Impact of artificial lights on foraging of Neotropical insectivorous bats

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ABSTRACT
Studies from the temperate zones have shown that artificial lights can either deter insectivorous bats by disorienting them and increasing exposure to predators, or attract them by providing concentrations of prey, depending on the life history of the species in question. This study looked at insectivorous bat responses to light pollution in the tropics for the first time. Bat echolocations were recorded at 11 pairs of light and dark sites in premontane and lower montane forest of Monteverde, Costa Rica. Bat foraging activity was higher at artificially lighted sites (mean ± standard error 123.64 ± 34.77 recorded echolocations per night) than dark sites (mean ± standard error 49.64 ±12.00 recorded echolocations per night), but species richness was not statistically different between sites. While the majority of bat species increased their activity in response to light, *Myotis pilosatibialis* and an unidentified bat were only recorded in dark sites, suggesting that like temperate bats, tropical species are differentially impacted by artificial lights. Increased light pollution in the tropics concentrates some species around human inhabited areas while harming others via habitat fragmentation, potentially shifting community structure.

RESUMEN
Los estudios de las zonas templadas han mostrado que las luces artificiales pueden desalentar los murciélagos insectívoros por desorientarlos y exponérselos a un mayor peligro de depredación, o atraerlos por proporcionar concentraciones de presas, dependiendo de la especie. Este estudio examinó la repuesta de los murciélagos insectívoros a la contaminación de luz en el trópico por primera vez. Los sonidos de los murciélagos fueron grabados en 11 parejas de lugares claros y oscuros en el bosque alrededor de Monteverde, Costa Rica. La actividad de forrajeo fue mayor en los lugares claros (promedio ± error estandár 123.64 ± 34.77 sonidos grabados por noche) que lugares oscuros (promedio ± error estandár 49.64 ± 12.00 sonidos grabados por noche), mientras la riqueza de especies no fue estadísticamente diferente entre los lugares claros y oscuros. Aunque la mayoría de las especies de murciélagos aumentaron su actividad en la presencia de luces, Myotis pilosatibialis y otra especie no identificada solamente fueron grabados en los lugares oscuros. Esto sugiere que como los murciélagos de zonas templadas, los especies tropicales son afectadas diferencialmente por las luces artificiales. Las niveles de contaminación de luz crecientes en el trópico concentran unas especies alrededor de las áreas habitadas por humanos mientras las luces dañan otros por la fragmentación del habitat, y pueden cambiar la composición de la comunidad.

INTRODUCTION
As human development continues to expand around the world, our species' impacts on nature become farther-reaching and more difficult to predict. One often overlooked but important consequence of human expansion is light pollution. As artificial lights rapidly expand into more and more ecosystems around the world, understanding how light pollution affects wildlife is increasingly important to conservation efforts (Gaston et al. 2013). Anthropogenic lighting drastically alters the nighttime landscape around areas of human influence, potentially shifting the behavior of nocturnal organisms and disturbing their ecological roles (Longcore & Rich 2004).

Bats (Order Chiroptera), as a major group of nocturnal animals, are both likely to be heavily impacted by brighter nights and are also globally important. Bats fulfill crucial ecosystem roles as pollinators, seed dispersers, and controllers of insect populations, among others. They also benefit humans as the primary predators of many disease-carrying and crop-destroying insect species (LaVal & Rodríguez-H 2002), yet almost one quarter of species globally are threatened, mostly due to human disruption of their natural habitats (Stone et al. 2015). Artificial lights have been found to affect different bats in different ways. A number of bat species prosper in urban environments and are known to forage around artificial lights (Polak et al. 2011). Certain species, particularly aerial insectivores adapted for fast flying and long-range echolocating, have been shown to be actively attracted to streetlamps where they can exploit the insects that are drawn to the light (Rydell 1992). On the other hand, gleaning bats—species adapted for maneuvering in cluttered environments and using short-range echolocation to find arthropods on vegetation — actively avoid artificially lit areas in their foraging routes and leave their roosts later in artificially lighted conditions (Stone et al. 2009). Other bat species have been shown to commute over lights but avoid foraging near them (Dries et al. 2008, Polak et al. 2011).

