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The Influence of Vegetation and Insect Abundance on Insectivorous Bat Activity during Dusk Emergence in an Urban Space in Metro Manila, Philippines

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ABSTRACT

Because of their importance in the maintenance of ecological processes and sensitivity to multiple stressors, bat activity is increasingly being used to study habitat associations, including the effects of urbanization and other landuse changes. However, to be effectively used as a bioindicator, baseline information on bat activity patterns must first be established. In this study, we aimed to determine patterns of insectivorous bat activity, richness, and assemblage within an urban green space in the Philippines' capital region in relation to habitat type, insect abundance, and environmental conditions, with particular focus on activity at dusk emergence. Bat activity was measured as the number of bat passes per minute using a portable bat recorder at five time intervals from 5:30 PM to 7:30 PM, and compared between 10 open and 10 forested sites. Bat calls were classified into sonotypes based on five call variables. There was no difference in bat activity between forested and open sites, but more sonotypes were recorded in open sites. Both bat activity and sonotype richness peaked between 6:00 PM and 6:30 PM, representing a short foraging bout upon dusk emergence. However, we did not observe significant relationships between bat activity and insect abundance, air temperature, and relative humidity. Our study found considerable bat activity and diversity in an urban ecosystem, a poorly explored field of research in the Philippines. Additional studies are necessary to understand the impact of landuse changes on Philippine bats, and to inform their conservation and management in anthropogenically altered habitats.

Keywords: Bioacoustic monitoring, urban ecosystems, insectivorous bats

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INTRODUCTION

The rapid development of urban areas in response to growing human populations often involve little to no planning in developing countries like the Philippines (Vallejo et al. 2009; de Araujo and Bernard 2016). Metro Manila, or the National Capital Region, is considered one of the five largest urban areas in the world, with an estimated population of 13 million in 2015 and an annual growth rate of 1.58% (Philippine Statistics Authority 2016). In the past 30 years, urbanization has also spilled over the fringes of Metro Manila, with rapid land use conversion resulting in the continued fragmentation and destruction of green spaces in the National Capital Region and its surrounding provinces (Bravo 2017).

Despite the fragmentation and destruction of natural habitats due to urbanization, several studies have shown that remaining green spaces in urban landscapes still support considerable diversity, acting as refuge for different species amidst a rapidly changing environment (Pickett et al. 2001). For example, an inventory of terrestrial vertebrates within two university campuses in the center of Metro Manila has documented the presence of six amphibian species, 13 reptile species, 47 bird species, and 10 mammal species, of which 11 are endemic to the country (Ong et al. 1999). More recent records of bird occurrences in Metro Manila from birdwatching hobbyists and clubs such as the Wild Bird Club of the Philippines (WBCP) place the species richness of birds at about 140 (WBCP2015). Compared to birds, significantly less monitoring and studies have been done on the diversity of other terrestrial vertebrates in Metro Manila and other urban areas of the Philippines.

Flight allows bats to cross environmental matrices otherwise unfavorable to other animals and to persist in altered habitats. These make bats important components of urban ecosystems, and likely crucial in the maintenance of ecological processes in urban landscapes. Ecosystem services provided by bats include pollination and seed dispersal of urban flora, and control of arthropod populations (Jones et al. 2009; de Araújo and Bernard 2016). Insectivorous bats, in particular, are considered excellent pest controllers, as their insect diet amounts to 25-50% of their body mass (Kunz et al. 2011; Boyles et al. 2013). They are also sensitive to a wide range of stressors, such as habitat alteration and fragmentation, climate change, agricultural expansion, and pollution, and thus have the potential to be excellent bioindicators (Jones et al. 2009). In addition, because bats are not influenced by regular direct human interactions that may influence community composition, studies in urban areas may offer insights more directly related to the urbanized elements of the environment (Krauel and LeBuhn 2016).

The insectivorous bat fauna of the Philippines consists of at least 55 species from six families, at least 10 of which are endemic (Ingle and Heaney 1992; Heaney et al. 2016). Because of their echolocation, insectivorous bats are difficult to sample using mist nets and require more labor-intensive capture techniques such as harp traps and tunnel traps (Heaney et al. 2016). As such, much less information is known on their taxonomy, distribution, and general ecology despite being more speciose than fruit bats (Heideman and Utzurrum 2003; Mildenstein et al. 2005).

The development of bioacoustic techniques to detect and assess insectivorous bats has helped fill this research gap in the past two decades (Sedlock 2001; Sedlock et al. 2014a; Sedlock et al. 2014b). Bats emit calls with frequencies ranging from 9 to 212 kHz, with considerable diversity in duration, bandwidth, and use of harmonics (Maltby et al. 2009). Using a combination of echolocation call parameters, bat calls can be distinguished between species, although significant intraspecific variation exists due to sex, age, geography, and habitat variations (Stathopoulos et al. 2018).

