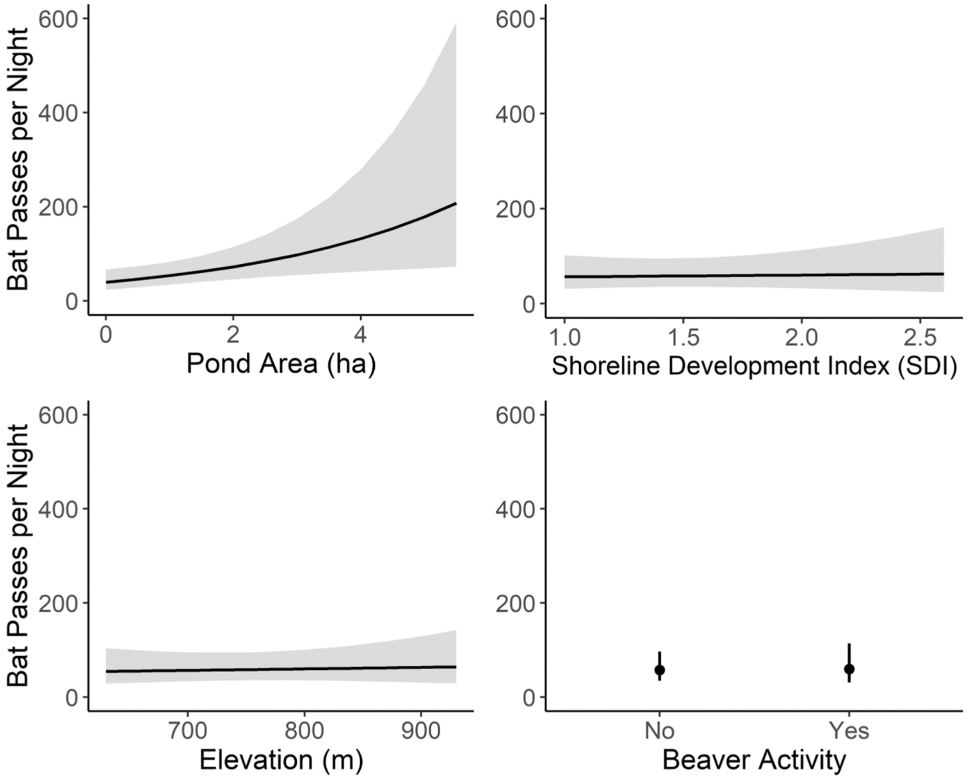

Fig. 3. Predicted activity of the little brown bat (*Myotis lucifugus*) in relation to pond characteristics in Yukon, Canada. Solid lines show the predicted covariate effect with 95% confidence intervals (shading) when all other variables are held constant at their mean.

geomorphology, or vegetative qualities, rather than waterbody shape (Heino et al., 2009, Law et al., 2019, Labat et al., 2022), and this may also be the case for the bats that prey on them. Unfortunately, data on prey abundance or other geomorphic (e.g., depth) characteristics were unavailable for ponds in our study area. Elevation was likely insignificant in our models because we did not sample high elevation ponds, and most ponds we sampled were located within a relatively narrow elevational band. We know from previous studies that bats are generally not found at higher elevations in our study area (>900 m asl; Slough and Jung, 2008). Bats are responsive to ambient temperature, which typically decreases in higher elevations, and survey temperature was a significant predictor of bat activity in our study. Additionally, our study failed to show positive impact of beaver presence on bat activity at ponds, although it was included in the top two models. Many beaver-impacted ponds in our study area were surrounded by additional water/wetland habitat, which may negate the potential benefits of beaver modification at these ponds. Further study is needed to determine in what context, if any, beaver activity may benefit bats in the boreal forest.