If certain species are benefitted by anthropogenic lights while others expend energy avoiding them while losing potential foraging sites, increasing light pollution has the potential to alter bat community structures and put some species at risk (Stone et al. 2015). Even bats that do take advantage of artificial lights could be negatively impacted. Increased abundance and decreased defenses of disoriented insects around streetlamps (Svensson & Rydell 1998) could lead these bats to rely on lights for easy foraging, relaxing stabilizing selection of foraging-related traits due to increased fitness across the entire population (Swaddle et al. 2015) and decreasing their ability to capture prey in a natural setting. Moreover, almost all bats rely on vision for determining when to leave their roosts and for some aspects of foraging (Fure 2006), so even species that can forage in bright artificial lights may do so for less of the night and with less efficiency (Stone et al. 2015).

The little we do know about bat responses to artificial light primarily comes from studies in the temperate zone (e.g. Dries et al. 2008, Polak et al. 2011, Rydell 1992, Stone et al. 2009), despite the fact that bats are far more functionally and taxonomically diverse at lower latitudes (LaVal & Rodríguez-H 2002). My study attempts to extend understanding of artificial light's effect on insectivorous bat behavior to more complex tropical communities by comparing the number of bat echolocations between dark and lighted sites in Costa Rica. Because the majority of recordable echolocations are from aerial insectivores, other types of bats such as frugivores and gleaners cannot be taken into account with this study. Unlike frugivores or gleaners, which have only been found to avoid lights (Lewanzik & Voigt 2014, Stone et al. 2009) aerial insectivores were expected to vary in their light preferences and allow study of a broader range of light pollution's effects (Stone et al. 2015). Moreover, as aerial insectivores are one of the few bat guilds that exist in temperate zones, focusing on them allowed me to compare the effect of artificial light on tropical bats with what has been found at higher latitudes. To the best of my knowledge, this is the first study to look at the effect of light pollution across a tropical bat community.

MATERIALS AND METHODS

STUDY SITES—The study was conducted at 11 pairs of sites in premontane and lower montane moist forest around Monteverde, Costa Rica (Fig.1). Monteverde is surrounded by large amounts of intact forest but has experienced a rapid increase in development in the past 50 years (Nadkarni & Wheelwright 2000), making it an ideal area to test how light pollution affects otherwise undisturbed ecosystems. Monteverde was particularly well suited for this study as its bat community has been relatively well studied (LaVal & Fitch 1977), and at least 25 different species have been recorded in the area (R. LaVal, unpubl. data).

