



Original research article

Green roofs provide habitat for urban bats



K.L. Parkins ^{*}, J.A. Clark

Department of Biological Sciences, Fordham University, 441 East Fordham Road, Bronx, NY, 10458, USA

ARTICLE INFO

Article history:

Received 2 June 2015

Received in revised form 22 July 2015

Accepted 23 July 2015

Keywords:

Acoustic monitoring

Bats

Green roof

Urban ecology

Urban wildlife

Urbanization

ABSTRACT

Understanding bat use of human-altered habitat is critical for developing effective conservation plans for this ecologically important taxon. Green roofs, building rooftops covered in growing medium and vegetation, are increasingly important conservation tools that make use of underutilized space to provide breeding and foraging grounds for urban wildlife. Green roofs are especially important in highly urbanized areas such as New York City (NYC), which has more rooftops (34%) than green space (13%). To date, no studies have examined the extent to which North American bats utilize urban green roofs. To investigate the role of green roofs in supporting urban bats, we monitored bat activity using ultrasonic recorders on four green and four conventional roofs located in highly developed areas of NYC, which were paired to control for location, height, and local variability in surrounding habitat and species diversity. We then identified bat vocalizations on these recordings to the species level. We documented the presence of five of nine possible bat species over both roof types: *Lasiusurus borealis*, *L. cinereus*, *L. noctivagans*, *P. subflavus*, and *E. fuscus*. Of the bat calls that could be identified to the species level, 66% were from *L. borealis*. Overall levels of bat activity were higher over green roofs than over conventional roofs. This study provides evidence that, in addition to well documented ecosystem benefits, urban green roofs contribute to urban habitat availability for several North American bat species.

© 2015 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

1. Introduction

Urbanization is a leading cause of species endangerment in the United States (Czech et al., 2000) with persistent trends of decreased species richness and diversity (McKinney, 2008, 2002) as well as a high degree of biotic homogenization for most taxa (Lockwood et al., 2000; McKinney and Lockwood, 1999). As of 2008, more than half the world's human population lived in cities, and this proportion is predicted to grow to 72% by 2050 (United Nations, 2012), significantly impacting biodiversity (McDonald et al., 2008). Hence, as the urban human population continues to increase, it becomes progressively more important to include urbanized areas in biological conservation efforts (Marzluff and Rodewald, 2008). Mitigating the negative consequences of urbanization, thus conserving biodiversity in urban habitats, has a positive impact on both humans and ecosystems (Savard et al., 2000). One potential tool in conserving urban biodiversity is the installation of green roofs.

Green roofs are vegetated rooftops. Built on flat or sloped rooftops, they consist of a root barrier, a drainage layer, a filter layer, growing medium, and vegetation (Getter and Rowe, 2006). Green roofs benefit urban ecosystems by providing services such as reducing stormwater runoff (Berndtsson, 2010; VanWoert et al., 2005) and mitigating the urban heat island effect (Getter and Rowe, 2006; Smith and Roebber, 2011). More recently, studies have begun to investigate the potential of green roofs to increase urban biodiversity by providing patches of suitable habitat (Oberndorfer et al., 2007). This may be

* Corresponding author. Tel.: +1 443 850 0792.

E-mail address: kaitlynlparkins@gmail.com (K.L. Parkins).

of particular importance in cities where there is more rooftop surface area than available green space. Several recent studies found that vegetated roofs can provide valuable habitat for a multitude of microorganisms and arthropods, especially when designed to replicate native habitat (Braaker et al., 2014; Brenneisen, 2007; Colla et al., 2009; Getter and Rowe, 2006; Kadas, 2007). Even small green roofs increase the connectivity of urban habitat patches, influencing the diversity of mobile arthropods positively (Braaker et al., 2014). An arthropod prey base and vegetative cover has the potential to provide usable habitat for vertebrates with the mobility to reach rooftops. Birds are known to use green roofs for foraging and nesting (Baumann, 2007) and, in some cases, green roof habitats are developed specifically for avian species of concern (Gedge and Kadas, 2005; Oberndorfer et al., 2007).

However, birds are not the only vertebrates with the potential to take advantage of urban rooftop habitats. Bats are an ecologically and economically important taxonomic group (Boyles et al., 2011; Kunz et al., 2011), and, presumably, volancy enables them to take advantage of small, elevated patches of habitat that are inaccessible to terrestrial mammals. While some bats are commonly observed in cities worldwide (e.g., Avila-Flores and Fenton, 2005; Hourigan et al., 2010 and Rydell, 1992), the effects of urbanization are species-specific and highly dependent on landscape context (Gehrt and Chelsvig, 2004, 2003) and level of disturbance (Hourigan et al., 2006; Jung and Kalko, 2011). Most studies of urban bats have found that urbanization results in a reduction of species diversity and the dominance of a few, open-adapted, generalist species (Avila-Flores and Fenton, 2005; Coleman and Barclay, 2012; Duchamp and Swihart, 2008; Loeb et al., 2008; Luck et al., 2013; Threlfall et al., 2011; Ulrey et al., 2005). Even among urban-adapted bats, however, activity is dependent on the availability of suitable habitat for roosting and foraging as well as prey within the urban matrix (Avila-Flores and Fenton, 2005; Dixon, 2011). Thus, the presence of green roofs with high arthropod abundance and diversity may be beneficial foraging grounds for bats in urban habitats.

