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Research article

Male and female bats differ in their use of a large urban park

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Abstract

Understanding how wildlife respond to ever-encroaching urbanization is of great concern. Bats are the second-most speciose mammalian order and while many appear to be urban adapted, we currently have a limited understanding of their demography and habitat use within urban environments. Using a combination of captures to obtain demographic data, radio-telemetry to examine foraging and roosting behaviour, and data on diet and prey availability, we examined how big brown bats (*Eptesicus fuscus*), a synurbic species, use an urban green space (High Park) in Canada's largest city centre, Toronto. We found that adult males outnumbered adult females more than two to one and that males were found throughout the park, while females were concentrated in an area with greater access to water, but lower prey availability. We also found that bats of both sexes were in poorer body condition than reported for other non-urban areas, including a site within southern Ontario. Our data suggest that High Park may not provide adequate resources for reproductive females as they were never found roosting in the park and beetles, their preferred prey, were limited. Although previous studies suggest urban green spaces may offer refuge to bats, most have not considered sex-specific responses to urbanization as they have largely been based on acoustic surveys. Our study therefore highlights the importance of considering demographic differences in response to urbanization to better inform urban management plans and green space development.

Key words: bats, diet, foraging, roosting, sexual partitioning

Introduction

Urbanization has ecological, evolutionary and conservation implications for non-human organisms (Johnson and Munshi-South 2017; Santangelo, Rivkin, and Johnson 2018). Covering between 1 and 3% of the Earth's terrestrial surface (Liu et al. 2014), urban areas are home to just over 50% of the worldwide human population (United Nations, Department of Economic and Social Affairs, Population Division 2019). In North America, over 80% of people live in cities that are often concentrated in the region's most biodiverse areas (Shwartz et al. 2014; Johnson and Munshi-South 2017). While species like pigeons and rats thrive alongside humans (Faeth, Bang, and Saari 2011; Santini et al. 2019), urbanization has often resulted in population declines and restricted gene flow for many species, as well as lower overall biodiversity and shifts in community structure (Hulme-Beaman et al. 2016; Munguía et al. 2016; Batáry et al. 2018; Santini et al. 2019). A better understanding of how species use space in urban landscapes is needed to inform the development of future wildlife management plans (Shwartz et al. 2014; Greggor et al. 2016).

It appears that no single strategy or set of traits defines success in urban landscapes (Santini et al. 2019). Instead, the ability to adapt to urbanization is highly dependent on life history, behavioural and ecological traits (Croci, Butet, and Clergeau

2008; Jung and Threlfall 2018; Santini et al. 2019). For instance, animals with larger litter sizes, dietary diversity, open space foraging and flexible in their shelter requirements have typically adapted to the challenges of urban living (e.g. pigeons, rats, cockroaches; Croci, Butet, and Clergeau 2008; Santini et al. 2019), sometimes even increasing in abundance within the urban matrix (Faeth, Bang, and Saari 2011). In contrast, those animals lacking these favourable traits have experienced declines, resulting in declining biodiversity with increasing urbanization for a variety of taxa (birds, Melles, Glen, and Martin 2003; insects, Fattorini 2011; amphibians, Scheffers and Paszkowski 2012; reviewed in McKinney 2008; Faeth, Bang, and Saari 2011; Aronson et al. 2014). Species-specific responses to urbanization are therefore highly heterogeneous (McKinney 2008; Jung and Threlfall 2016).

While bats (Order Chiroptera) may be one of the most diverse groups of mammals still inhabiting urbanized regions (Jung and Kalko 2010; Jung and Threlfall 2016), response to urbanization by bats is species-specific (Jung and Threlfall 2016; Moretto and Francis 2017). In general, acoustic surveys indicate that urbanization generally has a negative impact on bat diversity and community structure (Russo and Ancillotto 2015; Jung and Threlfall 2016; Moretto and Francis 2017). Nevertheless, several species are well-known for their ability to roost in anthropogenic structures (e.g. *Eptesicus fuscus*, *Rhinolophus ferrumequinum*, *Tadarida teniotis*, reviewed in Russo and Ancillotto 2015) and there is evidence for increased bat activity in some urban areas (Avila-Flores and Fenton 2005; Haupt, Menzler, and Schmidt 2006; Fabianek, Gagnon, and Delorme 2011; Russo and Ancillotto 2015; Jung and Threlfall 2016). Specifically, bats appear to use large (≥100 ha) urban green spaces within city landscapes, especially if forested (Geggie and Fenton 1985; Avila-Flores and Fenton 2005; Johnson, Gates, and Ford 2008; Loeb, Post, and Hall 2009). Urban parks may therefore be key for helping bats meet their needs in urban landscapes.

The above work has been important for expanding our understanding of bat biodiversity trends along urban gradients, but many of these studies have relied on acoustic and roost occupancy surveys (Geggie and Fenton 1985; Ancillotto, Tomassini, and Russo 2015; Jung and Threlfall 2018). While these methods provide information on relative bat activity and diversity, they do not provide the information needed to assess population health, such as body condition, sex ratios and number of births. For instance, a demographic study of *Myotis lucifugus* found that bats were more abundant in urban green spaces, but had lower body condition compared to bats in suburban transition zones (Coleman and Barclay 2011). Furthermore, acoustic surveys do not allow for examination of sex-specific patterns of habitat use or diet, which may be common among bat species (Altringham and Senior 2005; Senior, Butlin, and Altringham 2005). During the summer months, female bats often roost and forage in separate locations from males, likely owing to the energetic demands associated with pregnancy and lactation (Barclay 1991; Senior, Butlin, and Altringham 2005; Lintott et al. 2014; Istvanko, Risch, and Rolland 2016). Indeed, a study of the soprano pipistrelle, *Pipistrellus pygmaeus*, found females used higher quality habitat within urban settings while males were more widely distributed (Lintott et al. 2014). These studies highlight the importance of characterizing population demographics and intersexual differences in habitat use in urbanized areas.

Considering the need for more detailed studies examining the impact of urbanization on bats, we examined sex-specific patterns of habitat use of big brown bats, *E. fuscus*, in a large urban park. The big brown bat is one of the most widely distributed and most well-studied bats in North America (Agosta 2002). Furthermore, it is a commonly cited urban-adapted species as it is typically the most represented bat species in urban surveys continent-wide (Loeb, Post, and Hall 2009; Jung and Threlfall 2016; Schimpp, Li, and Kalcounis-Rueppell 2018). In fact, big brown bats likely owe their widespread distribution across North America to their ability to use human structures as roosts (McAlpine et al. 2002). At the same time, this close association with humans generates some concern, as big brown bats are a major reservoir for Rabies virus in north-eastern North America (Banyard et al. 2014), highlighting a need to understand how they use space in urban landscapes.