The sites ranged from 1274 m to 1440 m in elevation. Within each pair, sites differed from each other by no more than 60 m, with a mean difference of 14.6 m in elevation. Each pair consisted of one site at a streetlamp or similarly bright artificial light and one nearby without artificial lights. Eight of the light sites in the study were lit by sodium-vapor lamps that gave out an orange glow while three were lit by white lights—likely high intensity discharge lamps or LEDs (Longcore & Rich 2004). While insects have been found to be more attracted to white lights than sodium-vapor lamps (Stone et al. 2015), I assumed that the use of different lamp types would not disrupt the results as both types attract more insects than the dark areas I compared them to (Stone et al. 2015, per. obs.). Sites were chosen that lacked canopy cover overhead but were near forest edge, in order to: (1) avoid affecting the microphone's range with surrounding vegetation; (2) control for bat activity possibly differing under canopy cover; (3) take advantage of the fact that the highest bat activity is observed near forests (R. LaVal, pers. comm.).
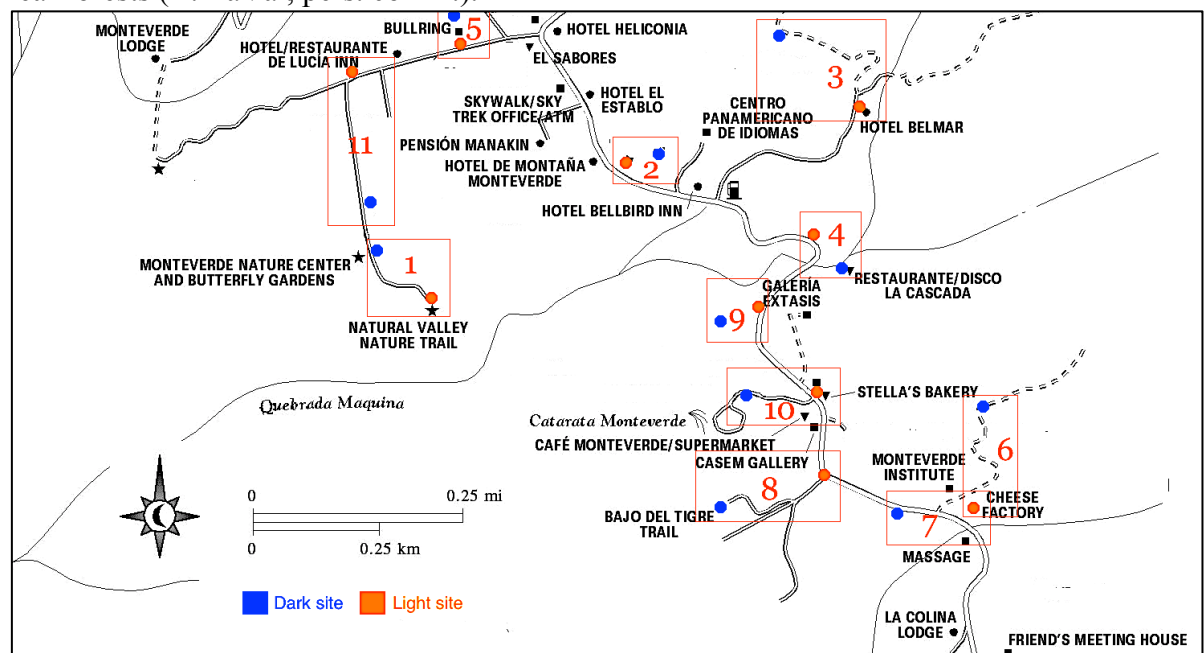

FIGURE 1. Map of Monteverde and Cerro Plano area in Costa Rica depicting the study sites used to record bats. Each pair of light and dark sites is numbered and outlined in red. Note that nights 6 and 7 overlap, as the Monteverde Cheese Factory was used as the light site for both. Sites were recorded over the period from October 22nd to November 17th. Original map taken from **http://moon.com/maps/**

PROCEDURE—To record bat calls and process them into legible data, I used an Echo Meter Touch (EMT) connected to an iPad Mini 2. The EMT's microphone can receive input from 8 kHz to 125 kHz, but was manually restricted to recording from

15 to 100 kHz, as all known bats from Monteverde fall into this range (R. LaVal, pers. comm.). The microphone recorded 5-10 m from directly below the light source at each site. Recordings were manually classified as the EMT's Auto-ID system is only accurate in low-clutter environments for a single individual at a time, an unrealistic assumption for Monteverde's field conditions. The EMT was set to retain files identified as noise.

By recording two sites each night and comparing their data rather than recording every site independently, the effect of changing lunar phase on bat activity (R. LaVal, unpub. data) was minimized, isolating the influence of artificial light. Recordings were made in four alternating 30-minute intervals between sites, for a total of 1 hour of recording at each site and 2 hours for the whole pair. To control for the disrupting variable of bat activity changing through the course of the night (R. LaVal, unpub. data), the order of recording sites in the pair was altered every night. As insectivorous bats do not usually forage in severe rain (R. LaVal, pers. comm.; pers. obs), I did not record on nights with heavy precipitation. On nights that started raining enough during recording to affect bat activity, the session was cut short. Thus, five out of the 11 total nights had fewer than the full 2 hours of recording—the minimum was 1 hour—but for every pair of sites the amount of analyzed recording time at each site was equal.

After recording, the .wav files from the EMT were converted to zero-crossing files using Kaleidoscope and examined in AnaLook. A reference library containing recordings of Monteverde's known bats (R. Laval, unpub. data) was used to assist in classifying the sound data.

RESULTS

BAT ACTIVITY—A total of 1906 bat passes were recorded across the 11 nights of recording. An average night had 173 passes between both sites, but nightly counts varied greatly between a minimum of 4 passes (it had rained earlier that night) and a maximum of 461.