Pearce and Walters (2012) provided preliminary evidence supporting this prediction in the UK: bat activity was higher over green roofs compared to roofs with only conventional roofing material. Because Pearce and Walters (2012) monitored each site in their study for only a total of seven nights during a single breeding season and because bat activity has high temporal variability (Hayes, 1997), their results are difficult to generalize.

The primary objective of this study is to expand the previous research investigating urban green roofs as habitat for bats. We collected a larger dataset than previous studies by comparing bat activity over urban green and conventional urban rooftop sites for an entire season. Using passive recording devices, we recorded bat passes and feeding buzzes (defined below), which can indicate foraging activity. We predicted that there would be more bat activity and higher species richness over urban green roofs than nearby comparable conventional roofs. Because surrounding landscape variables are likely to influence bat activity at a given site, we also investigated surrounding land cover on overall bat activity.

2. Methods

2.1. Study sites

Study sites were located within the Bronx, Queens, and Manhattan boroughs of New York, NY, USA. New York City (NYC) has an approximate population of 8.4 million people over 487 km² (US Census Bureau, 2014).

To compare bat activity between green and conventional roof sites, we used a paired study design as recommended by Hayes (1997) to help control for the large amount of temporal variation in bat activity within and among nights and seasons. Four green roofs were selected for this study. Each roof had a waterproof membrane and growing substrate, and all were completely covered in vegetation. For each green roof, a nearby conventional roof site was selected for comparison. Conventional roofs were the same number of stories tall as the paired green roof, were located within one city block of the green roof, and had conventional blacktop or concrete roofing material with no vegetation (Fig. 1). All paired sites were either six or eight stories tall and of similar height to surrounding buildings, and there was no difference in lighting on the roofs—no roofs had distinctive or exceptional nighttime lighting. One of the paired roof sites was connected but located a substantial distance away from each other so that recorders on each roof type were only recording bat activity over the roof on which they were installed. Examining recordings after the first week of deployment verified that each set of paired detectors did not record the same bats simultaneously.

2.2. Bat acoustic recording

Bat activity was recorded using passive SongMeter SM2BAT+ (Wildlife Acoustics, Concord, MA) full spectrum ultrasonic acoustic recording units (detectors) between 1 May and 5 September 2013. Passive sampling was used instead of active recording because personnel were not allowed on rooftops at night. One detector was deployed in the center of each roof and left for the duration of the study for a total of eight detectors on eight roofs. We attached external SMX-US omnidirectional microphones to the top of 2.7-m poles to minimize echolocation bounce off of hard surfaces and to maximize the number and quality of calls recorded. Microphones were calibrated before deployment (Parsons and Szewczak, 2009) using an Ultrasonic Calibrator (Wildlife Acoustics, Concord, MA) with a 40 kHz pulse.

Detectors were set to record calls continuously from civil twilight to civil twilight. Detectors were set with a 192 kHz sample rate, 12 kHz digital high pass filter, 18 dB trigger level, microphone bias off, and 36 dB gain. We used a 2.0 s trigger

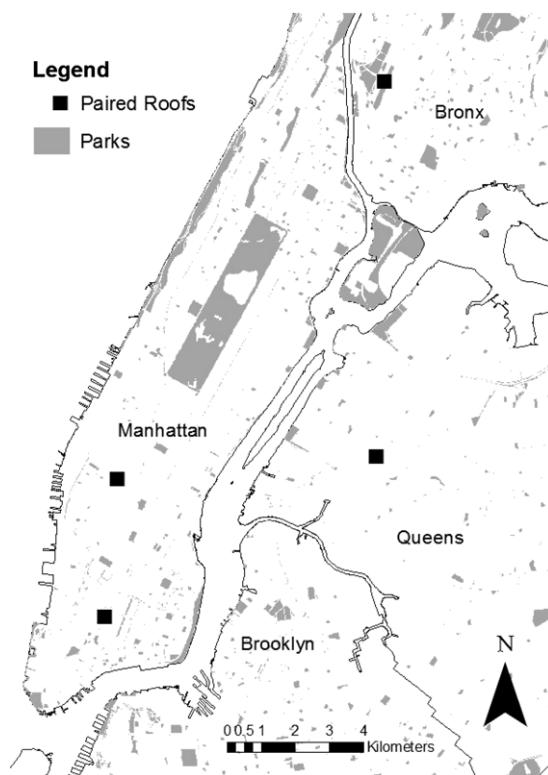


Fig. 1. Location of paired green and conventional roof sites in New York City, NY, USA used in this study of urban bat activity.

window minimum and 8.0 s maximum file length so that calls would be an appropriate length for the analysis software. Calls were recorded in WAV format onto data cards and copied to hard drives for later analysis. Data cards and batteries were changed every two weeks.