During an initial survey in the summer of 2015, we found a male-biased population of big brown bats and apparent sexual partitioning of foraging habitat in Toronto's High Park (see Supplementary Material). To better understand these apparent sex-specific patterns, we conducted an intensive study in the summer of 2016 to test the following hypotheses:

1. *Sex-specific flight constraints correlate with habitat use*: In bats, wing morphology plays an important role in the ecology of a species (Norberg and Rayner 1987). Previous work has indicated that success in urban environments correlates with wings designed for fast flight and open space foraging (Jung and Threlfall 2018). Furthermore, it has been hypothesized that differences in flight constraints between males and females may explain intersexual differences in habitat use (Lintott et al. 2014). Given that female big brown bats are typically larger than males (Kurta and Baker 1990), they may have higher wing-loading, making them relatively less manoeuvrable in cluttered habitat and more likely to fly in open areas. We therefore predict that males and females will differ in flight constraints (i.e. wing loading) and this will correlate with sex-specific differences in habitat use. Specifically, we predict females will have higher wing loading and will therefore be found more often in more open habitat.
2. *Prey availability correlates with female, but not male, habitat use*: Like nearly all North American temperate bats, big brown bats are insectivorous (Kurta and Baker 1990). Insect abundance and diversity vary with habitat type and bat activity often reflects this variation (Threlfall, Law, and Banks 2012). Females must locate high quality foraging habitat to support pup development and care, while males may potentially use lower quality habitat and offset low foraging success through torpor (a decrease in body temperature and metabolism to save energy; Altringham and Senior 2005). We therefore predict males will be uniformly distributed on the landscape with respect to prey availability (as determined through passive insect sampling), while females will be more common in areas with greater availability of preferred prey, as assessed based on the diet of captured individuals.
3. *Roosting activity within the park will be low*: Big brown bats are known to readily roost in anthropogenic structures (McAlpine et al. 2002). Building roosts may be advantageous for bats because of protection from predators and more stable, warmer microclimates (Russo and Ancillotto 2015). Warmer microclimates may be particularly favoured by female bats, as it reduces reliance on torpor and may increase reproductive success (Kerth, Weissmann, and König 2001; Agosta 2002). Male bats however may be less constrained in their use of torpor. Given anthropogenic roosts appear to provide considerable benefits (particularly to females) and are presumably more readily available in the surrounding urban landscape, we predict that fewer bats will be roosting in the park.

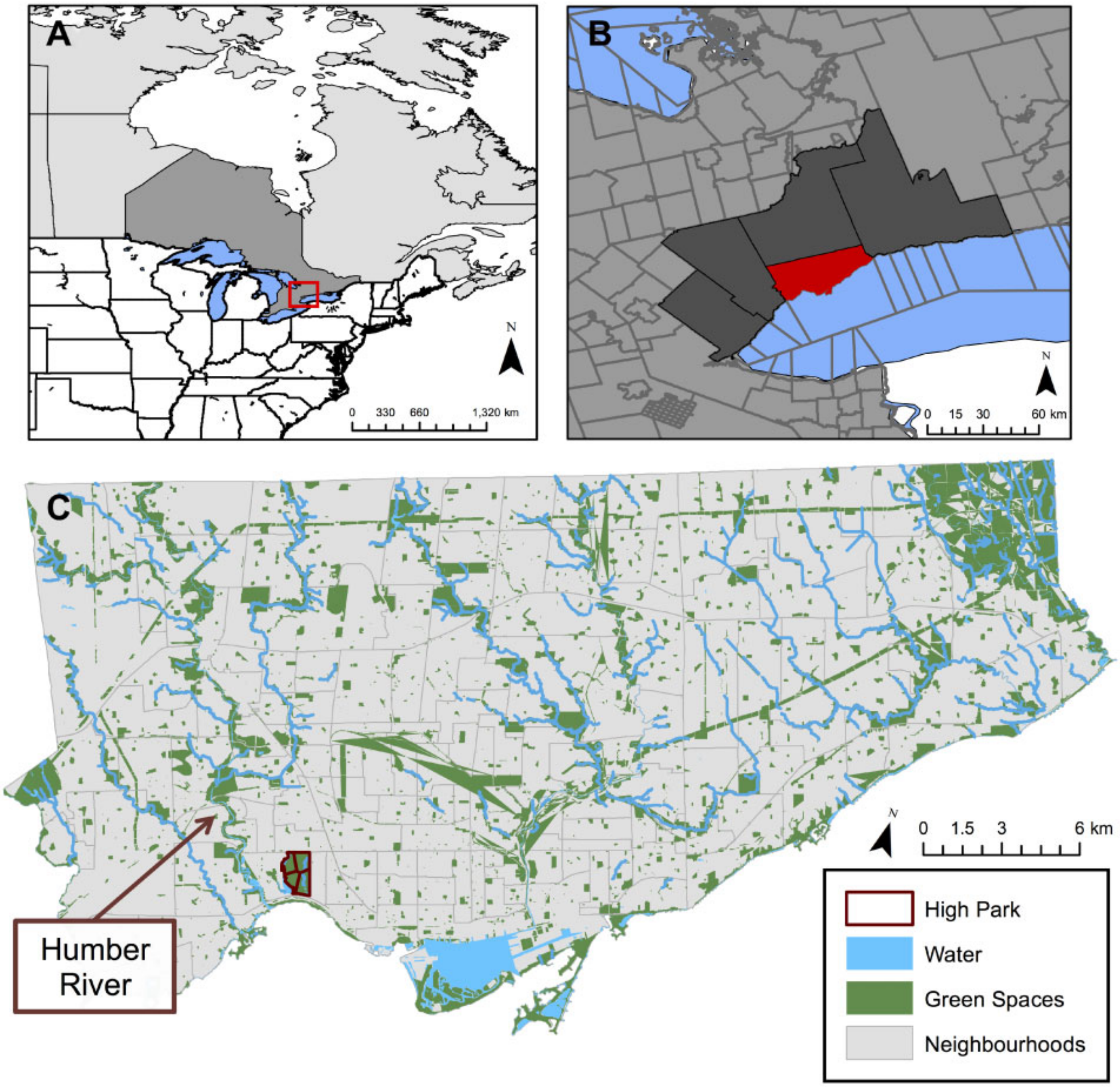

Figure 1: Location of study area (High Park, Toronto) in (A) Ontario, Canada, (B) among Southern Ontario municipalities (dark grey), with the Greater Toronto Area highlighted in red and (C) in the City of Toronto. The location of Humber River is also indicated (red arrow)

Methods

Study area

We conducted our study in High Park, located in Canada's most populated urban centre, the Greater Toronto Area (GTA), Ontario (7124.15 km^2; 6.4 million people, Fig. 1). At 161 ha (1.61 km^2), High Park is just under half the size of Central Park in New York City (341 ha) and is one of the largest entirely urban (vs suburban) parks in North America. Roughly half of High Park (83.25 ha) is made up of an Environmentally Sensitive/Significant Area consisting of provincially rare black oak (*Quercus velutina*) savannahs, regionally rare moist red oak (*Q. rubra*), and eastern hemlock (*Tsuga canadensis*) forests, regionally rare marshlands near a large pond and creek, and locally significant bottomland forests (City of Toronto 2002). The remainder of the park provides cultural and recreational areas, including manicured gardens, sports fields, family recreation areas and a small zoo (City of Toronto 2002).