Light sites had significantly higher bat activity than dark sites (paired t test, df = 10, t = -2.6045, p= 0.02629), with mean activity at light sites (123.64 passes ± 34.77) more than double that of dark sites (49.64 passes ± 12.00) (Fig. 2). While four of the 11 nights had a higher dark site activity (including the night with only 4 total passes), the other seven nights with higher light site activity had much more pronounced differences.
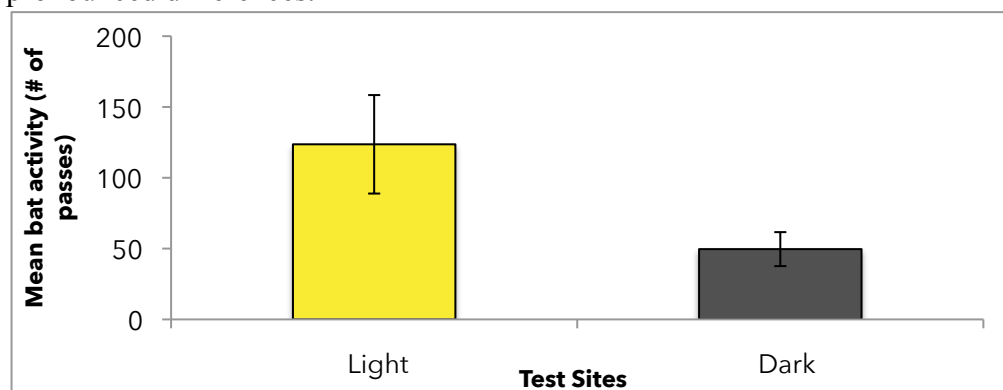

FIGURE 2. Mean bat activity per site (±1 sd) measured in number of bat passes recorded at 11 pairs of light and dark sights in premontane and lower montane forest of Monteverde, Costa Rica. One pair of sites was recorded per night. Recordings for most pairs were made in four periods of 30 minutes alternating between the light and dark site, although five of the 11 pairs had less than 2 full hours of recording.

SPECIES RICHNESS—Fifteen unique species were identified from the total dataset (see **Appendix** for the full list of species). An average night had 7.8 species between both sites with a maximum of 13 and a minimum of 3 (again, this was the night with only 4 total passes).

While light sites had a higher mean richness (5.91 species +/- 0.83) than dark sites (5.18 species +/- 0.82), the difference was nonsignificant (Paired Wilcoxon signed rank test, $V = 15$, $p = 0.404$). While light sites had a higher mean richness, it was a light site that accounted for the minimum richness of 0 (the same night with 4 total passes) while a dark site accounted for the maximum richness of 12 species (Fig. 3).

Sites were compared by species richness rather than using a more comprehensive measure of diversity that took evenness into account because: (1) I was not confident in the reliability of relative abundance data I would need to calculate evenness, due to ambiguity between some species' calls (particularly between *Eptesicus brasiliensis* and *Lasiurus ega*, two of the most frequently recorded bats) and (2) as an individual bat can, and often does, make many calls while foraging, the number of recorded echolocations does not necessarily correlate with abundance, meaning echolocation data cannot accurately show relative species abundance even if all of the identifications are absolutely reliable.
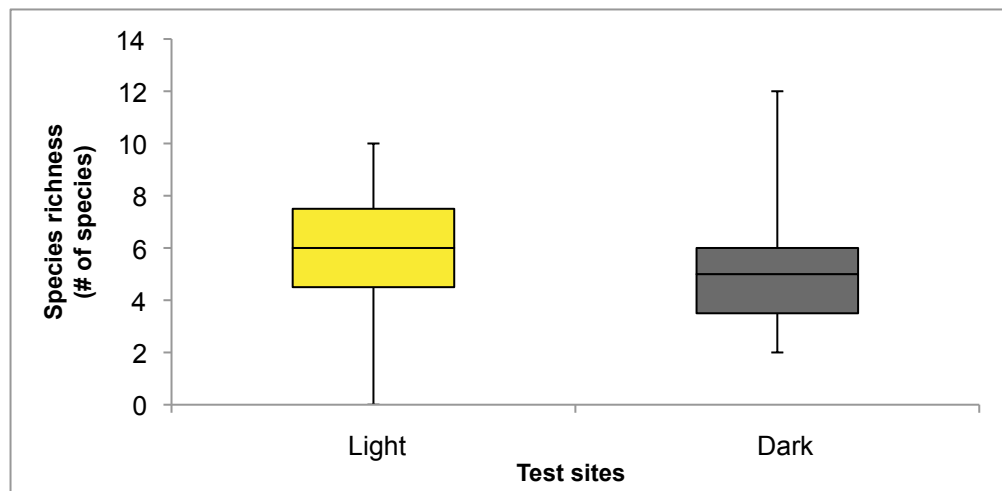