Regardless, acoustic monitoring has been used as a tool in conservation and biomonitoring schemes, particularly in determining the effect of anthropogenic activities on biodiversity (Barlow et al. 2015; Jung and Kalko 2010; Kelly et al. 2016; Newson et al. 2017).

Bat activity based on bioacoustics is increasingly being used to study habitat associations, including the effects of urbanization and other land use changes on bat assemblages. Generally, bat activity decreases with increased intensity of urbanization, with variations in degree across species and geography (Gehrt and Chelsvig 2003; Schimpp et al. 2018). Studies have shown, however, that urban green spaces, with abundant nocturnal invertebrates and tree hollows, may ameliorate the impact of urbanization on insectivorous bats (Avila-Flores and Fenton 2005; Basham et al. 2011).

Unfortunately, very few ecological studies have been done on the bats of the Philippines, much less so those targeted towards urban assemblages.Tanalgo and Hughes (2018), in their review of Philippine bat research in the last two decades, report that only 15% of all studies focus on ecology, majority of which looked at the seed dispersal ecology of frugivorous bats. In addition, the review found only seven studies conducted in urban and othermodified habitats. Thus, the impact of urbanization and other land use changes on bat assemblages is poorly understood in the Philippines and warrants investigation.

There is great untapped potential in the use of insectivorous bat acoustics for conservation and monitoring in the Philippines. However, there is still insufficient information on the most basic aspects of insectivorous bat ecology, especially in anthropogenically altered landscapes. As such, assessing the effects of urbanization on insectivorous bats requires first an understanding of local activity patterns and the factors that influence these patterns in urban environments.

In this study, we aimed to determine patterns of insectivorous bat activity, richness, and assemblage within an urban green space in the center of the Philippines' capital, with particular focus on activity at dusk emergence. We also assessed if habitat type, insect abundance, and environmental conditions influence these activity and richness patterns.

MATERIALS AND METHODS

Study area and site selection

The study was conducted within a 40-day sampling period from February to March 2018 within the University of the Philippines (UP) campus in Diliman district, Quezon City (14°37'50.37" N, 121°4'42.48" E). The university campus has academic use areas, residential areas, parks, commercial areas, and protected forest areas encompassing a total of 493 hectares. Over 900 buildings are scattered across the campus, majority of which are for housing and academic use (University of the Philippines 2012). According to data from 2009, daytime population within the campus averages at around 40,000, composed of students, academics, staff, and residents (Vallejo et al. 2009).

Based on the latest Land Use Plan of the campus (University of the Philippines 2012) and satellite images (Google Earth 2017), we randomly selected ten sampling sites each of forested and open sites (Figure 1). Based on a 50x50 m grid overlaid on satellite images of the campus, we selected forested sites as those with canopy cover greater than 60%, while open sites have less than 10% cover (Di Gregorio and Jansen 2000). Because the presence of built-up structures has an influence on measured bat activity as possible roosting areas, all sites selected were at least 150 m away from any buildings within the campus. All sampling sites were at least 100 m apart.The selected forested sites were located in two forested patches within the study area, about 0.16 km^2 and 0.05 km^2 in total area. On the other hand, the selected open sites were located in five open areas, 0.02 km^2, 0.05 km^2, 0.02 km^2, 0.10 km^2, and 0.04 km^2 in total area.

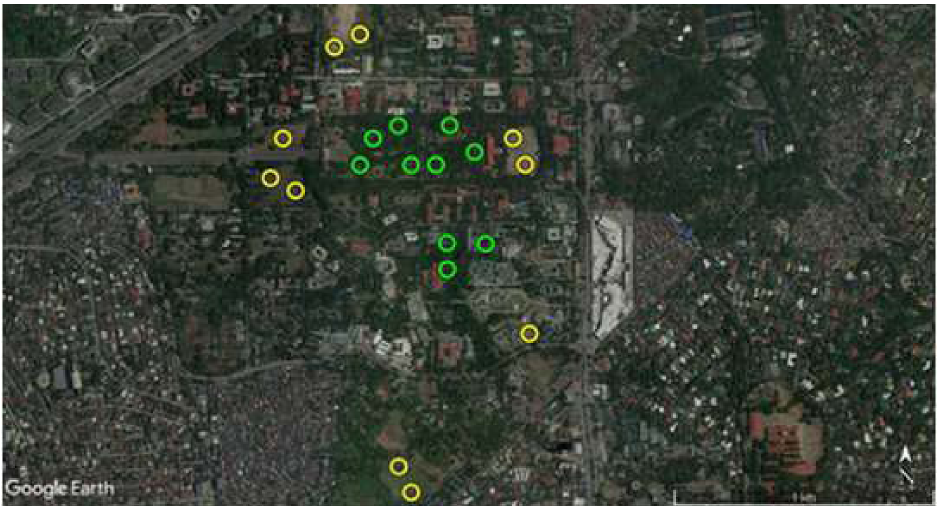

Figure 1. Ten open sites (yellow) and ten forested sites (green) within the University of the Philippines Diliman campus in Quezon City were chosen as sampling sites for the study.