General methods

We repeatedly sampled 16 sites throughout the park from 2 June to 23 September 2016 (Fig. 2). Sites were selected to: (i) reflect the habitat variability described above, (ii) ensure even coverage in each of four quadrants in the park to account for possible biases in spatial distribution independent of habitat type and (iii) optimize capture success of big brown bats (*E. fuscus*) by returning to sites which had been most productive during our 2015 survey (see Supplementary Fig. S1 and Table S1).

To account for potential temporal variation in habitat use, we sampled from sunset to sunrise roughly six nights per week from 2 June to 1 September 2016. To account for seasonal variation, we visited roughly 8 sites per week, rotating among all 16 sites in a semi-randomized order, where (i) the same site was not visited more than once a week, (ii) two sites in the same quadrant were not sampled on the same night and (iii) the same quadrant was not sampled on consecutive nights (Table 1; $N = 72$ calendar nights total). By visiting the same site no more

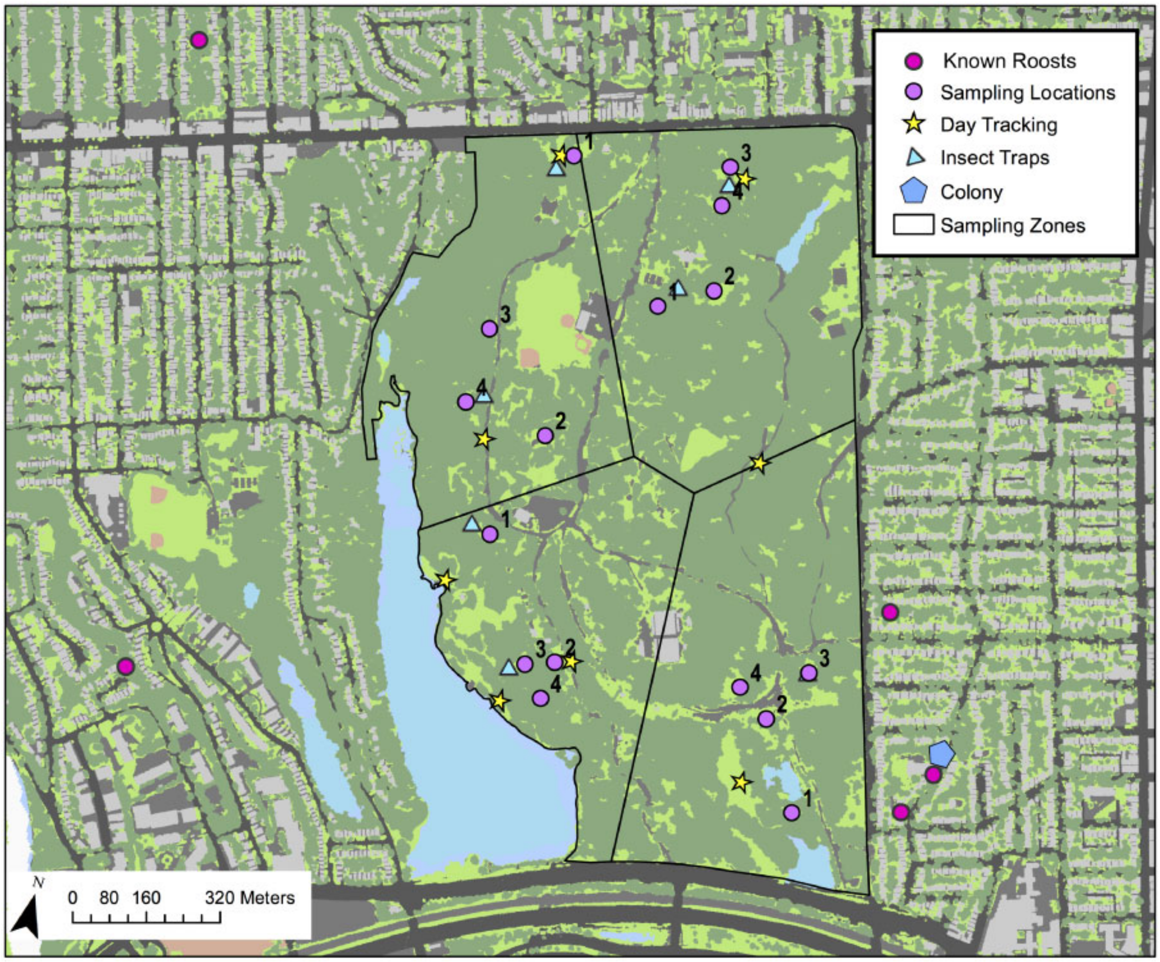

Figure 2: High Park, Toronto, Ontario, Canada with locations of sampling sites and insect traps. Demarcations for the sampling quadrants and numberings of sampling sites within those quadrants (see Table 1) are also displayed. Land cover classes present on the map include water (blue), forest (dark green), manicured grass (light green), paved surfaces (dark grey) and buildings (light grey)

Table 1: Summary of *E. fuscus* capture distribution in High Park, Toronto, Ontario, by sex and age group

Quadrant	Site	Total[a]	Adult males	Adult females	Juvenile males	Juvenile females
NE	1	3	1	0	2	0
	2	5	4	1	0	0
	3	5	4	0	1	0
	4	2	2	0	0	0
Quadrant total		15	11	1	3	0
NW	1	11	11 (1)	0	0	0
	2	16	12 (1)	1	3	0
	3	3	1	2	0	0
	4	4	4	0	0	0
Quadrant total		34	28	3	3	0
SE	1	14	7	1	4	2
	2	9	7	0	1	1 (1)
	3	2	2 (1)	0	0	0
	4	5	4	0	0	1
Quadrant total		30	20	1	5	4
SW	1	26	12 (1)	8 (2)	5	1
	2	12	4 (1)	5	2	1
	3	30	5	8 (1)	7 (1)	10 (1)
	4	32	16 (1)	15	1	0
Quadrant total		100	37	36	15	12
Overall total		179	96	41	26	16

[a] Given that we are interested in the distribution by site, summary of captures here includes recaptures (six adult males, three adult females, one juvenile male, two juvenile females). However, at sites with re-captures, the number of recaptures is noted in brackets to the right of the total number of captures.

than once a week, we reduced the potential for 'net-shyness', where low capture rates may be attributed to bats learning to avoid areas (Robbins, Murray, and Mckenzie 2008; Winhold and Kurta 2008). To better allow comparison among quadrants, on two nights of the week, we sampled two sites concurrently, one in each of two quadrants. On the remaining four sampling nights in a given week, we sampled only one site per night to allow more time for radio-tracking (see below). To establish when bats leave the park for mating and hibernation, after the 3-month intensive sampling period (i.e. 2 June 2 to 1 September), we resampled the site with the highest summer capture success in each of the four quadrants (NE Site 2, NW Site 2, SW Site 3 and SE Site 1; see Supplementary Table S1) once per week from 2 September to 16 September 2016. Of these four sites, we then selected the site with the highest captures (SW Site 3) and resampled it on 23 September. By resampling sites with the highest capture rates, we could be more confident that failure to capture bats was because the bats had left the park for the year rather than because we chose sites known to be typically bat-poor. For a breakdown of sampling effort by site, see Supplementary Table S3.