We found reduced bat activity at ponds that were surrounded by additional open water/wetland habitat, which was surprising because we predicted that larger feeding areas, or feeding area networks, would attract more bat activity. Bats may have avoided open habitats, because nocturnal periods in our study area are short and illuminated by twilight in summer, and bats may avoid large open areas to reduce predation risk (Slough and Jung, 2008, Talerico, 2008, Shively et al., 2018). There is no true darkness (i.e., astronomical night when the sun is 18° or more below the horizon) in our study area, which is located above 60°N, between 20 April and 23 August, and there is no civil twilight (i.e., when the sun is 6° or more below the horizon) between 18 and 25 June. Bat activity at high latitudes is likely a function of prey abundance and minimizing the risk of predation (Jones and Rydell, 1994, Speakman et al., 2000). Thus, bats may prefer ponds that are less exposed, such as those surrounded by forest, and focus their feeding activity along shaded pond edges (Talerico, 2008).

It is also possible that roosting habitat was a limiting factor at ponds surrounded by open wetland with open water (Lookingbill et al., 2010). Reproductive bats, particularly while lactating, may prefer foraging areas near their maternal roost (Nelson and Gillam, 2017). Ponds closely linked to roosting habitats have been found to be more important to bats than ponds in open habitat types in other studies (Johnson et al., 2008, Heim et al., 2018, Slough et al., 2023). While mature forest cover around ponds was included in our top models, it did not have a significant effect, likely because adult female little brown bats prefer to roost in buildings in our study area. Thus, the importance of individual ponds is likely dependent on their spatiotemporal context related to their quality for feeding, drinking, and avoidance of predators during nights that do not get completely dark. Additionally, bat activity at foraging areas are not static; for example, other studies have shown that bat activity may decrease at individual ponds when water levels or insect abundance changes temporally (e.g., during the rainy season; Lopez-Gonzales et al., 2015, Nystrom and Bennett, 2019), or during insect emergence events (Fukui et al., 2006, Rainey et al., 2006, Salvarina et al., 2018). However, we did not have data on insect abundance at our sample ponds to examine this potentially important factor.

A final key finding from our study is that the human footprint on the landscape (e.g., buildings, roads, and forest clearings) was not retained in our top models, suggesting that ponds are important both in natural and anthropogenic landscapes. While artificial lighting may deter bats in some urban settings (Barre et al., 2023, Seewagen et al., 2023), none of our sample ponds were near strong sources of artificial illumination. However, protection of dark habitat from artificial lights should be included in conservation planning for bats (Russo et al., 2017, 2019). Bats may have less prey in urbanized landscapes (e.g., due to insect control, land clearing, and infilling of ponds and wetlands), and available ponds may be even more important habitat features in these contexts where waterbodies may be limited.

5. Conservation implications

Our study adds to similar studies that point to small waterbodies, such as ponds, being key habitat for several species of bats (e.g., Francl, 2008, Nummi et al., 2011, Lison and Calvo, 2014, Heim et al., 2018, Ancillotto et al., 2019), especially in (semi-)arid or (peri-) urban landscapes. Specific to endangered little brown bats in developing boreal landscapes, we urge that ponds of comparatively high value be identified and that these ponds be protected from development, draining, and degradation, and that the surrounding forest remains intact. The conservation of ponds is particularly important for little brown bats because they are synurbic and attracted to human settlements, which is often where land development is most pronounced. Additionally, bats living at high latitudes may avoid ponds in open wetland complexes despite their potential for increased prey, likely due to a perceived risk of predation (Talerico, 2008). Darker habitats, such as isolated ponds surrounded by mature forest may be particularly valuable for foraging. Thus, clearing forests around ponds may reduce their value to little brown bats, so retention of mature forest immediately around ponds should be a priority. More broadly, ponds provide bats and other wildlife species with necessary drinking and foraging habitats. Recognition and conservation of ponds and their surroundings as key habitat for wildlife requires further attention. The value of ponds for wildlife in developing landscapes needs to be considered during land-use planning processes (Crous et al., 2012, Ancillotto et al., 2019, Oertli and Parris, 2019). Understanding the characteristics of ponds selected by wildlife can help inform conservation priorities and measures that ensure the aquatic habitats they require are maintained in developing landscapes.

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CRediT authorship contribution statement

Piia M. Kukka: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Hannah A. Miller:** Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. **Julie P. Thomas:** Conceptualization, Investigation, Methodology, Writing – review & editing. **Fiona K.A. Schmiegelow:** Methodology, Supervision, Validation, Writing – review & editing. **Thomas S. Jung:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft.

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 will be made available on request.

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Appendix A. Supporting information

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