2.3. Bat call analysis

Due to occasional unexpected detector failures (e.g., because of battery displacement or vandalism), only data from nights when both detectors in a pair were functioning for the entire night were included for analysis. This approach helped maintain the integrity of the paired design. Recordings from all sites were first passed through SonoBat Batch Scrubber Utility 5.2 (DND Design, Arcata, CA) using default settings to remove the majority of files that did not contain bat passes. A bat pass (or “call”) was defined as a file with two or more pulses and with each pass separated by one or more seconds (Kalcounis et al., 1999; White and Ghert, 2001). Due to the large amount of regular, high- and low-frequency ambient noise in our urban setting, files were then visually inspected on a time–frequency sonogram for the presence of bat echolocation calls in order to manually eliminate files that contained only non-bat noise.

All passes identified as “bats”, including those that were not suitable for species identification, were used to calculate an index of bat activity. Relative bat activity at each site was quantified as the number of bat passes per night (Gehrt and Chelsvig, 2003). The activity index does not provide an estimate of abundance of bats in an area (Hayes, 2000) but is, instead, an estimate of the relative use of a site and can be used to make relative comparisons between sites (Hayes, 2000; Parsons and Szewczak, 2009).

2.3.1. Foraging activity

Quantification of passes containing “feeding buzzes” or “terminal buzzes” (see Griffin, 1958 and Griffin et al., 1960) is often used to indicate foraging activity in acoustic monitoring studies (e.g., Avila-Flores and Fenton, 2005; Fukui et al., 2006; Grindal et al., 1999; Kalcounis et al., 1999; McCracken et al., 2007; Pearce and Walters, 2012 and Vaughan et al., 1997). We examined passes visually for the characteristic high inter-pulse repetition rate, steep pulse slope, and short pulse duration of a feeding buzz (Griffin et al., 1960; McCracken et al., 2007; Schnitzler and Kalko, 2001) as in Kalcounis et al. (1999). Passes containing feeding buzzes were labeled as such, tallied for each site, and used to calculate a “buzz ratio” or ratio of feeding buzzes to bat passes (Vaughan et al., 1996). Passes containing feeding buzzes were only quantified for overall bat activity, not for each species specifically.

2.3.2. Species identification

Bat passes were examined for quality before species analysis, and only regular, search phase calls with a single echolocating bat were used for species analysis as low-quality, fragmented calls are likely to result in misidentification (Szewczak, 2002). Any obviously fragmented calls were not included for analysis (Miller, 2001). These calls were then analyzed using default settings in SonoBat NNE 3.2.0 automated classifier: a required call quality of 0.80 and a 0.90 decision threshold (as in Kalcounis-Ruppell et al., 2013 and Jameson and Willis, 2014). Identifications were then checked using an acoustic identification key to confirm species presence at each site and to investigate any unusual identifications made by the automated classifier.

The ability to make interspecific comparisons among sites using acoustic recordings is limited, and the ability to record and correctly identify calls varies between species (Hayes, 2000; O'Farrell and Gannon, 1999), as species composition can be skewed by the presence of a small number of highly active bats. To account for species-specific differences in activity, we used the Miller activity index (Miller, 2001) to examine relative activity between species. The Miller activity index is determined by the number of one-minute time blocks that each species is present at each site. We also examined the difference in species richness between sites using only species presence.

2.4. Vegetation cover analysis

Land cover was analyzed using ArcMap 10.2 (ESRI, Redlands, CA). The data source was the 2010 Landcover Raster Dataset, a high resolution (3 ft²) raster available from NYC OpenData (<https://data.cityofnewyork.us>). We reclassified seven land cover classes into the following four classes: impervious surface (includes road, buildings and other paved surfaces), water, bare earth, and vegetative cover (includes tree canopy cover and grass/shrubs). We defined concentric circular buffers at 100, 500, and 1000 m around each site (Dixon, 2011) and extracted land cover data from these buffers. Buffers larger than 1000 m could not be used because this resulted in the overlapping of buffers from two of the sites that were only slightly more than 2 km apart.

2.5. Statistical analysis

All statistical analyses used R version 3.1.1 (R Core Development Team, 2014), and a significance level of $\alpha = 0.05$ was set for all tests. We used a linear mixed effect model with roof type as a fixed effect and week as the random effect to examine bat activity over the duration of the sampling period. Differences in proportion of feeding buzzes between roof types and intraspecific differences in activity were tested using a chi-square test.

We tested for differences in the amount of vegetation at 100, 500, and 1000 m between green and conventional roof sites using a paired *t*-test to confirm the integrity of the paired design. We tested for covariance between vegetation at 100, 500, and 1000 m using Pearson's correlation. Linear regression models were run to examine the relationship between surrounding vegetation and bat activity.

3. Results

3.1. Overall bat activity

Bat detectors ran for a total of 676 detector nights (where one detector night = one detector deployed at one site for one night) between 1 May and 5 September 2013. Detectors functioned for an average of 85 nights per site over the sampling period, and 965 bat passes were recorded. Taking into account the effect of week, the effect of roof type was significant; green roofs had higher average bat activity per night ($F_{(1,93.25)} = 4.45$ $p = 0.04$) (Fig. 2).