We captured bats using three mist-nets (2.6, 6 and 9 m in length; all 2.6 m in height; Avinet, Dryden, NY, USA) placed in areas expected to be frequented by bats, such as along treed edges and near ponds (Winhold and Kurta 2008, see Supplementary Fig. S1). We followed all capture and handling protocol guidelines according to the American Society of Mammalogists (Sikes, Gannon, and Animal Care and Use Committee of the American Society of Mammalogists 2011). To estimate capture rates, we used three different metrics as there is no consistency among previous studies. We determined the number of bats caught: per net night (89 net-nights: one site sampled/night = one net-night; two sites sampled/night = two net-nights), per net hour (572 net hours: total # of hours each net was open) and per net area (45.76 m^2).

Demographics and condition

For all captured big brown bats, we documented age, reproductive condition, mass and forearm size. We also implanted RFID tags (12.5 mm, model HPT 12, Biomark, Boise, ID, USA) subcutaneously between the scapulae of all captured individuals to document recapture rates. To assess age, adults and juveniles were differentiated based on the ossification of the epiphyseal gap on the fourth metacarpal (Anthony 1988). Reproductive condition of females was assessed as either pregnant through palpation of the abdomen, nursing by the presence of worn fur around the nipples and expression of milk, or weaning by the presence of worn fur around the nipples but no expression of milk (Racey 2009). Reproductive condition of males was determined as either scrotal by the presence of enlarged testes, or non-scrotal by the absence of enlarged testes (Racey 2009).

As in similar studies (Kurta and Teramino 1992; Coleman and Barclay 2011), we estimated reproductive success based on the ratio of captured juveniles to reproductively active adult females, specifically lactating females to account for the possibility that some pregnant females may have aborted foetuses. This is because we could not gain access to maternity colonies to establish reproductive success of specific individuals. We assessed the general health of individuals using body mass index (BMI), a ratio of mass (g) to forearm size (mm) (Senior, Butlin, and Altringham 2005; Pearce, O'Shea, and Wunder 2008; Speakman and Racey 2009; Jonasson and Willis 2011). After verifying that our data met the assumptions for using an independent sample *t*-test we used this to compare average adult female and adult male BMI within High Park, both across the entire summer and just in the month of August after females had weaned pups. In addition, to examine differences in body condition on a larger scale, we compared adult BMI of bats caught in High Park to those caught at other study sites. To do this, we compiled information on body mass and forearm size of adult big brown bats captured from May to August in other urban and natural areas to calculate BMI (see references in Table 2). In some instances, we also used unpublished datasets provided to us by the authors (Table 2). For those sites which we obtained raw data, we confirmed that all data met the assumptions for using an ANOVA and Tukey HSD *post hoc* comparisons. Then, because we only had summary data (means and standard deviation) available for one site (Hamilton), we used summary data to compare body condition across sites based on average BMI for males and females combined, due to smaller sample sizes from some study areas. For a summary of all individual data and samples collected, see Supplementary Table S4.

Table 2: Mean ± SD BMI for *E. fuscus* in rural and urban areas across their range

	Mean ± SD forearm size (mm)	Mean ± SD mass (g)	Mean ± SD BMI	N
High Park, Ontario (urban)[1]	45.33 ± 1.67^{a}	16.11 ± 2.35^{a}	0.35 ± 0.04^{a}	127
Hamilton, Ontario (rural)[2]	44.6 ± 0.24^{b}	17.7 ± 0.63^{b}	0.40 ± 0.03^{b}	168
New Hampshire (rural)[3]	45.8 ± 1.65^{a}	17.5 ± 2.46^{b}	0.40 ± 0.05^{b}	123
New Hampshire (rural; post WNS)[3]	46.2 ± 1.57^{c}	17.35 ± 2.04^{b}	0.37 ± 0.04^{a}	22
Alberta (rural)[4]	47.09 ± 1.54^{d}	18.8 ± 3.39^{c}	0.49 ± 0.09^{c}	15
Alberta (urban)[4]	47.6 ± 1.99^{d}	23.22 ± 4.6^{df}	0.40 ± 0.07^{b}	12

Superscripts indicate results of Tukey HSD *post hoc* tests, where values with different superscripts are statistically significantly different ($P < 0.05$).

[1] Data from this study.

[2] Data from Mayberry and Faure (2015).

[3] Unpublished data from P. Moosman, Virginia Military Institute, Lexington, Virginia.

[4] Unpublished data from J. Coleman, University of Calgary and Department of Biological Sciences, National University of Singapore.

To test if differences in manoeuverability correlate with differences in habitat use (see Sex-specific patterns of habitat use below), we used an iPhone 5 s camera (Apple, Inc., Cupertino, CA, USA) to take pictures of the right wing of each bat spread out on flat 5 × 5 mm graph paper. Using ImageJ (National Institutes of Health, v. 1.46r), we measured wing area to then calculate relative wing loading [(mass(M)*acceleration due to gravitation(g)/wing area)/$M^{0.33}$] (Norberg and Fenton 1988). We used an independent samples *t*-test to compare wing loading of adult males and females. For a summary of all individual data and samples collected, see Supplementary Table S4.

Diet and prey availability

To examine diet and compare it to prey availability within the park, we obtained faecal samples from bats (N = 131 total; Supplementary Table S4). We dissolved faecal samples in 95% ethanol and used a light microscope (Zeiss, Stemi508) to identify undigested prey remains to Order based on methods outlined in

Whitaker, McCracken, and Siemers (2009). It can be difficult to accurately assess the relative contribution of different insect Orders to an individual's diet due to differences in size and degree of digestion (Whitaker, McCracken, and Siemers 2009). Soft-bodied insects, like dipterans, are often digested more completely and may therefore be underrepresented in diet analyses, while beetle exoskeleton and moth scales remain intact and may therefore appear more common in the diet (Whitaker, McCracken, and Siemers 2009). At the same time, wings and antennae often persist in faeces and can be used to identify dipterans (Whitaker, McCracken, and Siemers 2009). We therefore simply examined faeces for any trace of each group and assessed presence/absence of each Order so that even small traces of more easily digested prey should be visible if present in the diet. Because we were dealing with proportional data, we used z-tests to compare the proportion of individuals that ate each of the three most common insect Orders to the total proportion of insect traps containing each Order.

To examine prey availability, insect traps were erected each night for the same duration and in the same quadrant as mist-nets were deployed (Fig. 2; number of nights sampled: NE = 23, NW = 21, SW = 21, SE = 20). Traps consisted of a vertical array made up of a sticky trap both above and below a four-sided Malaise trap (L110 × W110 × H110 cm SLAM trap BT1004; Bugdorm.com; see Supplementary Fig. S6) that included a sampling vial filled with ethanol placed at the top and bottom. Cylindrical sticky traps like those used here are believed to be effective in capturing flying insects, particularly smaller insects, while Malaise traps are considered one of the most versatile traps (Kunz 1988). To ensure insect samples reflected insects available at the same heights as bats would be foraging, we set traps at a height to ensure that the lowest of our sticky traps aligned with the middle tiers of our lowest set net (~1.8 m off the ground). We also attached temperature loggers to the upper and lower sticky traps to measure nightly temperature.