Bat recordings

Recordings were collected using a Pettersson Elektronik M500 USB Ultrasound Microphone attached to a laptop PC. The M500 has a sampling frequency of 500 kHz and a frequency range of 10 to 210 kHz. Sampling was only done on nights without rain, and avoiding the two nights prior to and following a full moon. One to three sampling sites were sampled per night, alternating between forested and open sites. We recorded for three minutes at each point, following Barros et al. (2014) and de Araujo and Bernard (2016), with 30-minute intervals from 5:30 PM to 7:30 PM. The M500 was held about 1.3 m above the ground, angled at 45° relative to the ground. For each sampling point and time interval, the number of bat passes per minute were counted and used as a measure of bat activity. Only search calls were used in this study. For each search call, the following call variables were extracted using BatSound 4.2.0: call duration (D, in ms), frequency with maximum energy (Fmax, in kHz), initial frequency (Fi, in kHz), terminal frequency (Ft, in kHz), and frequency range (R, in kHz). The following settings were used for spectrograms: FFT size = 1024; FFT overlap = 0; Hanning window). Using these call variables, a Euclidean distance matrix was generated and used to construct a non-metric multidimensional scaling (NMDS) biplot using the function “metaMDS” of the Community Ecology Package (“vegan” v. 2.5-3) (Oksanen et al. 2019) in the R statistical software (v. 3.5.1) (R Core Team 2018). Clustering in the NMDS biplot was used to classify calls into sonotypes. Clusters of less than five calls were assessed as outliers and not classified into any sonotype. Discriminant function analysis (DFA) was then performed using SPSS Statistics v. 20 (IBM 2011) to evaluate validity of the classification into distinct sonotypes.

Insect sampling and environmental data collection

Insect sampling was conducted simultaneously with bat activity recording using a sweep net. Systematic sweeping within a 20 m x 20 m quadrat centered on the sampling point was conducted to obtain an estimate of nocturnal insect abundance. The insect sampling protocol used covers only the lower strata of the habitats sampled. This reduces the likelihood of our sampling interfering with the foraging bats in the area, majority of which have been observed to fly at least 15 m above the ground. However, it presumes a positive, but not necessarily close, correlation between insect abundance at different vertical strata (Taylor 1960). Collected insects were preserved in 70% ethanol and then identified to order level and quantified as abundances per order. Air temperature and relative humidity were recorded at every sampling session, simultaneous with bat recording and insect sampling.

Data analyses

Kruskal-Wallis tests were conducted to test for differences in bat activity and sonotype richness across different time points, and between open and forested sites. Variations in insect abundance, air temperature, and relative humidity were also compared using Kruskal-Wallis tests. NMDS biplots from Bray-Curtis distances and permutational MANOVA were used to assess differences in bat assemblage using the “vegan” package in R (Oksanen et al. 2019). Sonotypes were used as proxy for taxa and bat activity as proxy for abundance.

Generalized linear models were constructed with quasi-Poisson distribution to analyze the influence of time, habitat type, air temperature, and insect abundance on bat activity and sonotype richness. Relative humidity was not included in the model due to collinearity with air temperature. A quasi-Poisson model was used to correct for overdispersion. The model with the smallest corrected Akaike’s information criterion (AICc) was considered the best-fitting model.

RESULTS

A total of 824 bat passes were recorded over 300 minutes of recordings. Of the 100 files analyzed, 39 did not contain search calls (24 from forested and 15 from open sites). Majority of the empty recordings were sampled at 5:30 PM (n = 18) and at 7:30 PM (n = 11). The number of bat passes per recording ranged from 0 to 54 in forested sites (mean± SEM = 6.84 ± 1.81) and from 0 to 57 in open sites (mean = 9.64 ± 2.05). Across sampling times, the number of bat passes per recording was lowest at 5:30 PM (mean = 0.35 ± 0.30) and highest at 6:30 PM (mean = 19.75 ± 4.05).

Five calls with low detail were not used to measure call characters. Based on five call characters, the NMDS biplot constructed revealed seven potential sonotypes and 15 outliers. Each bat pass was classified into these seven sonotypes (Figure 2). DFA confirmed the validity of the grouping, with 64.4% of original grouped cases correctly classified. The first two canonical functions cumulatively account for 98.0% of the discriminating ability, while including the third function explains 99.9% of the characters'discriminating ability. The two functions with the highest eigenvalues are most correlated with call duration (CV = 0.95) and both maximum frequency (CV = 0.96) and terminal frequency (CV = 0.92). The third canonical function is most highly correlated with frequency range (CV = 0.99).