Passes containing feeding buzzes constituted only 2% of all passes, with only 12 and 8 buzzes over green and conventional roof types respectively. This difference in buzz ratio over green versus conventional roofs was not significant (chi-square test, $p = 0.99$); however, the number of passes containing feeding buzzes were strongly correlated with total bat passes at each site ($r = 0.98$, $p < 0.001$).

3.2. Species specific bat activity

Of the 965 total passes, 67% were categorized into the Sonobat designated high frequency call clade, which for the NY region includes *Lasiurus borealis*, *Perimyotis subflavus*, and *Myotis* spp. The remaining 33% were classified into the low frequency call clade comprising *Eptesicus fuscus*, *Lasionycteris noctivagans*, and *L. cinereus*. Overall, 579 of passes (60%) could be identified to species.

Over green roofs, five species were recorded with Sonobat estimated likelihoods of 0.90 or above: *L. borealis*, *L. noctivagans*, *E. fuscus*, *P. subflavus* and *L. cinereus*. The most prominent species, *L. borealis*, accounted for 69% of all identified passes; 15% were *L. cinereus*, 15% *L. noctivagans*, 4% *P. subflavus*, and 3% *E. fuscus*.

Over conventional roofs, three species were recorded with Sonobat estimated likelihoods of 0.90 or above: *L. borealis*, *L. noctivagans*, and *L. cinereus*. There were three passes from *P. subflavus* and one from *E. fuscus*, which gave estimated likelihood

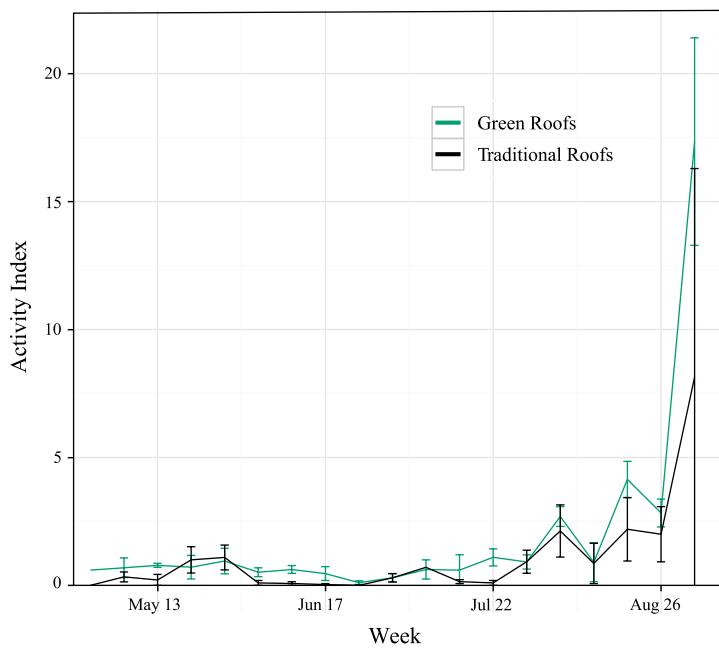


Fig. 2. Bat activity index (passes per night) (\pm SE) over green and conventional roofs in New York City, NY, between 1 May and 5 September 2013. Green roofs had higher levels of bat activity than conventional roofs ($p = 0.04$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

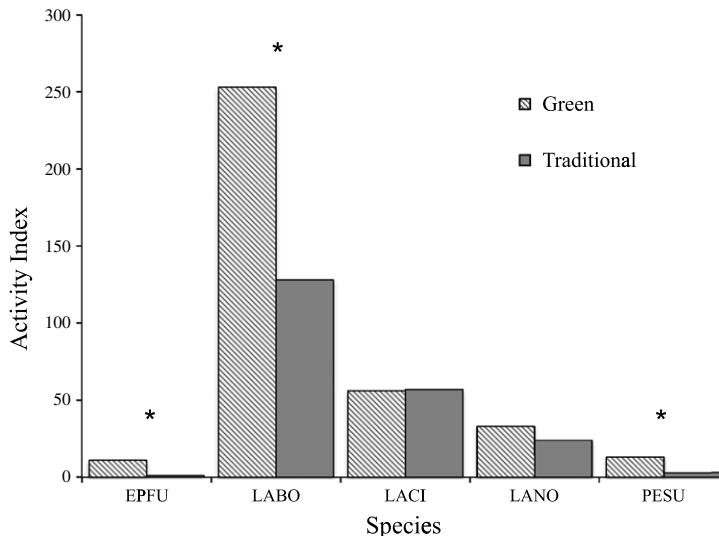


Fig. 3. Total activity index (Miller, 2001) for each bat species recorded over green and conventional roofs in New York City, NY, USA: *Eptesicus fuscus* (EPFU), *Lasius borealis* (LABO), *L. cinereus* (LACI), *Lasionycteris noctivagans* (LANO), *Perimyotis subflavus* (PESU). Differences in activity were found for only for EPFU, LABO, and PESU (* $p < 0.05$).

values of 0.58 and 0.23 respectively; however, upon inspection and analysis with an acoustic key, all of these passes were confirmed to be from the species assigned by Sonobat, thus *P. subflavus* and *E. fuscus* were also considered confirmed over conventional roofs. The most prominent species, *L. borealis*, accounted for 60% of all identified passes; 26.5% were *L. cinereus*, 11% *L. noctivagans*, 1% *P. subflavus*, and 0.5% *E. fuscus*.

