

Temporal variation in vertical stratification of neotropical bats

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Abstract

Previous research has shown diverse vertical space use by various taxa, highlighting the importance of forest canopy. Yet, we often fail to explore how this three-dimensional space use changes over time. Here we use canopy tower systems in French Guiana to monitor neotropical bat activity above and below the forest canopy throughout nine nights in the wet season. We show that different bats use both canopy and understory space differently, and that this can change throughout the night. We find that bats are overall more active in the canopy, but multiple species/acoustic complexes are more active in the understory. We also find that species that do not seem to prefer understory or canopy, when data are aggregated by night, do show temporally changing preferences in hourly activity. This work highlights the need to consider temporal axes in studies of space use, both throughout daily cycles and across seasons.

Introduction

The study of space use has long interested ecologists (Elton, 1927), and more recently three-dimensional space use has been shown to be important for many taxa including arthropods (Schulze, Linsenmair & Fiedler, 2001; Basset et al., 2003), birds (Pearson, 1971; Walther, 2002), rodents, marsupials (Vieira & Monteiro-Filho, 2003), and bats (Francis, 1994; Bernard, 2001). From an applied perspective, failing to survey animals above the forest canopy can lead to biased conclusions about management decisions. For example, European bats that have higher risk of wind turbine mortality were later found to be more common in higher vertical strata (Müller et al., 2013). Had we understood how these animals use space over time, we may have made different decisions about where to place wind turbines, and when to shut them down. Exploring how animals use vertical strata across time is important to understanding conservation strategies for forests and the animals that use that space. This is especially true in the tropics where biodiversity loss from deforestation is high (Laurance, 1999; Giam, 2017).

Bats are ideal study organisms for exploring vertical stratification of space-use. They comprise a group that is diverse, ecologically and economically important (Kalka, Smith & Kalko, 2008;

Boyles et al., 2011; Kasso & Balakrishnan, 2013), highly sensitive to deforestation (Garcia-Morales et al., 2016), and are relatively easy to monitor with recent advances in passive acoustic monitoring. Passive monitoring of tropical bats during the dry season suggests that bat activity and species diversity is higher in the canopy, relative to mid- or below-canopy (Marques, Ramos Pereira & Palmeirim, 2016). This may be a result of high insect abundance in the canopy (Basset et al., 2003). Many nectar feeding Lepidoptera (e.g. Sphingidae), for example, are more abundant high in the canopy, where more flowers are present (Schulze, Linsenmair & Fiedler, 2001). Yet, it is likely that vertical space use by flowers, arthropod prey, and bat foragers would vary both seasonally, and throughout the night. Indeed, some tropical insectivorous bat species adjust their activity during the night to take advantage of more favorable periods to forage (Appel et al., 2019).

Yet little is known about temporal patterns of vertical space use of aerial insectivorous bats. Here we survey the vertical space use by ~~neotropical~~ bats in French Guiana over the course of the entire night, for nine nights.

Methods

Setup

We sampled above and below two canopy towers, part of the COPAS infrastructure, at the Nourages research station, French Guiana from the evening of 10 April 2018, to the morning of 19 April 2018 in the wet season. We conducted paired sampling on top of the canopy towers (~40 m high), to get a measure of activity above the forest canopy, and below canopy towers (~1.5 m high), to get a measure of bat activity in the forest understory. At each sample site, we deployed a passive acoustic monitoring unit (Song Meter SM3) with an omnidirectional ultrasonic microphone (SMU; Wildlife Acoustics, Massachusetts, USA). We programmed acoustic monitors to run continuously from sunset to sunrise (~12 hours) and to record with a 16-bit depth, 384 kHz sample rate, with an internal 16 kHz high pass filter, and a 1.5 ms minimum trigger duration.