FIGURE 3. Species richness per site based on identified bat recordings at 11 pairs of light and dark sights in premontane and lower montane forest of Monteverde, Costa Rica. The middle line represents median richness, the boxes constrain the 25 to 75 percentiles, and the whiskers extend to minimums and maximums of the data. One pair of sites was recorded per night. Recordings for each pair were made in four periods of 30 minutes alternating between the light and dark site, although five of the 11 pairs had less than 2 full hours of recording. There were 15 unique species observed across all sites.

INDIVIDUAL SPECIES ACTIVITY—I chose seven bat species that I had identified confidently to perform individual activity analyses on, as well as one unidentified bat with a call in the 70-90 kHz range which appeared on five nights (Table 1). Activity data was only taken from nights where the species was recorded at a minimum of one site because the absence of a species at both sites does not indicate its preference for light versus dark.

Most of the analyzed species showed increased activity at light sites, but only the change in activity of *Diclidurus albus* was strictly statistically significant at $p <$

0.05 (Table 1; Fig. 4). *Myotis pilosatibialis* and the unidentified bat showed a trend ($0.05 < p < 0.10$) towards dark sites, having only been recorded there (Table 1; Fig. 5). *Myotis oxyotus* was found in similar abundances at both sites (Table 1). These trends were likely non-significant at $p < 0.05$ due to low sample sizes.

TABLE 1. *Results of Wilcoxon signed rank tests on difference in bat activity at light versus dark sites for eight insectivorous bat species. Activity was measured as the number of identified calls of each species from recordings at 11 pairs of light and dark sights in premontane and lower montane forest of Monteverde, Costa Rica. Nights where a given species wasn't found at either pair of sites were excluded from the analysis of that species. The third column displays the general trend for each species based on the difference in medians between sites. The data for* Eumops auripendulus *excluded one night in which the dark site was located at a known roost for that species.*