There was no difference in species richness between the roof types: all five species were recorded over both green and conventional roofs. We found differences between total activity index over each roof type for *L. borealis* ($p < 0.001$), *E. fuscus* ($p = 0.03$), and *P. subflavus* ($p = 0.01$) (Fig. 3).

Table 1

Vegetation cover at 100, 500, and 1000 m around green and conventional roof sites (QU = Queens, BX = Bronx, FI = Fashion Institute, GS = Grand St.).

Buffer (m)	Site	Percent cover		
		Green roof	Conventional roof	<i>p</i> -value
100	BX	6.09	5.87	0.27
	FI	5.70	1.60	
	GS	3.21	1.03	
	QU	10.94	10.49	
	Mean	6.48	4.75	
500	BX	15.80	15.47	0.39
	FI	10.72	9.28	
	GS	6.47	4.09	
	QU	8.26	8.96	
	Mean	10.31	9.45	
1000	BX	28.2	27.56	0.41
	FI	15.64	15.51	
	GS	19.07	18.04	
	QU	31.86	29.05	
	Mean	23.69	22.54	

3.3. Surrounding land cover

Surrounding vegetation ranged from 1.0% to 10.9% at 100 m, 4.1% to 15.8% at 500 m, and 15.5% to 31.9% at 1000 m (Table 1). We found no difference in the amount of surrounding vegetation between green and conventional roofs sites at any of the three buffer distances (paired *t*-test, *p* > 0.05). Surrounding vegetation was correlated at 100 and 1000 m ($r = 0.82$, *p* = 0.01). Bat activity was correlated with surrounding vegetation at 1000 m ($r^2 = 0.50$, *p* = 0.05).

4. Discussion

4.1. The effect of green roofs

Our prediction that bats would be recorded more often over green than conventional roofs in NYC was based on the assumption that there would be more arthropod prey available to bats over vegetated roofs; hence, we expected that more bats would be present over green roofs due to increased foraging activity. Arthropod samples using sticky and bowl traps collected from three of the four green and conventional roof pairs in this study for a separate research study each showed higher species richness and abundance of arthropods (D. Partridge, unpublished data). Our initial measure of foraging activity, the buzz ratio, did not differ between site types, most likely due to an exceptionally low number of passes containing feeding buzzes recorded. Feeding buzzes are more difficult to record than search phase calls due to faster attenuation of the feeding buzz over shorter distances (see McCracken et al., 2007), an effect that is likely intensified by the presence of constant high frequency urban noise. However, the strong correlation between passes containing feeding buzzes and total passes indicates that total passes may be used as a proxy for foraging activity as in other studies (e.g., Fukui et al., 2006). The difference in average passes per night between the two roof types was small, but significant, and in agreement with the results of Pearce and Walters (2012) in the UK. Because we did not record many feeding buzzes, we could not definitively conclude that bats are foraging over green roofs, and it is possible that they are only commuting in the airspace over the roofs. However, the significantly greater amount of bat activity over green roofs, combined with evidence of more arthropods on green roofs, is a likely explanation of increased foraging activity in these patches. The green and conventional roofs in our study were otherwise similar, and we can think of no other explanation for why bats would choose to commute in green roof airspace over conventional roof airspace.

The presence of bats at a site does not directly give information on the quality of the site as habitat. Bats may be foraging over green roofs, but actual prey capture ratios, as well as quality of prey items, are unknown. We also did not compare between green roofs and other habitat patches, so our conclusions are limited to a comparison of green roofs to conventional roofs. Green roofs may not perform as well when compared to larger habitat patches or those containing resources other than just prey, such as water or trees for roosting. There are also other factors that may affect bat activity of both roof types. The factor “week” included in the analysis shows that bat activity is highly variable and is likely affected by date (seasonal bat activity) and temperature.

4.2. Surrounding landscape

While we found no difference in surrounding vegetation between the site types, the effect of surrounding vegetation at 1000 m on bat activity regardless of roof type was strong. Even though green roofs had, on average, more bat activity than conventional roofs, surrounding vegetation explained 50% of bat activity. The roofs with highest activity levels within each

roof type were those with more surrounding green space in the form of trees, shrubs, and grass. This result suggests that the availability of nearby habitat is important in contributing to the effectiveness of the green roof as a habitat patch. A visual inspection of aerial photos of the sites reveals that the vast majority of green space near these sites is tree canopy, mostly in the form of street trees and small parks. Given that the three species recorded most frequently are tree roosting bats – *L. borealis*, *L. noctivagans*, and *L. cinereus* – the presence of roosting habitat nearby may increase the ability of these species to utilize the green roof as foraging habitat or the frequency with which they encounter this habitat and subsequently stay to forage. Another possibility is that, in locations with densely packed buildings and tree canopy, green roofs provide a patch of open space in which bats can more easily forage. In either case, the combination of green roof and surrounding vegetation results in the highest bat activity.