To ensure sampled insects were not drawn to our traps from outside our quadrant of interest, we relied on passive sampling rather than attractants, such as lights or pheromones. Insects and other arthropods were identified to Order. To determine if bat distribution is explained by prey distribution, we first quantified the total number of captured arthropods belonging to each Order per quadrant. We also quantified the proportion of traps containing each Order per quadrant and compared this to the proportion of faecal samples containing each Order (see below) from bats captured in matching quadrants on the same dates. Finally, analyses for understanding the importance of prey availability for predicting male and female presence, relative to other landscape variables, is discussed below.

Sex-specific patterns of habitat use

To determine if males and females differed in their use of the park, we used Pearson's Chi-squared test to compare observed captures of adult males and females in each of the four quadrants to expected captures. We assumed a uniform distribution to generate expected values, which were calculated by taking the total number of adults captured and dividing by 8 (2 sexes * 4 quadrants).

We also examined which landscape variables predicted male and female presence at sampling sites throughout the park. In ArcGIS 10.1 (ESRI 2011), we created a 150 m buffer around the boundary of High Park. This distance was the median straight-line distance between located bat roosts and park borders (Fig. 2). Using the buffered park boundary, for each of the four quadrants we calculated the proportion of the quadrant covered by roadways and buildings, obtained from the City of Toronto's Works and Emergency Services Property Data Maps (City of Toronto 2015), and the proportion of the quadrant covered by water, recreational/open space and canopy, obtained from the City of Toronto's Forest and Land cover dataset (Parks, Forestry, and Recreation 2007). Given that our land cover data were collected at the level of quadrant, sampling sites within each quadrant have the same land cover information. This was in part because some sampling sites were too close in proximity to obtain separate land cover data. As detailed above, sites were selected to maximize coverage of the park as well as captures, based on capture success in 2015 (see above). As a result, sites in different quadrants and within the same quadrant may be in close proximity. In an effort to account for this, site was included as a random variable in our models (see below).

Using an information theoretic approach (Burnham and Anderson 2002), we constructed a set of candidate models predicting the distribution of females and males throughout the park (Supplementary Tables S8 and S10). We fit generalized linear mixed models (GLMM) with a negative binomial error structure (given overdispersion in the count response) using the number of either adult males or adult females captured at each sampling site on nights throughout the summer as the responses ($N = 52$ nights for which we had complete data, see following). In addition to the landscape variables described above, we also included information on the temperature (collected using temperature loggers) and the proportion of beetles captured on nights that sites were sampled. The proportion of beetles captured at sites was calculated by dividing the number of beetles in each trap by the total abundance of all arthropods found in faecal samples (see above) captured in each trap. This included coleopterans, dipterans, lepidopterans and hymenopterans. In addition to these fixed effects, we included the total number of adult bats caught at each site on a given night as an offset term in the model. We also included date, and sampling site nested within sampling quadrant as random effects. We compared the difference in AIC scores of all competing models. All models with a $\Delta_{\mathrm{AIC}} < 2$ were considered to have equal support (Burnham and Anderson 2002). Where multiple models had similar support, we adopted a principle of parsimony and assumed that the best model was the one with the fewest parameters (Burnham and Anderson 2002). All GLMMs were fit in R (R Core Team 2018) using the lme4 (*v. 1.1-21*) package (Bates et al. 2015).

Roosting and foraging patterns

To locate day-roosts, we used surgical adhesive (Osto-Bond, Montreal Ostomy, Montreal, QC, Canada) to attach radio-tags (PipAg379; 0.47 g; Lotek, Newmarket, ON, Canada) between the scapulae of a subset of individuals ($N = 20$; 7 adult males, 3 juvenile males, 8 adult females, 2 juvenile females). We located radio-tagged bats using 5-element Yagi antennae and Lotek SRX-800 receivers (Lotek, Newmarket, ON, Canada). Because our goal was to determine how bats were using High Park, we began our tracking efforts within the park. To do this, we first established the range of detection of our tags in the park (see Supplementary Section 2.1 for detailed methods). Based on this, we designated a series of scanning locations throughout the park that would ensure we could detect bats if they were roosting within the park's boundaries (Fig. 2). We scanned for tagged bats from each of these locations on a daily basis for as long as the tag remained active (range = 7–17 days/bat). If we were unable to detect a signal from any of these locations, we concluded bats were not roosting within the park. When a signal was detected, we located the strongest signal to identify roosts.

We did not quantify roost characteristics because the only roosts we located were outside the park's boundary, which were not part of the scope of this study. Unlike some previous studies of natural bat roosts (reviewed in Kalcounis-Rüppell, Psyllakis, and Brigham 2005), we also did not attempt to quantify the availability of potential roosts based on a set of assumptions about what constitutes a set of roost characteristics (e.g. tree species, decay stage, canopy cover). To do so would presuppose what might constitute a suitable roost in an urban environment, for which there is little precedent.

To examine foraging behaviour, we also tracked the 20-tagged bats nightly from sunset to sunrise (range = 7–17 nights/bat). Logistical constraints limited our ability to actively follow bats while they foraged. Instead, two teams radio-tracked bats simultaneously from our previously established fixed positions to maximize detection range within the park (Fig. 2; see Supplementary Section 2.1). Concurrent bearings were taken every 10 min and used to biangulate the locations of foraging bats using LOAS 4.0 (Ecological Software Solution LLC). Because bats often moved beyond the park's borders, we did not have enough data (e.g. >100 for Minimum Convex Polygons; Harris et al. 1990, minimum 30 for Kernel Density Estimation; Seaman et al. 1999) for any individual bat to meet the recommended sample sizes to estimate utilization distributions (defined as the relative intensity or probability of use of areas, Millspaugh et al. 2012). As such, detailed methods and results of our efforts to examine bat movement can be found in the Supplementary Section 2.3. We do, however, provide information on the timing of detections to provide insight to the relative use of the park. We also present kernel density estimates (KDE) with 95% contours (Seaman et al. 1999) of bat utilization distributions based on pooled detections for adult males ($N = 36$ observations; 4 individuals), adult females ($N = 48$ observations; 7 individuals) and juveniles ($N = 50$ observations; 4 individuals) across the season. We provide this information to give a general sense of animal movement within the park.

Results

See Supplementary material for 2015 pilot survey results.

In 2016, we caught a total of 179 big brown bats (*E. fuscus*). The majority of these captures occurred primarily near dusk and dawn, with relatively few captures through the remainder of the night (Fig. 3). Based on our nightly sampling effort of 89 net-nights, our captures translate to 2 bats/net-night. Given a total sampling time of 572 net hours, our capture rate translates to 0.31 bats/net-hour. Based on our total net area of 45.76 m^2 in each site, this translates to 3.9 bats/m^2 and 0.007 bats/m^2/h. Of the 179 big brown bats caught in the park, 12 (6.7% of total) were recaptures from that same year, for a total of 167 unique individuals caught in the park in 2016. Sixteen (9.6%) of these 167 individuals were recaptures from 2015.