Sonar sequence identification

Bat recordings were batch processed with Sonobatch scrubbing software to exclude non-bat calls. We then visualized the remaining 16,123 sequences with Kaleidoscope Software (version 4.3.2; Wildlife Acoustics, Massachusetts, USA) and identified the calls following the libraries of Amazonian bat echolocation (López-Baucells, 2018) and echolocation characteristics from the literature (Barataud et al., 2013; Arias-Aguilar et al., 2018). When possible, we identified bat calls to the species level or identified the call as an acoustic complex when species-level identification was impossible (Torrent et al., 2018). Our analysis included a total of 11 species and eight acoustic complexes, with a total of 19 sonotypes from the families Emballonuridae, Molossidae, Mormoopidae and Vespertilionidae (Table 1). We defined bat activity as the number of bat passes per hour and night. A bat pass is a sequence of 5-s recording that has a minimum of two recognizable search-phase calls per species (Torrent et al., 2018; Appel et al., 2019)).

Statistical analysis

All our models were generalized linear (mixed) effects models that we ran in a Bayesian framework with the R (R Core Team, 2017) package `rstanarm` (Gabry & Goodrich, 2016). We visually checked model residuals and trace plots, and inspected predictors for collinearity. There were no divergent transitions or issues with convergence. All priors were uninformed.

Since all response data were counts of bat passes, we modelled these data with a negative binomial distribution and log link function. In our ‘all bats’ model (~~presented in Figs 1 and 2~~) we set a random (~~varying~~) intercept for bat species, with varying slopes for hour after sunset (0-12), vertical strata (canopy vs understory), and the interaction between the two (which were also fitted as fixed effects to make inferences on ‘all bats’ overall). We did not include site as a random effect, as we did not have at least five levels (Harrison et al., 2018).

We included horizontal moon illumination (measured following Kyba, Conrad & Shatwell, 2020) as a fixed effect to control for any influences that moon light might have on vertical bat activity (Hecker & Brigham, 1999; Appel et al., 2017), as well as any latent processes occurring over the course of the nine day experiment (either due to moonlight or day of the year). In this model, we removed all bat species (or acoustic complexes) that contained 5 or fewer observations, since these data are not robust enough for inference.



To further elucidate patterns of bat activity over the course of the night, we separately analyzed the four most common bat species (*Peropteryx macrotis*, *Saccopteryx bilineata*, *Centronycteris maximiliani*, and *Peropteryx kappleri*) with hour after sunset as a second-order polynomial, vertical strata (canopy vs understory), and the interaction between the two all fitted as fixed effects in a generalized linear model. We did not run similar models for other species, as we did not feel like we had an adequate number of counts for those species, and did not think inferences on minimal data were appropriate.

Throughout the results we report 80% and 90% credible intervals, from a Bayesian framework. While these choices are always largely arbitrary, we chose these values because both display a wide interval spanning a high probability range of parameter values. We avoid using a 95% credible interval for a number of reasons. Firstly, these can often be misinterpreted as 95% confidence intervals. The latter, in contrast to Bayesian credible intervals, assume that the interval is random and the parameter is fixed, and are often interpreted as a hypothesis test. Secondly, both 80% and 90% credible intervals reduce concerns with the computational stability of wider (e.g. 95%) intervals. In the following text we generally use 80% CI to suggest broad-scale trends, whereas we use 90% CI in the reporting of parameter estimates, to give a narrower estimate band, with higher certainty.

Results

Overall, bats were more active in the canopy, versus the understory. That is, bat activity was estimated to be 9.5 times (90% CI: 4.3 – 21.1) higher in the canopy, than in the understory. Yet, patterns for individual species (or acoustic complexes) were mixed (Fig 1). Broad patterns at 80% credible intervals suggest six species/complexes are more active in the canopy, five in the understory, and six aren't more or less active in any particular strata. Of the strongest trends, *Peropteryx macrotis* was 21.8 times more likely to be found in the canopy (90% CI: 6.01 – 84.6), whereas *Myotis riparius* was a factor of 132.8 more likely to be in the understory (90% CI: 31.2 – 586.6). There was a 92.2% probability that moonlight has a positive effect on overall bat activity, but we did not have the data resolution to look at individual species effects.

Overall bat activity decreased 22.0% (90% CI: 14.8 – 29.6%) for every hour in the canopy as the night progressed, whereas activity in the understory did not change over time (90% CI: -8.2 – 10.7%). Individual bat species/complexes differed in their activity above and below the canopy as the evening progressed, depending on the species/complex (Fig 2). Three bat complexes increased understory use over the night, whereas none of them decreased their use of that space over time (90% CI). The *Lasiurus sp.* complex, for example, was 52.5% more active in the understory (90% CI: 32.4 – 83.1), each hour of the night (Fig 2). Canopy use throughout the night, however, increased for two groups, and decreased for one at the 90% CI, but trended that direction for two other groups (80% CI; Fig 2). Two of the complexes (Molossidae group A & B) increased the use of both understory and canopy throughout the night.