4.3. Species-specific effects

While little information is available on the bat community composition in NYC, anecdotal evidence from naturalists and park employees in NYC, as well as studies on bats in other metropolitan areas in the US (e.g., [Loeb et al., 2008](#) and [Kurta and Teramoto, 1992](#)) led us to expect that *E. fuscus* would be the dominant species recorded during this study. Instead, *E. fuscus* was the least recorded of all species, and *L. borealis* dominated our recordings. It is likely that nearly all of the high frequency passes recorded (67% of the sample) are from *L. borealis*. The only other possible high frequency species in the region are *P. subflavus* and the *Myotis* spp. Due to the low numbers of *P. subflavus* and complete lack of *Myotis* bats in the subset of passes that were identified to the species level, the majority of unidentified high frequency passes were probably *L. borealis*. Although differences exist in detection rates between bat species that can skew the proportions of species in a sample, the dominance of *L. borealis* and low numbers of *E. fuscus* are substantial enough to challenge conventional wisdom on the community structure of bats in NYC and warrants further investigation to determine if this pattern holds true in other areas of NYC or is an artifact of the type of habitats we surveyed (i.e., parks versus building dense areas).

The lack of a difference in the number of recordings of *L. noctivagans* and *L. cinereus* over each roof type suggests that these species were recorded while commuting through the city. The low overall number of passes each for *E. fuscus* and *P. subflavus* suggests that green roofs may not benefit these two species to any great extent. *E. fuscus* is known to roost in highly urbanized areas and commute long distances to forage outside the city ([Everette et al., 2001](#)), so there is a possibility that these individuals we recorded are only being recorded over green roofs on their commute to more rural foraging grounds; however, we would then expect to record *E. fuscus* near sunset after emergence and again in the early hours of the morning upon their return. After examining the timing of *E. fuscus* recordings, we observed no patterns that would indicate that this is the case; calls from this species were dispersed throughout the night.

The proportion of *L. borealis* recorded and the greater number of passes recorded over green roofs for this species, suggest that green roofs may be particularly beneficial for this common, generalist species. The peak in activity during the fall migratory season may be due to increased presence of this species during the migratory period.

5. Conclusions

While we controlled for roof height in this study, green roofs can vary from only a few to tens of stories in height, and vegetation positioned at certain locations within the three-dimensional space of a city may be more or less beneficial to bats. Green roofs can also differ in vegetative composition, e.g., from low-lying drought tolerant species to flourishing native gardens. Our study included representative roofs from both of these classifications. The type of invertebrate habitat a roof's vegetation provides likely has an effect on the type and density of prey species available for bats; hence, some green roofs will provide better foraging habitat than others. There also may be an interaction between activity over green roofs, vegetation type, date, and temperature. For example, green roofs may be particularly beneficial during the reproductive season or conversely, during migration. All of these factors deserve additional examination. Further studies that examine the role of roof height and vegetation type along with recent research on green roof arthropod and avian communities can be used to inform stakeholders on how best to design green roofs for wildlife habitat. Our study provides a basis for future investigation of the many factors that may affect bat use of green roofs.

More specifically, our study suggests that bats that reside in urban areas may benefit from the presence of green roofs over conventional rooftops. Further, green roofs contribute to the diversity and abundance of arthropods in the urban landscape and, as such, may be beneficial as both direct foraging grounds and by contributing to prey abundance throughout the urban landscape. We do not suggest that green roofs be used in lieu of other green spaces but, instead, that they be used in conjunction with larger green spaces that provide roosts and additional foraging habitat for urban bats. In short, green roofs have greater potential to benefit bats than conventional roofs.

Acknowledgments

We thank the following institutions and individuals for access to field sites: Chris and Lisa Goode, Joe Arcoleo, The Fashion Institute of Technology, Extra Space Storage Inc., Kate Shackford, Matthew Casuccio, Anastasia Cole Plakias, and Brooklyn Grange Rooftop Farm. Thanks to Dustin Partridge for his input and help with experimental design. We would also like to thank J.D. Lewis for input on earlier versions of this manuscript.