Demographics and condition

Of the 167 unique individuals, we caught 126 adults with a sex ratio of 2.4 males: 1 female, and 41 juveniles with a sex ratio of 1.8 males: 1 female (Table 1). The number of captured juveniles ($N = 39$, excluding recaptures) relative to lactating females ($N = 20$, excluding recaptures) was 1.95:1. Adult females had significantly higher BMI ($\mu = 0.38$, $SD = 0.03$, $N = 34$) than adult males ($\mu = 0.34$, $SD = 0.04$, $N = 89$) throughout most of the summer ($t = 2.39$, $P = 0.01$). However, by the end of the summer (August) when most females had weaned pups, there was no significant difference in BMI between adult males (μ_{August}=0.36, $SD = 0.06$, $N = 7$) and females (μ_{August}=0.38, $SD = 0.01$, $N = 4$) ($t = 0.67$, $P = 0.52$). Wing loading was also significantly higher ($t = 2.40$, $P = 0.02$) in adult females ($\mu = 35.39$, $SD = 4.78$, $N = 31$) than adult males ($\mu = 33.27$, $SD = 3.66$, $N = 65$). When compared to big brown bats caught elsewhere during the same period (i.e. May–August), those caught in High Park had significantly lower BMI (males and females combined in all cases; $F_{5,461} = 42.48$, $P < 0.00001$). Tukey HSD *post hoc* comparisons revealed that bats in High Park had significantly lower BMI compared to bats in rural areas of Ontario, New Hampshire and Alberta, as well as urban regions in Alberta (Table 2). In addition, a comparison of forearm sizes and masses shows that these differences are not driven by geographic differences in morphology. For instance, bats in Hamilton (~50 km from High Park) had significantly smaller forearms than bats in High Park, but were statistically heavier (Table 2).

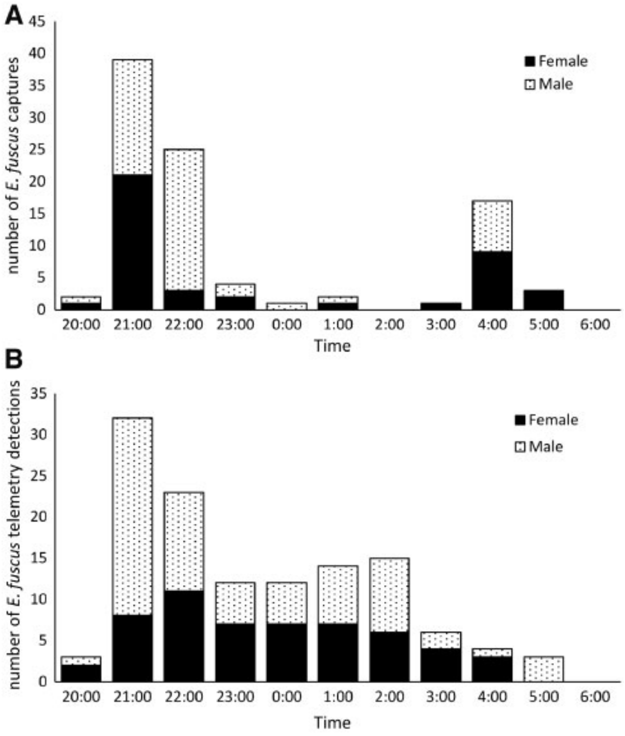

Figure 3: Histogram of (A) captures and (B) pooled radio-telemetry detections recorded in and around High Park, Toronto, Ontario, Canada throughout the night. Sunset ranged from 9 pm earlier in the season to 7 pm later in the season, while sunrise ranged from 5:40 am to 7:15 am

Diet and prey availability

Of the 131 faecal samples collected, nearly all contained Coleoptera (99.2%) with fewer samples containing Lepidoptera (67.2%). There was no significant difference in diet across demographic groups, with the exception of adult males who consumed Lepidopterans more often than did juveniles (Supplementary Tables S5 and S6). A comparison of the proportion of faecal samples and traps containing beetles, suggests a greater proportion of faecal samples contained beetles than expected based on their occurrence in traps, regardless of demographic group (Supplementary Table S7). A comparison of the proportion of faecal samples and traps containing

Table 3: Summary of number of insects sampled in each of four quadrants in High Park, Toronto (Ontario)

Quadrant	Coleoptera	Lepidoptera	Diptera	Other[a]	Unidentified	Total
NE	49	385	46	91	15	586
NW	29	246	39	70	17	401
SE	15	204	77	41	19	356
SW	21	394	198	68	14	695
Totals	114	1229	360	270	65	2038

[a] Other may include Hymenoptera, Homoptera and Arachnidae.

Lepidoptera and Diptera suggests fewer faecal samples contained moths and flies than expected based on their occurrence in traps, regardless of demographic group (Supplementary Table S7).

Data from passive insect traps indicate that overall insect availability was highest in the SW quadrant (34.1%) followed by the NE quadrant (28.7%) (Table 3). Coleoptera, however, were less abundant in the SW and most abundant in the NE (43%). Overall, Lepidoptera (60.3%) was the most common insect Order collected in High Park and Diptera was the second most common (17.9%), while Coleoptera (6.6%) were less abundant (Table 3). Other Orders, including Hymenoptera, Hemiptera, Neuroptera and Orthoptera, made up roughly 13% of insect samples (Table 3). The importance of this prey availability for predicting male and female presence is presented below in Sex-specific patterns of habitat use.

Sex-specific patterns of habitat use

Capture data indicate that adult big brown bats were not randomly distributed throughout the park ($\chi^2_{7,137} = 95.47$, $P < 0.001$). Generally, more bats were captured in the SW quadrant (56% of captures) than in all the other quadrants combined, with the fewest captures in the NE quadrant (8% of captures) (Table 1). Adult females were nearly absent from most of the park, with the exception of the SW quadrant, an area characterized by open space and water cover, where 88% of all females were caught. In contrast, adult males were more uniformly distributed throughout the park (11%, 29%, 21%, 39% of adult male captures in the NE, NW, SE and SW quadrants, respectively; Table 3). Sex ratios in three quadrants were heavily male-biased, the exception being the SW quadrant where the sex ratio was 1:1 (Table 1). Juvenile distribution closely matched adult female distribution and was also not random ($\chi^2_{3,42} = 36.86$, $P < 0.001$), with most captures in the SW quadrant (57% of juvenile males and 75% of juvenile females).

A comparison of AIC scores for candidate models for female capture abundance on sampling nights indicates that a model containing temperature, proportion of beetles in traps and proportion of water in sampling quadrants best fits the data (Supplementary Table S8). Examination of model fixed effects suggests proportion of water had positive effects on female capture abundance, while proportion of beetles and temperature had a negative effect (Supplementary Table S9). However, the effect of temperature was small, and did not differ significantly from zero (Supplementary Table S9).