Centronycteris maximiliani activity showed a peak of activity in the middle of the night. This species is slightly more active in the understory, relative to the canopy, during early and late parts of the night, whereas they are more active above the canopy during the middle of the night (Fig 3A). *Saccopteryx bilineata* has higher activity in the understory at the beginning and end of the night (~~dusk and dawn~~), and higher canopy activity in the early-middle of the night (Fig 3B). Both *Peropteryx kappleri* and *P. macrotis* are far more active above the canopy (relative to understory), but there is a small, ~~difficult to visualize~~, spike in understory activity late in the night (Fig 3C, D).

Discussion

Understanding space use over time is vital if we hope to accurately assess habitat use and quality for bats (Bernard, 2001; Müller et al., 2013; Appel et al., 2019). Since it is difficult to directly observe bats flying in the night, spatio-temporal resolution from passive acoustic monitoring may offer important insights about the natural history of bats, and ultimately their conservation (Marques, Ramos Pereira & Palmeirim, 2016). Here we show that both the canopy and understory are used differently by different ~~neotropical~~ bats, throughout the night.

We find that bats are overall more active in the canopy, which corroborates previous work (Marques, Ramos Pereira & Palmeirim, 2016) and that overall bat activity decreases in the canopy throughout the night. We also find multiple species that are more active in the understory

(only *Myotis riparius* in Marques, Ramos Pereira & Palmeirim, 2016). Other Myotid species ~~are~~
~~thought to~~ prefer to forage in the understory elsewhere in the world (Kennedy, Sillett &
 suggesting that this characteristic may be a trait of the
 genus independent of the geographic location.

~~It is possible that~~ some differences between this study and Marques et al. (2016) ~~are~~ explained by
 seasonal differences in prey communities within the canopy and understory, as this study was
 during the wet season and Marques et al. (2016) occurred during the dry season. ~~Arthropod prey~~
~~vary seasonally in their abundance (Wolda, 1988; Lister & Aguayo, 1992; Pinheiro et al., 2002)~~
~~and those prey likely spend time in different vertical strata (Schulze, Linsenmair & Fiedler,~~
~~2001). Indeed, seasonal changes in arthropod abundances in the neotropics have been linked to~~
~~changes in diets of many taxa, including bats (Lister & Aguayo, 1992; Jahn et al., 2010; Salinas-~~
~~Ramos et al., 2015).~~ However, there are likely many other idiosyncratic differences between the
 French Guiana and Brazilian forests studied here and in Marques et al. (2016), respectively, that
 could contribute to these differences as well. Future work should aim to understand three-
 dimensional space use over longer periods of time within the same forest.

For many bats, there were no clear preferences between canopy and understory (~~Fig 1~~). This may
 be because these bats are just as active in the various vertical strata. Bernard (2001), for example,
 found the same lack of vertical stratification pattern as we did for *Saccopteryx bilineata* and *S.*
leptura, and the author suggests that this may be because these species fly in large spiral
 movements occupying both the higher and lower strata. Instead, this apparent lack of a pattern
 may suggest that bats partition the night and are more active in different strata at different times.
S. bilineata provides an example, as they were not more active in either stratum when their
 activity was integrated over the entire night (~~Fig1~~), yet they partition their use of the canopy and
 understory across the night. *S. bilineata* has a “U”-shaped change in activity in the understory
 over time. This suggests that these bats roost somewhere near our detectors, likely inside tree
 cavities and on exposed trunks (Voss et al., 2016), but spend the middle hours of the night
 foraging above the canopy (~~Fig 3B~~). If bats are virtually non-existent in a survey of the
 understory during early hours of the night, but common in the canopy during later hours, it is
 likely that they are roosting elsewhere and commuting to forage (Voss et al., 2016).