| Bat species	Nights sampled	Activity change in response to light (difference between median light site activity and median dark site activity)	V	p
Diclidurus albus	6	6	0	**0.03351***
Eptesicus fuscus	5	5	0	**0.05676**
Eumops auripendulus	6	3	0	**0.05791**
Molossus molossus	8	7	2.5	**0.06251**
Myotis nigricans	9	11	8	**0.09661**
Myotis oxyotus	5	0	6	0.8539
Myotis pilosatibialis	4	-2	10	**0.09751**
Unidentified bat	5	-1	15	**0.0547**
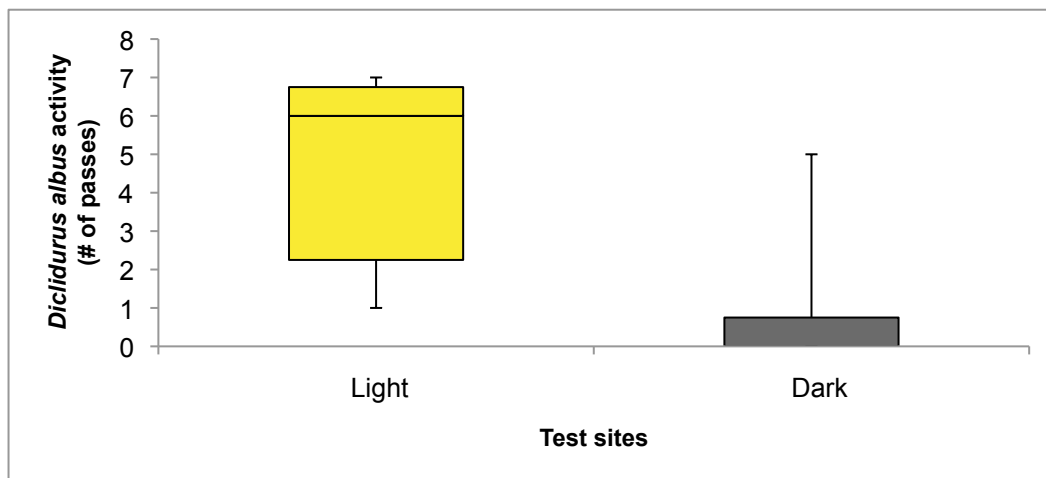
FIGURE 4. *Diclidurus albus* activity per site identified in Analook from recordings at 6 pairs of light and dark sights in premontane and lower montane forest of Monteverde, Costa Rica. The middle line represents median richness, the boxes constrain the 25 to 75 percentiles, and the whiskers extend to minimums and maxiumums of the data. Five of 11 sampled nights where *D. albus* was not found were excluded from this dataset. One pair of sites was recorded per night. Recordings for each pair were made in four periods of 30 minutes alternating between the light and dark site, except for one pair where the second set of recordings was only 15 minutes due to rain.
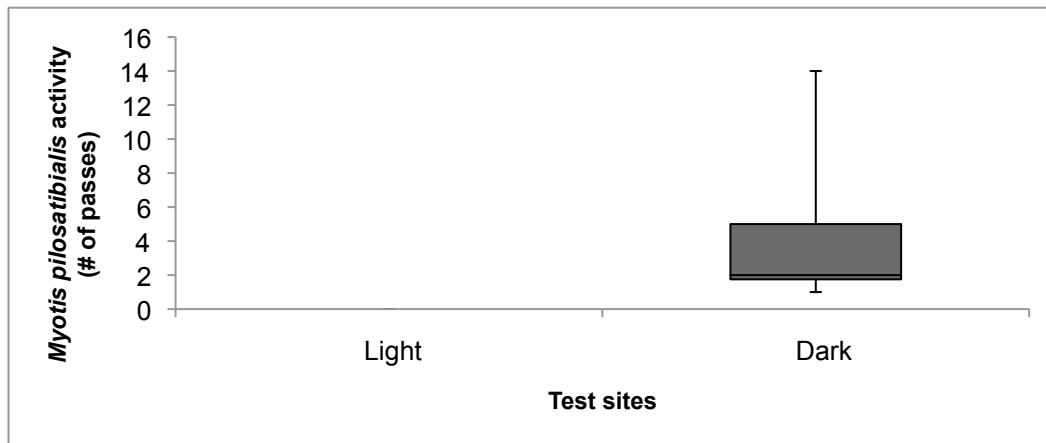
FIGURE 5. *Myotis pilosatibialis* activity per site identified in Analook from recordings at 4 pairs of light and dark sights in the premontane and lower montane forest of Monteverde, Costa Rica. The middle line represents median richness, the boxes constrain the 25 to 75 percentiles, and the whiskers extend to minimums and maxiumums of the data. Seven of 11 sampled nights where *D. albus* was not found were excluded from this dataset. One pair of sites was recorded per night. Recordings for two pairs of sites were made in four periods of 30 minutes alternating between the light and dark site, the other two only had 30 minutes measured at each site due to rain.

ADDITIONAL OBSERVATIONS—Of the 15 bat species identified, none were present in light sites that were not also found at dark sites, whereas three species were found uniquely at dark sites: *M. pilosatibialis*, *Pteronotus gymnonotus*, and the unidentified bat. As only a single pass of *P. gymnonotus* was recorded, it was not included in the individual analyses.

DISCUSSION

Artificial lights attracted substantially more bat activity than dark areas. This implies that that a significant amount of bats were taking advantage of the insects attracted to artificial lights, congregating in higher numbers around lights or making more frequent echolocations, or both. Both the magnitude of the difference between sites and the results of the individual species analyses support the idea that like aerial insectivorous bats studied in the temperate zone (Stone et al. 2015), the majority of aerial insectivores in Monteverde are attracted to artificial light sources.