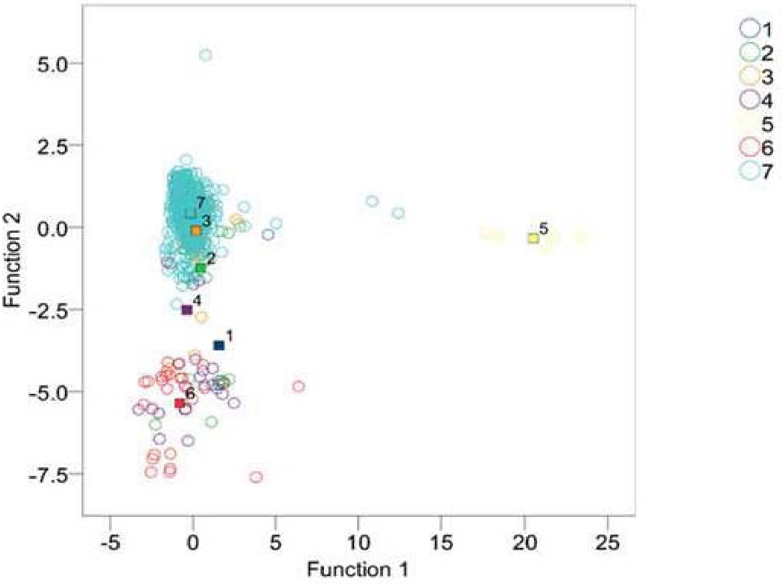

Figure 2. Canonical discriminant functions biplot showing classification of 804 bat calls into seven distinct sonotypes.

Majority of the calls were classified into Sonotype 7 (n = 659), most distinctly characterized by the shortest call duration, the widest frequency range, and the highest initial frequency. The six other sonotypes were only represented by five to 49 search calls (Table 1). Six sonotypes were recorded from both open and forested sites. Sonotype 5 was recorded only in the open sites.

Table 1. Call characteristics of the seven distinct sonotypes recorded within the University of the Philippines Diliman campus. Values are shown as mean ± SEM.

Sonotype (number of samples)	Initial frequency, F_i (kHz)	Terminal frequency, F_i (kHz)	Frequency at maximum energy, F_{max} (kHz)	Call duration, D (ms)	Frequency range, R (kHz)
1 (8)	30.88 ± 2.47	29.00 ± 2.73	30.20 ± 2.60	19.29 ± 1.58	1.88 ± 0.61
2 (28)	39.48 ± 1.45	37.19 ± 1.43	38.31 ± 1.41	12.45 ± 0.81	2.30 ± 0.40
3 (49)	44.52 ± 0.78	41.20 ± 0.57	42.39 ± 0.55	9.99 ± 0.40	3.32 ± 0.47
4 (29)	39.84 ± 2.07	32.19 ± 2.04	34.56 ± 1.88	10.92 ± 1.07	7.65 ± 0.91
5 (5)	50.70 ± 2.80	43.36 ± 0.46	44.14 ± 0.37	85.22 ± 3.99	7.34 ± 2.43
6 (26)	32.02 ± 1.42	22.82 ± 1.14	24.52 ± 1.13	12.63 ± 1.58	9.20 ± 1.24
7 (659)	52.29 ± 0.31	43.09 ± 0.11	44.88 ± 0.10	8.15 ± 0.14	9.20 ± 0.27

Bat activity, richness, and assemblage

Bat activity was not significantly different between open and forested sites (H = 1.60, df = 1, p = 0.11), with open sites having 3.21 ± 0.68 bat passes per minute and forested sites having 2.28 ± 0.60 bat passes per minute. However, bat activity differed significantly across time points, both when forested and open sites are combined (H = 44.23, df = 4, $p < 0.00$) and when analyzed separately (H = 23.32, df = 4, $p < 0.00$ and H = 23.80, df = 4, $p < 0.00$ for forested and open sites, respectively) (Figure 3). Peak bat activity within our sampling time period was from 6:00 PM to 6:30 PM, with 4.13 ± 4.41 and 6.30 ± 6.13 bat passes per minute in forested sites and 5.63 ± 6.08 and 6.87 ± 5.62 bat passes per minute in open sites. Between open and forested sites within each time point, there was no significant difference in bat activity.

Significantly more sonotypes were detected in open (n = 7; mean = 1.50 ± 0.21) than forested (n = 6; mean = 1.04 ± 0.21) sites (H = 2.01, df = 1, p = 0.045). In addition, there was a significant difference among sonotype richness across time points (H = 35.23, df= 4, p = 0.00). Within each time point, there was no significant difference in sonotype richness between forested and open sites except at 7:00PM, when sonotype richness was higher in open areas (H = 2.16, df = 1, p = 0.04) (Figure 4).