For nightly male capture abundance, comparison of AIC scores for candidate models suggest that two models had similar support and were equally parsimonious (i.e. had the same number of parameters) (Supplementary Tables S10 and S11). The first model contained temperature, proportion of beetles in traps and proportion of water in the sampling zone (Supplementary Table S10). Both temperature and water had negative effects on male abundance, while proportion of beetles had a positive effect. However, no terms in the model were significant (Supplementary Table S11). The second model contained temperature, proportion of tree cover and proportion of buildings in each sampling zone (Supplementary Table S10). Fixed effects indicated that temperature and proportion of buildings had positive effects on nightly male capture abundance, while tree cover had a negative effect (Supplementary Table S11). However, proportion of buildings in the sampling zone was the only significant term in the model (Supplementary Table S11).

Roosting and foraging patterns

We tracked 20 bats almost daily in an effort to locate day-roosts. No roosts were found in High Park (Fig. 2). In addition to the maternity colony and another roost located in a residential area to the southwest of the park both first located in 2015, we tracked five individual bats to four separate locations outside the park (Fig. 2). The exact nature of these roosts is unknown as they were located on private property and therefore could not be confirmed. In each instance, however, the private property contained a single dwelling house and one or more large trees. Roosts for all other individuals could not be located.

Similar to captures, radio-telemetry detections in the park for the 20 bats tagged peaked at dusk, but remained relatively constant until sunrise (Fig. 3). Of the 20 bats tagged, we were able to bi-angulate GPS locations for 15 individuals at night (average ± SD number of fixes per bat 10.27 ± 8.8, range = 1–27). However, individuals were only detected intermittently throughout the night. Nevertheless, we can make some general inferences about patterns of habitat use. When detected, adult females were concentrated in the southern half of the park, particularly in the SW quadrant (Fig. 4). Males had a wider distribution throughout the park, exhibiting greater presence in the NE quadrant than females (Fig. 4). Juveniles overlapped adult females more than they overlapped adult males (Fig. 4). More detailed exploratory models of spatial patterns can be found in the Supplementary Figs S2–S5.

Discussion

With continued human encroachment into natural spaces, there is a need to understand how human habitat modification affects synurbic wildlife. We examined demographics, condition and sex-specific habitat-use of big brown bats, *E. fuscus*, in Toronto's High Park. We identified a strong male sex bias in captures, with females having higher body condition compared to males. However, compared to big brown bats elsewhere in their range, bats in High Park had lower body condition. Within the park, adult males were more common and widely distributed relative to adult females, which were found primarily in the southwest quadrant of the park—an open area characterized by a large amount of water cover. As we discuss below, and as originally hypothesized, we postulate that presence of females in this area may be partially related to observed differences in wing loading. However, in contrast to our original hypotheses, presence of females at sampling sites is not related to preferred prey availability. Finally, in line with our predictions, none of the bats could be found roosting in High Park during the day despite radio-tag detections of both males and females moving through the park at night. Together, our data suggest

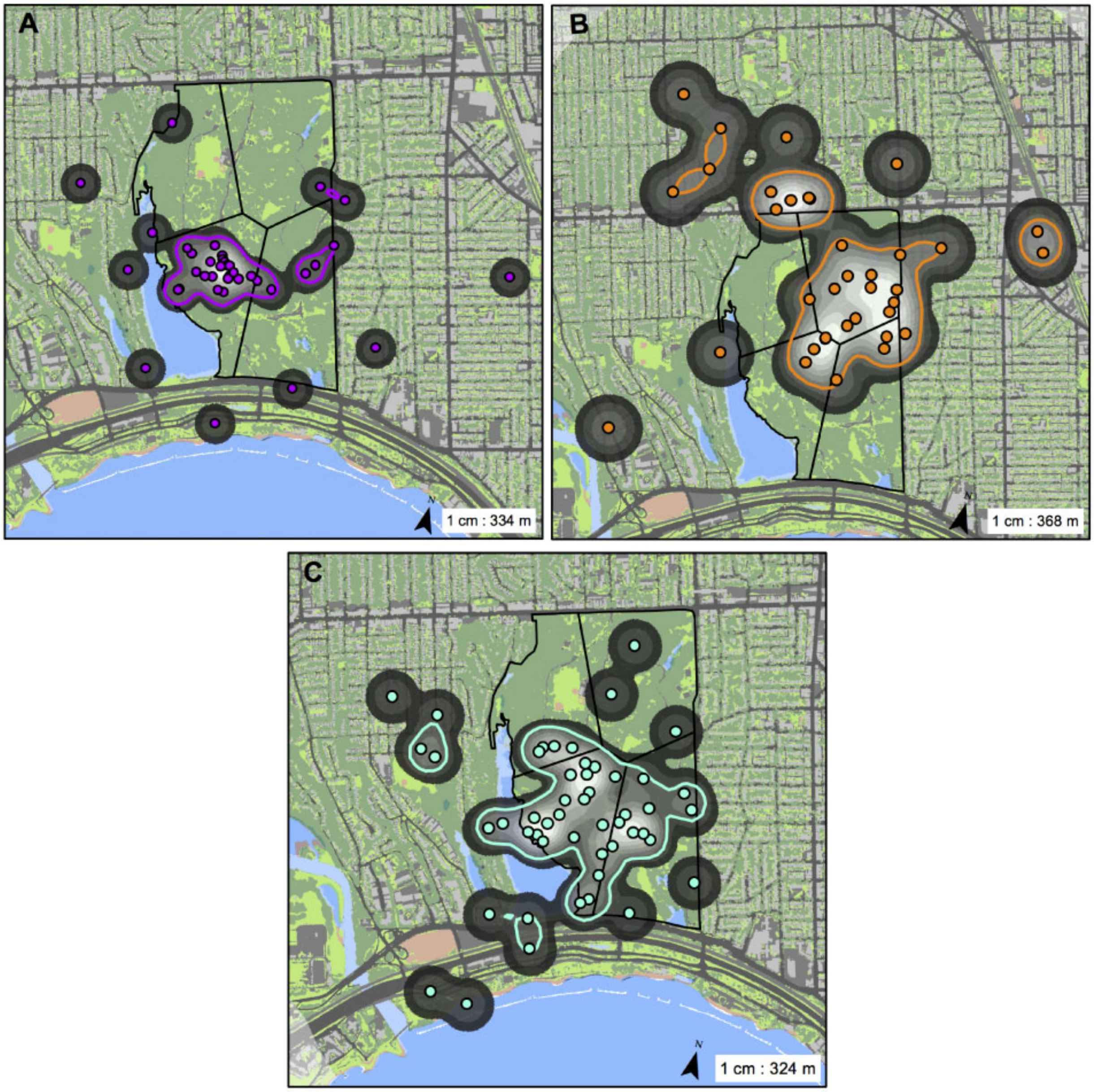

Figure 4: KDE of pooled (**A**) adult female, (**B**) adult male and (**C**) juvenile radio-telemetry data recorded in and around High Park, Toronto, Ontario, Canada. Lines represent the 95% KDE contours. Land cover classes present on the map include water (blue), forest (dark green), manicured grass (light green), paved surfaces (dark grey) and buildings (light grey)

High Park represents a lower quality habitat patch where bats show sexual segregation of habitat use.