References

- Avila-Flores, R., Fenton, M.B., 2005. Use of spatial features by foraging insectivorous bats in a large urban landscape. *J. Mammal.* 86, 1193–1204.
- Baumann, N., 2007. Ground-nesting birds on green roofs in Switzerland: Preliminary observations. *Urban Habitats* 4, 1–14.
- Berndtsson, J.C., 2010. Green roof performance towards management of runoff water quantity and quality: A review. *Ecol. Eng.* 36, 351–360.
- Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.H., 2011. Economic importance of bats in agriculture. *Science* 332, 41–42. <http://dx.doi.org/10.1126/science.1201366>.
- Braaker, S., Ghazoul, J., Obrist, M.K., Moretti, M., 2014. Habitat connectivity shapes urban arthropod communities: the key role of green roofs. *Ecology* 95, 1010–1021.
- Brenneisen, S., 2007. Space for urban wildlife: Designing green roofs as habitats in Switzerland. *Urban Habitats* 4, 27–36.
- Coleman, J.L., Barclay, R.M.R., 2012. Urbanization and the abundance and diversity of Prairie bats. *Urban Ecosyst.* 15, 87–102.
- Colla, S.R., Willis, E., Packer, L., 2009. Can green roofs provide habitat for urban bees (*Hymenoptera: Apidae*)? *Cities Environ.* 2, 1–12.
- Czech, B., Krausman, P., Devers, P., 2000. Economic associations among causes of species endangerment in the United States. *BioScience* 50, 593–601.
- Dixon, M.D., 2011. Relationship between land cover and insectivorous bat activity in an urban landscape. *Urban Ecosyst.* 15, 683–695. <http://dx.doi.org/10.1007/s11252-011-0219-y>.
- Duchamp, J.E., Swihart, R.K., 2008. Shifts in bat community structure related to evolved traits and features of human-altered landscapes. *Landsc. Ecol.* 23, 849–860.
- Everette, A.L., OShea, T.J., Ellison, L.E., Stone, L.A., McCance, J.L., 2001. Bat use of a high-plains urban wildlife refuge. *Wildl. Soc. Bull.* 29, 967–973.
- Fukui, D., Murakami, M., Nakano, S., Aoi, T., 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. *J. Anim. Ecol.* 75, 1252–1258.
- Gedge, D., Kadas, G., 2005. Green roofs and biodiversity. *Biologist* 52, 1–9.
- Gehrt, S.D., Chelvig, J.E., 2003. Bat activity in an urban landscape: Patterns at the landscape and microhabitat scale. *Ecology* 13, 939–950.
- Gehrt, S.D., Chelvig, J.E., 2004. Species-specific patterns of bat activity in an urban landscape. *Ecology* 14, 1–12.
- Getter, K.L., Rowe, D.B., 2006. The role of extensive green roofs in sustainable development. *HortScience* 41, 1276–1285.
- Griffin, D.R., 1958. *Listening in the Dark*. Yale University Press, New Haven, CT.
- Griffin, D.R., Webster, F.A., Michael, C.R., 1960. The echolocation of flying insects by bats. *Anim. Behav.* 8, 141–154.
- Grindal, S.D., Morissette, J.L., Brigham, R.M., 1999. Concentration of bat activity in riparian habitats over an elevational gradient. *Can. J. Zool.* 77, 972–977.
- Hayes, J.P., 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. *J. Mammal.* 78, 514–524.
- Hayes, J.P., 2000. Assumptions and practical considerations in the design and interpretation of echolocation-monitoring studies. *Acta Chiropterol.* 2, 225–236.
- Hourigan, C.L., Catterall, C.P., Jones, D., Rhodes, M., 2010. The diversity of insectivorous bat assemblages among habitats within a subtropical urban landscape. *Austral Ecol.* 35, 849–857.
- Hourigan, C.L., Johnson, C., Robson, S.K.A., 2006. The structure of a micro-bat community in relation to gradients of environmental variation in a tropical urban area. *Urban Ecosyst.* 9, 67–82. <http://dx.doi.org/10.1007/s11252-006-7902-4>.
- Jameson, J.W., Willis, C.K.R., 2014. Activity of tree bats at anthropogenic tall structures: Implications for mortality of bats at wind turbines. *Anim. Behav.* 97, 145–152.
- Jung, K., Kalko, E.K.V., 2011. Adaptability and vulnerability of high flying Neotropical aerial insectivorous bats to urbanization. *Divers. Distrib.* 17, 262–274.
- Kadas, G., 2007. Rare invertebrates colonizing green roofs in London. *Urban Habitats* 4, 66–86.
- Kalcounis, M.C., Hobson, K.A., Brigham, R.M., Hecker, K.R., 1999. Bat activity in the boreal forest: Importance of stand type and vertical strata. *J. Mammal.* 80, 673–682.
- Kalcounis-Ruppell, M.C., Briones, K.M., Homyack, J.A., Petric, R., Marshall, M.M., Miller, D.A., 2013. Hard forest edges act as conduits, not filters, for bats. *Wildl. Soc. Bull.* 37, 571–576.
- Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. *Ann. New York Acad. Sci.* 1223, 1–38. <http://dx.doi.org/10.1111/j.1749-6632.2011.06004.x>.
- Kurta, A., Teramoto, J.A., 1992. Bat community structure in an urban park. *Ecography* 15, 257–261.
- Lockwood, J.L., Brooks, T.M., McKinney, M.L., 2000. Taxonomic homogenization of the global avifauna. *Anim. Conserv.* 3, 27–35.