We did not find significant differences in assemblage between open and forested sites, based on both permutational MANOVA (F = 1.03, p = 0.45) and NMDS biplots. On the other hand, permutational MANOVA showed significant differences in assemblage across time points (F = 2.04, p = 0.02), although this is not readily apparent in the constructed NMDS biplot (Figure 4).

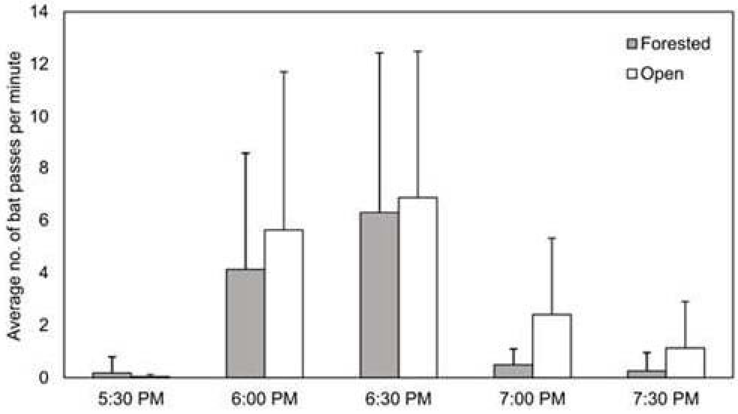

Figure 3. Bat activity, quantified as average number of bat passes per minute per time point from 5:30 PM to 7:30 PM in open and forested sites within the University of the Philippines Diliman campus. Bars indicate standard errors.

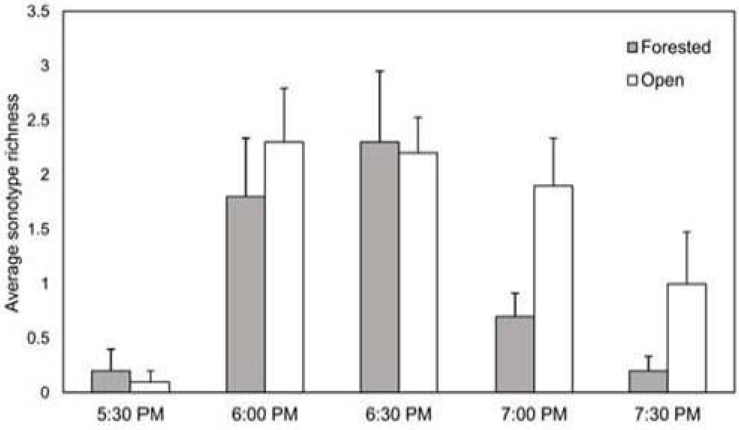

Figure 4. Average sonotype richness per time point from 5:30 PM to 7:30 PM in open and forested sites within the University of the Philippines Diliman campus. Bars indicate standard errors.

Insect abundance, air temperature, and relative humidity

To determine whether prey availability is associated with bat activity, insect sampling was done simultaneously with bat recording. A total of 721 insects distributed among nine orders (Lepidoptera, Trichoptera, Blattodea, Psocoptera, Orthoptera, Coleoptera, Diptera, Hemiptera and Hymenoptera) were captured. More than half (62.3%) were identified as members of Diptera, followed in abundance by Hemiptera (11.1%). Insect abundance significantly varied across time (H = 11.21, df = 4, p = 0.02) and between forested and open sites (H = 2.23, df = 1, p = 0.03) (Figure 5).

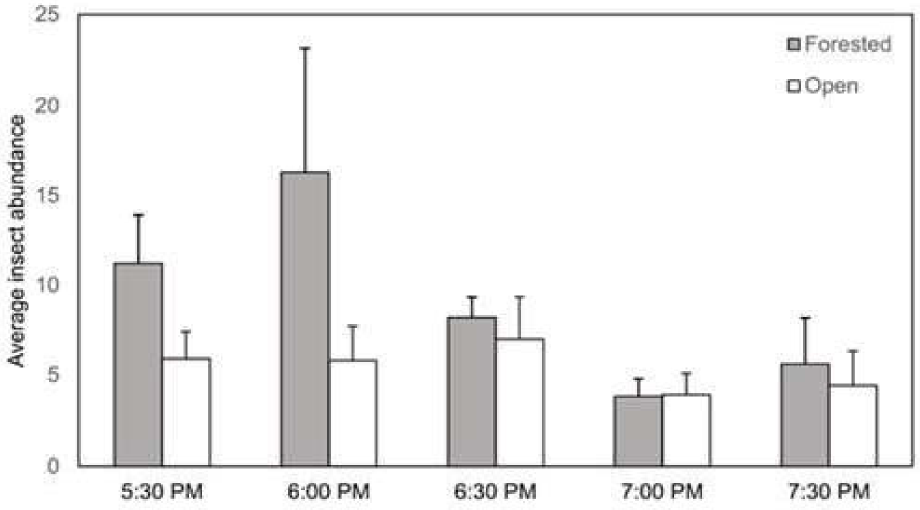

Figure 5. Average insect abundance per time point from 5:30 PM to 7:30 PM in open and forested sites within the University of the Philippines Diliman campus. Bars indicate standard errors.