Similar to other species of temperate, insectivorous Vespertilionids (e.g. *M. lucifugus*, Barclay 1991; *Myotis daubentonii*, Senior, Butlin, and Altringham 2005; *Nycticeius humeralis*, Istvanko, Risch, and Rolland 2016) our capture data suggest sexual segregation of habitat use by big brown bats within an urban environment. While we could not confirm the extent of this segregation during foraging due to sparse radio-tracking data, the few detections that we did have also weakly support intersexual differences in space use. Previous work (Barclay 1991, Senior, Butlin, and Altringham 2005) has suggested that differences in habitat use are driven by the differential energetic demands associated with reproduction, given that females must locate high quality foraging habitat to support pup development and care (Altringham and Senior 2005). In line with this, we hypothesized that female presence would be predicted by preferred prey availability (i.e. beetles). While adult males in our study site made greater use of areas with more beetles (i.e. the northeast quadrant), females did not. Instead, the proportion of females captured at sampling locations was best predicted by the amount of water present. Indeed, proximity to water is an important predictor of overall distribution for several bat species (e.g. *Myotis californicus*, *M. evotis*, *M. lucifugus*, *M. yumanensis* and *Tadarida brasilienis*; Grindal, Morissette, and Brigham 1999; Krauel and LeBuhn 2016), often because water is critical habitat in the life cycle of prey (Salvarina 2016). However, this may not entirely explain sex-specific differences in habitat use in High Park, given that abundance of preferred prey was lower in areas with higher water cover.

The association of females with open water may also relate to differences in flight constraints between the sexes. As seen in other species (Myers 1978; Jones and Kokurewicz 1994; Kalcounis and Brigham 1995), adult female big brown bats in High Park had higher wing loading than males, likely making them less manoeuverable. Consistent with the expectation that less manoeuverable bats are more commonly found in open habitat and along forested edges, rather than in more cluttered environments (Norberg and Rayner 1987; Swartz, Freeman, and Stockwell 2003), we caught the majority of females in an area characterized by open water and lower vegetation cover. This could explain the importance of water in our models predicting female presence. We also note that we caught the majority of juveniles in the southwest quadrant. While this is likely due in part to the fact that juveniles associate with mothers during early foraging flights (Brigham and Brigham 1989), they are also likely less manoeuverable while learning to fly (Buchler 1980). Access to open water may therefore provide a clutter-free corridor for females and juveniles with limited manoeuverability. However, the influence, and interaction, of seasonal water requirement, open space manoeuvrability and diet preference on female bats' association with open water remains to be determined.

Our dietary analyses suggest that, like elsewhere in their range (reviewed in Agosta 2002), beetles dominate the diet of big brown bats in our sampled urban environment. However, beetles were relatively uncommon in High Park. It is possible that, despite being relatively uncommon, beetles may have been larger and therefore represented greater biomass in the park, and for this reason were targeted by big brown bats. As we did not measure prey size to measure biomass, we cannot dismiss this possibility. Nevertheless, evidence that both male and female bats were caught primarily at dusk and dawn, together with low beetle abundance, suggests that bats spent little time foraging in High Park. We therefore argue that prey may be limited and speculate that bats, particularly females, were moving through High Park to forage elsewhere, especially considering that female capture success related negatively to beetle abundance within the park. Big brown bats are known to commute ~4 km (and up to 19 km) from roosts to foraging sites (Brigham 1991; Everette et al. 2001; Arbuthnott and Brigham 2007) and travel outside urban areas for more profitable foraging (Everette et al. 2001; Duchamp, Sparks, and Whitaker Jr. 2004; Duchamp and Swihart 2008). While we could not confirm foraging movements, we propose that bats are moving through High Park to forage along the Humber River. Given previous work has indicated that bat activity is higher in riparian areas (Grindal, Morissette, and Brigham 1999; Gallo et al. 2018), use of the Humber River by urban bats warrants further investigation.

Despite establishing a series of scanning locations that would ensure our ability to detect bats, we did not locate bats roosting within High Park. Those bats we did locate roosted on private residential properties outside the park where we could not confirm the exact nature (i.e. trees or buildings) of the roosts—the exception being one maternity colony in the chimney of a house. This is consistent with the fact that big brown bats in eastern North America are well-known for roosting in human-made structures (Agosta 2002; Lausen and Barclay 2006), likely because buildings provide warmer, more stable microclimates for female bats and pups (reviewed in Russo and Ancillotto 2015). Considering the thermoregulatory benefits provided by buildings, it seems reasonable that bats were not found roosting within the park where the few existing buildings are inaccessible to bats. Instead, it is likely bats were roosting outside the park where they could not be detected. Evidence that the ratio of volant young to nursing females was 2:1, which is consistent with other big brown bats in eastern North America (including southern Ontario, Mayberry and Faure 2015) that commonly produce twins (Kurta and Baker 1990; O'Shea et al. 2010), further suggests bats were finding suitable roosts elsewhere.

Our findings highlight the importance of collecting detailed demographics on urban bat populations. Although females at our study site were in better body condition than males, the bats of High Park were generally in poorer condition compared to big brown bats captured at other localities. We acknowledge that condition measures taken from bats at different localities and different times are not perfectly comparable due to geographic variation in morphology and life history traits (Turmelle, Kunz, and Sorenson 2011). That said, a comparison of forearm sizes and masses across sites shows that geographic variation in morphology is not likely driving differences in BMI. Nevertheless, this information provides impetus for future work comparing body condition and reproductive rates of High Park bats across multiple seasons and to bats captured at other sites along an urbanized gradient. In particular, given that BMI is a strong predictor of overwinter survival during hibernation for both male and female bats (Stawski, Willis, and Geiser 2014), this information about bat condition could be useful for informing future management decisions.

Bats, common or otherwise, warrant our protection as they provide critical ecosystem services in the form of pollination, seed dispersal, and, in the case of insectivorous Vespertilionids like big brown bats, pest control (Kunz et al. 2011). However, bats face a variety of threats including, but not limited to, death at wind farms, indiscriminate killing by vandals and property owners, and habitat loss due to urbanization (Mickleburgh, Hutson, and Racey 2002; Jung and Threlfall 2016). Considering that urbanization will continue to impact wildlife, there is a need for more detailed information about the behaviour, genetics, demographics and habitat use patterns of urban-adapted species to inform their conservation in highly modified landscapes. Although we can draw limited conclusions based on a single season of data collected at a single urban site, this work highlights the importance of considering sex-specific patterns in habitat use and collecting detailed demographic information. While additional work will be needed to elucidate if patterns of sexual segregation, offspring sex ratios and body condition hold across seasons and at different study sites in the urbanized landscape, this detailed understanding of habitat use will be necessary moving forward for management of species living at the human wildlife interface.

Animal welfare

Bats were captured with permission from the Ontario Ministry of Natural Resources. Animal handling protocols used in this study conformed to the guidelines of the Canadian Council on Animal Care and were approved by the University of Toronto animal care committee.

Data availability

Data presented in this article is available at datadryad.org (doi: 10.5061/dryad.4nn6dv0).

Supplementary data

Supplementary data are available at *JUECOL* online.

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Conflict of interest statement. None declared.

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