While bats were more active at the light sites, the species richness of light and dark sites did not significantly differ. This implies that artificial lights in Monteverde do not support more species than their surroundings. Considering that no species were found uniquely at light sites, it appears that artificial lights do not bring in a significant amount of locally rare species. Instead, they concentrate the activity of many of the species already present in the area. Studies in the temperate zone have have also shown that the bats attracted to lights tend to be more widespread and common (Polak et al. 2011, Stone et al. 2015).

The majority of the individual-species analyses displayed clear trends suggesting most species were attracted towards lighted areas (Fig. 4). However, three of the eight species did not prefer lighted areas (Table 1), with two seeming to avoid them entirely (Fig. 5). The varied responses of different species to light sites imply that light pollution selectively benefits the tropical bat community just as it does in the temperate zone (Stone et al. 2015).

Why might *M. pilosatibialis* avoid artificial lights? Like the other studied species, it is an aerial insectivore (LaVal & Rodríguez-H 2002). It is mostly recorded

in or near forest, and like most aerial insectivores its prey largely consists of beetles and moths (LaVal & Rodríguez-H 2002). One differentiating characteristic of *M. pilosatibialis* is that it is a particularly low flyer (R. LaVal, pers. comm.). A low flight pattern under or at streetlamp-level might increase *M. pilosatibialis'* visibility to predators more so than less exposed, higher-flying bats. Moreover, *M. pilosatibialis* flying around the level of streetlamps may disorient it more than higher flying bat species; studies in the temperate zone have shown that bats' eyes are sensitive to the bright, UV-rich light emitted by most artificial lamps (Fure 2006). An alternative, or complementary explanation is that the prey of *M. pilosatibialis* may not be as concentrated at lights. Larger insects are tend to be more attracted to lights (van Langevelde et al. 2011) and also fly at higher altitudes (Taylor 1974), so it may be that artificial lights host a higher ratio of high flying to low-flying insects than their surroundings—especially since most artificial lights are several meters above the ground. If so, low flying bats like *M. pilosatibialis* would be ill suited to take advantage of the insects at artificial lights.

Species that cannot benefit from artificial lights' associated insect concentrations would be selected to avoid them, given increased exposure to predators near lights and the fact that bats' eyes are sensitive to artificial light (Stone et al. 2015, Fure 2006). Thus, I likely would have found more species avoiding light if I could have accounted for other bat guilds that cannot take advantage of artificial lights. The only prior study focusing on light pollution's effect on tropical bats found that the frugivorous *Carollia sowelli* preferred to forage for away from artificial lights (Lewanzik & Voigt 2014), supporting this idea. It may be that the unidentified bat species I only found at dark sites was a member of another guild flying close to the microphone. The fact that some tropical aerial insectivores were not found to congregate near artificial lights despite being the guild most expected to take advantage of them combined with the existence of many primarily tropical guilds that don't like lights implies that tropical bat communities may have more species susceptible to light pollution than in temperate zones.

The effects of light pollution observed in this study on tropical populations of aerial insectivorous bats have important implications for the conservation of tropical ecosystems. Rapidly expanding artificial lighting in many tropical areas may lead to increasingly concentrated populations of the majority of aerial insectivorous species near human-inhabited areas. While increased prey abundance might benefit them in the short term, these species could come to rely on lights for food, and also become more vulnerable to other anthropogenic disturbances such as artificial noise and deforestation that often accompany human settlements. Other species that do not take advantage of artificial lights, like *M. pilosabilialis*, will likely suffer declines due to fragmentation of foraging grounds by light pollution (Stone et al. 2015). These changes in insectivorous bat foraging and community structures could have cascading effects down the food chain, with repercussions for entire tropical communities.

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APPENDIX

Recorded species list:
1. *Diclidurus albus*
2. *Eptesicus brasiliensis*
3. *Eptesicus fuscus*

4. *Eumops auripendulus*
5. *Lasiurus blossevilii*
6. *Lasiurus ega*
7. *Lasiurus intermedius*
8. *Myotis nigricans*
9. *Myotis oxotus*
10. *Myotis pilosatibialis*
11. *Molossus molossus*
12. *Molossus sinaloae*
13. *Molossus rufus*
14. *Pteronotus gymnonotus*
15. Unidentified species (see **Results**)