Environmental conditions, specifically air temperature and relative humidity, were also taken into consideration (Figure 6). Between 5:30 PM and 7:30 PM, air temperature ranged from 26.77°C to 29.03°C in forested sites (mean = 27.86 ± 0.43), and from 26.34°C to 29.88°C in open sites (mean = 28.42 ± 0.62). Relative humidity ranged from 73.73% to 76.76% in forested sites (mean = 75.14 ± 0.58), and from 67.04% to 73.5% in open sites (mean = 69.36 ± 1.15). Average relative humidity in forested sites was significantly higher than in open sites (H=5.58, df =1, p = 0.00).

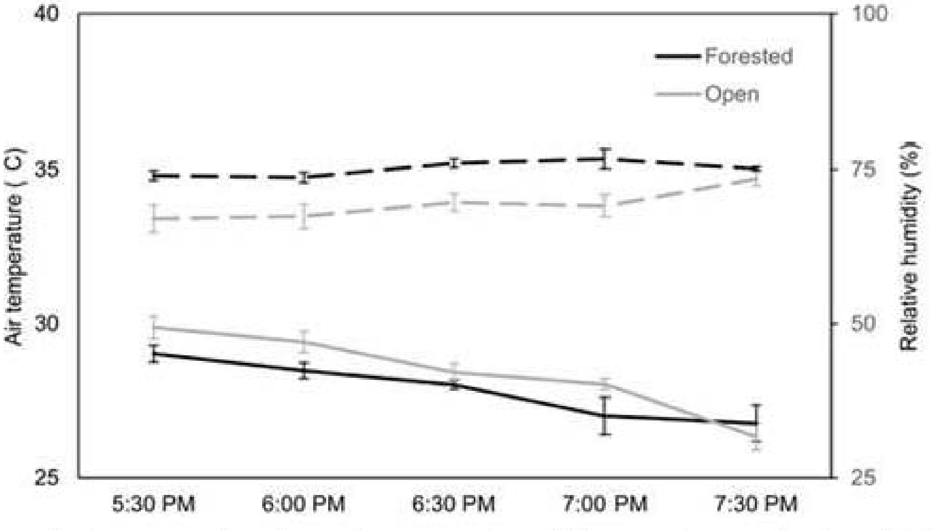

Figure 6. Average values for environmental variables per time point from 5:30 PM to 7:30 PM in open and forested sites within the University of the Philippines Diliman campus. (Air temperature– solid lines; relative humidity –dashed lines).

Bat activity and sonotype richness models

The model that best explained bat activity included all predictor variables-habitat type, time, insect abundance, and air temperature, based on corrected Akaike information criteria (AICc) (Table 2). However, bat activity was significantly influenced only by time, being significantly higher at 6:00 PM, 6:30 PM, and 7:00 PM (Table 3).

The best model for sonotype richness, on the other hand, only included habitat type and time as explanatory variables (Table 2). However, only time was a significant predictor. As with bat activity, sonotype richness was significantly higher at 6:00 PM, 6:30 PM, and 7:00 PM (Table 3). While habitat type wasnot a significant predictor of sonotype richness in our best model, we note that Kruskal-Wallis tests of sonotype richness found a significant difference between open and forested sites (p = 0.045).

Table 2. Differences in corrected Akaike information criterion (ΔAICc) scores between the top-ranked model and other models assessing the association of bat activity and sonotype richness with habitat type (Habitat), time (Time), insect abundance (Insects), and air temperature (Temp).

Model	ΔAICc
Bat activity	
Habitat + Time + Insects + Temp	0.0
Habitat + Time + Insects	12.31
Time + Insects + Temp	17.92
Habitat + Time + Temp	21.48
Habitat + Time	24.77
Sonotype richness	
Habitat + Time	0.0
Habitat + Time + Insects	1.69
Time	1.92
Habitat + Time + Temp	2.31
Time + Temp	3.73

Table 3. Summary of results of generalized linearmodels for bat activity and sonotype richness as a function of habitat type, time, insect abundance, and air temperature.

	Estimate	SE	t-value	p
Bat activity				
6:00 PM	3.766	1.324	2.844	0.0055
6:30 PM	4.247	1.332	3.188	0.0020
7:00 PM	2.879	1.387	2.076	0.0407
7:30 PM	2.302	1.472	1.563	0.1214
Air temperature	0.152	0.138	1.099	0.2746
Insect abundance	0.016	0.010	1.538	0.1274
Open sites	0.338	0.261	1.294	0.1990
Sonotype richness				
6:00 PM	2.611	0.731	3.571	0.0006
6:30 PM	2.754	0.741	3.717	0.0003
7:00 PM	2.255	0.778	2.900	0.0047
7:30 PM	1.510	0.860	1.755	0.0826
Air temperature	0.032	0.111	0.291	0.7718
Insect abundance	0.008	0.011	0.742	0.4599
Open sites	0.382	0.232	1.649	0.1025

DISCUSSION

The results of our study demonstrated variation in bat activity, sonotype richness, and sonotype assemblage across time during dusk emergence. However, we did not find significant associations of bat activity with habitat type, insect abundance, air temperature, and relative humidity.