- Loeb, S.C., Post, C.J., Hall, S.T., 2008. Relationship between urbanization and bat community structure in national parks of the southeastern US. *Urban Ecosyst.* 12, 197–214.
- Luck, G.W., Smallbone, L., Threlfall, C., Law, B., 2013. Patterns in bat functional guilds across multiple urban centres in south-eastern Australia. *Landsc. Ecol.* 28, 455–469. <http://dx.doi.org/10.1007/s10980-012-9842-0>.
- Marzluff, J.M., Rodewald, A.D., 2008. Conserving biodiversity in urbanizing areas: Nontraditional views from a bird's perspective. *Cities Environ.* 1, 1–27.
- McCracken, G.F., Gillam, E.H., Westbrook, J.K., Lee, Y.F., Jensen, M.L., Balsley, B.B., 2007. Brazilian free-tailed bats (*Tadarida brasiliensis*: Molossidae, Chiroptera) at high altitude: links to migratory insect populations. *Integr. Comp. Biol.* 48, 107–118. <http://dx.doi.org/10.1093/icb/icn033>.
- McDonald, R.J., Marty, K.L., Forman, R.T.T., 2008. The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biol. Conserv.* 141, 1695–1703.
- McKinney, M.L., 2002. Urbanization, biodiversity, and conservation. *BioScience* 52, 883–890.
- McKinney, M.L., 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst.* 11, 161–176.
- McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Science* 285, 1834–1836.
- Miller, B.W., 2001. A new method for determining relative activity of free flying bats using a new activity index for acoustic monitoring. *Acta Chiropterol.* 3, 93–105.
- Oberndorfer, E., Lundholm, J., Bass, B., Coffman, R.R., Doshi, H., Dunnett, N., Gaffin, S., Kohler, M., Liu, K.K.Y., Rowe, B., 2007. Green roofs as urban ecosystems: Ecological structures, functions, and services. *BioScience* 57, 823–833.
- O'Farrell, M.J., Gannon, W.L., 1999. A comparison of acoustic versus capture techniques for the inventory of bats. *J. Mammal.* 80, 24–30.
- Parsons, S., Szewczak, J.M., 2009. Detecting, recording, and analyzing the vocalizations of bats. In: Kunz, T.H., Parsons, S. (Eds.), *Ecological and Behavioral Methods for the Study of Bats*. The Johns Hopkins University Press, Baltimore, MD, pp. 91–111.
- Pearce, H., Walters, C.L., 2012. Do green roofs provide habitat for bats in urban areas? *Acta Chiropterol.* 14, 469–478. <http://dx.doi.org/10.3161/150811012X661774>.
- R Core Development Team, 2014. R: A language and environment for statistical computing.
- Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. *Funct. Ecol.* 6, 744–750.
- Savard, J.-P.L., Clergeau, P., Mennecier, G., 2000. Biodiversity concepts and urban ecosystems. *Landsc. Urban Plann.* 48, 131–142.
- Schnitzler, H.-U., Kalko, E.K.V., 2001. Echolocation by insect-eating bats. *BioScience* 51, 557–569.
- Smith, K.R., Roebber, P.J., 2011. Green roof mitigation potential for a proxy future climate scenario in Chicago, Illinois. *J. Appl. Meteorol. Climatol.* 50, 507–522. <http://dx.doi.org/10.1175/2010JAMC2337.1>.
- Szewczak, J.M., 2002. Advanced analysis techniques for identifying bat species. In: Brigham, R.M., Kalko, E.K.V., Jones, G., Parsons, S., Limpens, H.J.G.A. (Eds.), *Bat Echolocation Research: Tools, Techniques, Analysis, Bat Conservation International*, Austin, TX.
- Threlfall, C., Law, B., Penman, T., Banks, P.B., 2011. Ecological processes in urban landscapes: mechanisms influencing the distribution and activity of insectivorous bats. *Ecography* 34, 814–826. <http://dx.doi.org/10.1111/j.1600-0587.2010.06939.x>.
- Ulrey, W.A., Sparks, D.W., Ritz, C.M., 2005. Bat communities in highly impacted areas: Comparing Camp Atterbury to the Indianapolis airport. *Proc. Indian Acad. Sci.* 114, 73–76.
- United Nations, 2012. World urbanization prospects: The 2011 revision. United Nations, Department of Economic and Social Affairs Population Division, New York, New York, USA.

- US Census Bureau, 2014. Annual estimates of the resident population: April 1, 2010 to July 1, 2014—Metropolitan Statistical Area. Available online at: <http://factfinder.census.gov> (accessed 15.05.15).
- VanWoert, N.D., Rowe, D.B., Andresen, J.A., Rugh, C.L., Fernandez, R.T., Xiao, L., 2005. Green roof stormwater retention. *J. Environ. Qual.* 34, 1036. <http://dx.doi.org/10.2134/jeq2004.0364>.
- Vaughan, N., Jones, G., Harris, S., 1996. Effects of sewage effluent on the activity of bats (Chiroptera: Vespertilionidae) foraging along rivers. *Biol. Conserv.* 78, 337–343.
- Vaughan, N., Jones, G., Harris, S., 1997. Habitat use by bats (Chiroptera) assessed by means of a broad-band acoustic method. *J. Appl. Ecol.* 34, 716–730.
- White, E.P., Ghert, S.D., 2001. Effects of recording media on echolocation data from broadband bat detectors. *Wildl. Soc. Bull.* 29, 974–978.