With the constant increase of deforestation of Amazonian primary forests (Fearnside, 2005; Lovejoy & Nobre, 2018) and consequent loss of vertical stratification of these forests (Silva et al., 2020), aerial insectivorous bat activity is being affected by forest removal and degradation. Delineating specifically how vertical structure shapes bat communities and activity adds critical insight for ecologists and managers. Here we show that monitoring for bats in one vertical stratum only, or during just the early ‘golden’ hours of the night clearly misses important information. On the more speculative side, given enough information about a species’ emergence timing (Rydell, Entwistle & Racey, 1996; Duvergé et al., 2000; Russo, Cistrone & Jones, 2007), it may even be possible to estimate distances to roosts from these data. If this were the case, multiple passive acoustic monitors scattered throughout a forest could roughly triangulate on the location of these roosts (Svaizer, Matassoni & Omologo, 1997; Chang et al., 2002), which could then be preferentially protected from deforestation or development.

Conclusions

~~We used passive acoustic monitoring to explore how neotropical bats use space over time. While bats generally were more active in the forest canopy,~~ we show that individual groups of bats use space differently over the course of a night. Those who fail to survey habitat in three dimensions, and for the entire duration of a night may form erroneous conclusions about the quality of that habitat, or make poor management decisions. We hope that future work continues to explore how animals and their prey use space throughout the night, and over the course of different seasons, which will surely expand our knowledge of these understudied creatures.

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312

Figure 1

Model coefficient estimates for activity in vertical strata, by bat species/complex.

Positive values on y axis indicate that bats were more active in the canopy, whereas negative values indicate that bats were more active near the forest floor.