Bat activity and prey availability

The peak in activity we observed after sunset is typical for insectivorous bats (Hayes 1997; Taylor and O'Neill 1988). This peak presumably represents initial foraging at dusk. Other studies have detected another rise in activity just before sunrise, likely representing foraging bouts and commuting back to day roosts, creating a bimodal activity pattern (Hayes 1997). Extended survey until dawn may detect other similarly short bouts of activity in our study area. Unfortunately, limitations in equipment capability and manpower resources limited the focus of this study to the activity of insectivorous bats during dusk emergence. Despite these limitations, our findings provide some baseline for future studies on the relationship of bat activity with insect abundance, air temperature, and relative humidity. The short foraging bout we observed at dusk emergence should be taken into account when conducting monitoring work, especially when resources are limited.

The foraging period shortly after sunset is explained by Kunz and Brock (1975) to be a response to a peak in prey abundance. However, we did not observe this association between insect abundance and bat activity. Support for such a relationship is variable in literature. Rautenbach et al. (1996) and Hayes (1997) found a positive correlation between bat activity and insect abundance, measured as number of individuals and dry mass, respectively. On the other hand, Rydell et al. (1996) found a delay in the dusk emergence of two aerial-hawking species after the peak in insect activity, and presumed this to be a compromise between prey availability and predation risk (Jones and Rydell 1994). Thus, the influence of insect abundance on bat activity may be species-specific, both on bats and on their preferred insect prey. Indeed, Muller et al. (2012) found that the response of insectivorous bats to prey availability differed between foraging guilds. Open-habitat foragers, but not edge-and closed-habitat foragers, responded significantly to increasing prey abundance.

While the insect sampling conducted was able to eliminate the possibility of interfering with bat foraging by positioning the sampling at ground level, the presumption of correlation between bat abundance across different vertical strata may not always be true. Patterns of vertical stratification vary widely among different insect groups and are also influenced by the habitat type (Davis et al. 2011). To circumvent the possibility of affecting bat foraging activity during insect sampling, some studies do not sample insects the same night as bat data collection (i.e., Threlfall et al. 2012) while some collect insects both prior to and during bat activity recording and use both sets of data separately (i.e., Salvarina et al. 2017).

In addition, the diversity of insects that bats prey on in our study area may not have been sampled extensively using only sweep nets. Different types of traps have their own limitations, and several studies have suggested that multiple trap types should be employed for a better estimate of insect abundance in a given area (Brigham and Saunders 1990; Sleep and Brigham 2003). These biases may partly explain the variability in the observed influence of prey availability on bat activity especially in older literature, as no standardized methodology of insect sampling has been employed across studies. Consequently, it is likely that the lack of relationship we found between bat activity and insect abundance may be affected by the same bias.

Bat activity, air temperature, and relative humidity

Environmental conditions could affect insectivorous bat activity either through direct effect on bat energetic costs or through indirect effect on prey abundance (Bender and Hartman 2015). Previous studies have observed a positive relationship between air temperature and bat activity due to thermoregulation costs (Lacki 1984; Gaisler et al. 1998). We did not observe any significant relationship in our study, but this may be due to the small variation in air temperature (2.9°C) between the two hours our sampling covered.

Existing literature showed varying relationships between relative humidity and bat activity. Lacki (1984) attributes an observed positive relationship to the high relative humidity creating a more equal vapor pressure between the respiratory tract of bats and the environment, leading to less water loss. Amorim et al. (2012) also found a positive correlation between bat activity and relative humidity, which they link to an increase in insect activity due to the combination of humidity and temperature. On the other hand, Gaisler et al. (1998) found a negative correlation between the activity of Eptesicusserotinus and relative humidity, but attributed it only to the effect of temperature on humidity. Similarly, Smith and McWilliams (2016) expect a negative correlation, but note that humidity is correlated with other environmental variables such as air temperature and atmospheric pressure.

Habitat preferences

We did not find significant differences in bat activity between forested and open areas within the campus. Our classification of habitat types was limited to only two discrete categories based on ranges of percentage of canopy cover—above 60% for forested sites and below 10% for open sites. This allowed for a simple way of classifying sampling sites and establishing contrast between the habitat types we were evaluating, as transition types between these two extremes were excluded from the study (i.e., built-up areas with scattered canopy). Because of this limitation, however, association of the observed patterns of bat activity with different aspects of vegetation structure of the sampling area cannot be evaluated.

Bat foraging activity is influenced in varying ways by different aspects of a habitat's vegetation structure, including canopy cover (Threlfall et al. 2012), distance between trees (Ghert and Chelsvig 2003), vegetation clutter, and ground cover (Suarez-Rubio et al. 2018). In our study, the presence or absence of canopy cover did not significantly affect bat activity. Our results were similar to that of Threlfall et al. (2012), who found that vegetation cover, including canopy and ground cover, had no direct influence on both insect biomass and bat activity in an urban landscape.

We recommend looking at other aspects of vegetation structure and their influence on bat activity in the Philippines. We also recommend assessing the influence of other aspects of urban landscapes on bat activity, including proximity to built-up structures, distance from bodies of water, and the presence of artificial lighting.

Echolocation call characters and habitat preferences

Differences in foraging strategy, including habitat preferences, are ultimately linked to both the characteristics of each species' echolocation calls and their wing morphology (Norberg and Rayner 1987; Sedlock 2016). Echolocation call characteristics have been associated with the habitat preferences of insectivorous bat species. For example, the echolocation calls of forest species are characterized by short durations and long intervals, which minimize call-echo and echo-echo overlaps caused by vegetation. On the other hand, open habitat species have calls with relatively long durations and low frequencies, which travel greater distances but are not as precise (Sedlock 2016).

Our analysis of five call characters identified seven distinct sonotypes, all of which were recorded from open sites and all but one from forested sites. It is likely that the bat detector has recorded open-adapted bats foraging above the canopy in forested sites. All of the search calls recorded within the campus had dominant frequency-modulated (FM) components, characteristic of species from the families Vespertilionidae and Molossidae. We did not record any calls characteristic of species from the families Hipposideridae and Rhinolophidae, both of which have characteristic constant frequency (CF) components (Sun et al. 2008). This is expected, because of the latter families' known habitat associations with caves and well-developed forests, both of which are absent in the study area.

Because there is no baseline library of calls recorded from captured insectivorous bats within the campus, identification to species level is not possible. However, De Dios (2015) captured three species of insectivorous bats within the campus using mist nets: *Scotophilus kuhlii*, *Pipistrellus javanicus*, and *Myotis muricola*. Available call characters in literature do not match any of our sonotypes, including data for the aforementioned three species from Mt. Makiling, Laguna, approximately 60 km south of the study site (Sedlock 2001). Variability in calls could be due to geographic variation, as populations from different localities may exhibit differences in bat call characters (Conole 2000; Chen et al. 2009; Jiang et al. 2015). Because of these geographic differences, and other sources of interspecific and intraspecific echolocation call variation, Russo et al. (2017) suggest limiting identification to species with distinctive calls and combining acoustic surveys with capture sampling.

Our study on the activity of insectivorous bats in one of the last remaining green spaces in the Philippines' most urbanized region is one of the few in the country that has utilized bioacoustics to study this group's ecology. Furthermore, urban biodiversity and ecology in the Philippines have often been overlooked fields of study, perhaps due to the already existing gaps in knowledge about Philippine biodiversity and ecology in increasingly threatened natural habitats. Indeed, majority of bat research has targeted forest habitats, followed by caves and karst areas (Tanalgo and Hughes 2018). This prioritization of natural habitats where more species are expected and are more threatened is unsurprising, especially given limited resources in a developing country. However, several studies have demonstrated that the green spaces of Metro Manila are able to harbor significant levels of biodiversity, including some endemic and threatened species (Ong et al. 1999; Vallejo Jr. et al. 2008; Vallejo Jr. et al. 2009). Because the impact of land use changes on Philippine bats is poorly understood, especially in urban landscapes, more comprehensive and long-term monitoring of bat assemblages is needed.

Baseline studies on the activity patterns of insectivorous bats in urban ecosystems such as this thus contribute to filling this research gap, and provide useful starting points for future research. Bioacoustics technology provides an opportunity to conduct studies on insectivorous bats passively, utilizing less manpower. However, especially for the Philippines where sufficient baseline has yet to be established, acoustic surveys should be combined with capture sampling using harp traps or mist nets due to interspecific and intraspecific variations that make identification challenging (Russo et al. 2017). Building a bat call library using captured bats would be an important step to allow attribution of call recordings to species. We also recommend studying temporal variation over a 12-hour period to identify other peaks in bat activity post-dusk emergence. Lastly, we recommend exploring how bat activity is influenced by other landscape elements such as presence of artificial light, distance to a water body or forest edge, and proximity to man-made structures, as these are important aspects of urban landscapes that have been assessed to influence activity of bats in other studies. Understanding the influence of different elements in an urban landscape can help inform the conservation and management of biodiversity in these anthropogenically altered habitats.

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