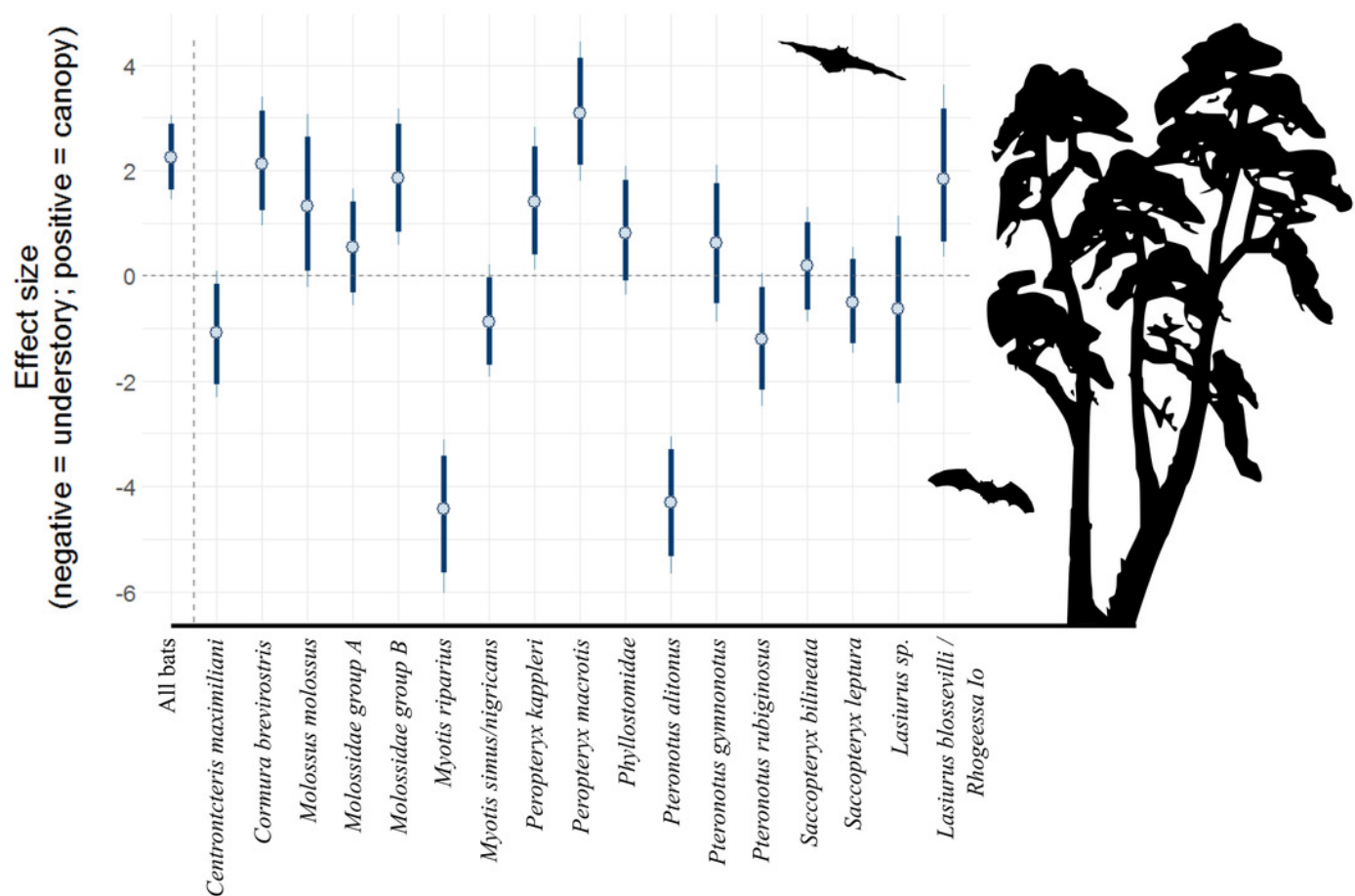


Figure 2

Model coefficient estimates for activity over the course of the night by bat species.

Estimates on left are for understory activity, whereas those on right are for canopy activity. Positive values on x axis indicate that bats were more active as time passed within a night, whereas negative values indicate that bats were more active earlier in the night.

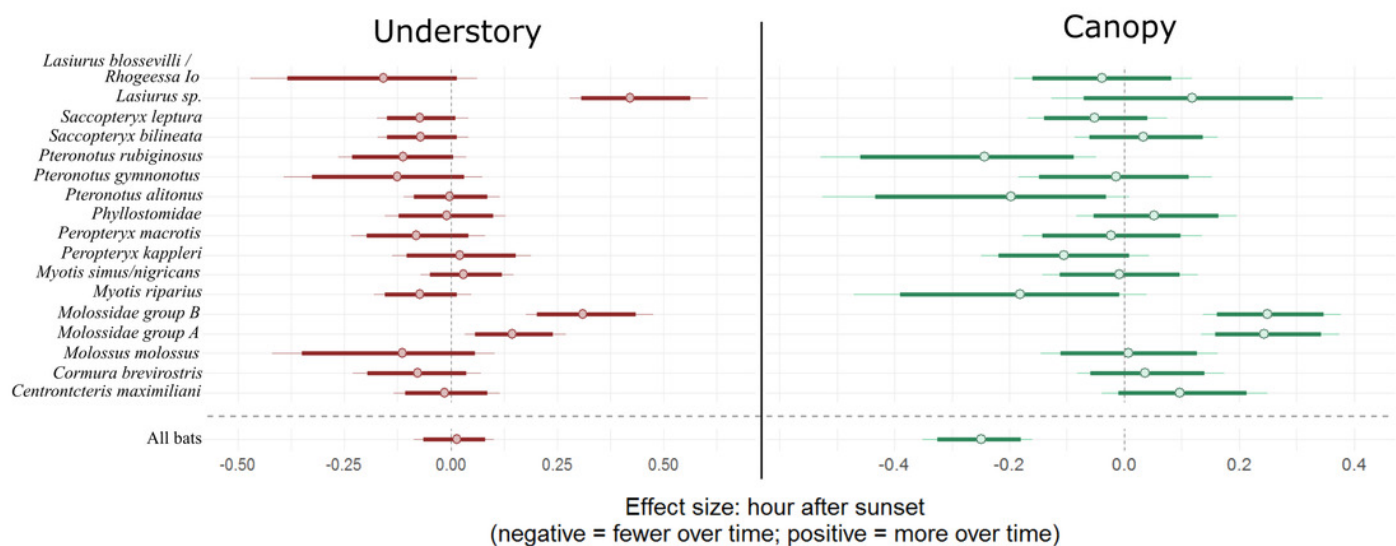


Figure 3

Activity of four most common species recorded at the Nouragues Research Station in French Guiana, plotted by hour since sunset.

Points indicate raw data by understory (red) and canopy (blue). Lines indicate 95% of 1000 posterior draws from Bayesian models.

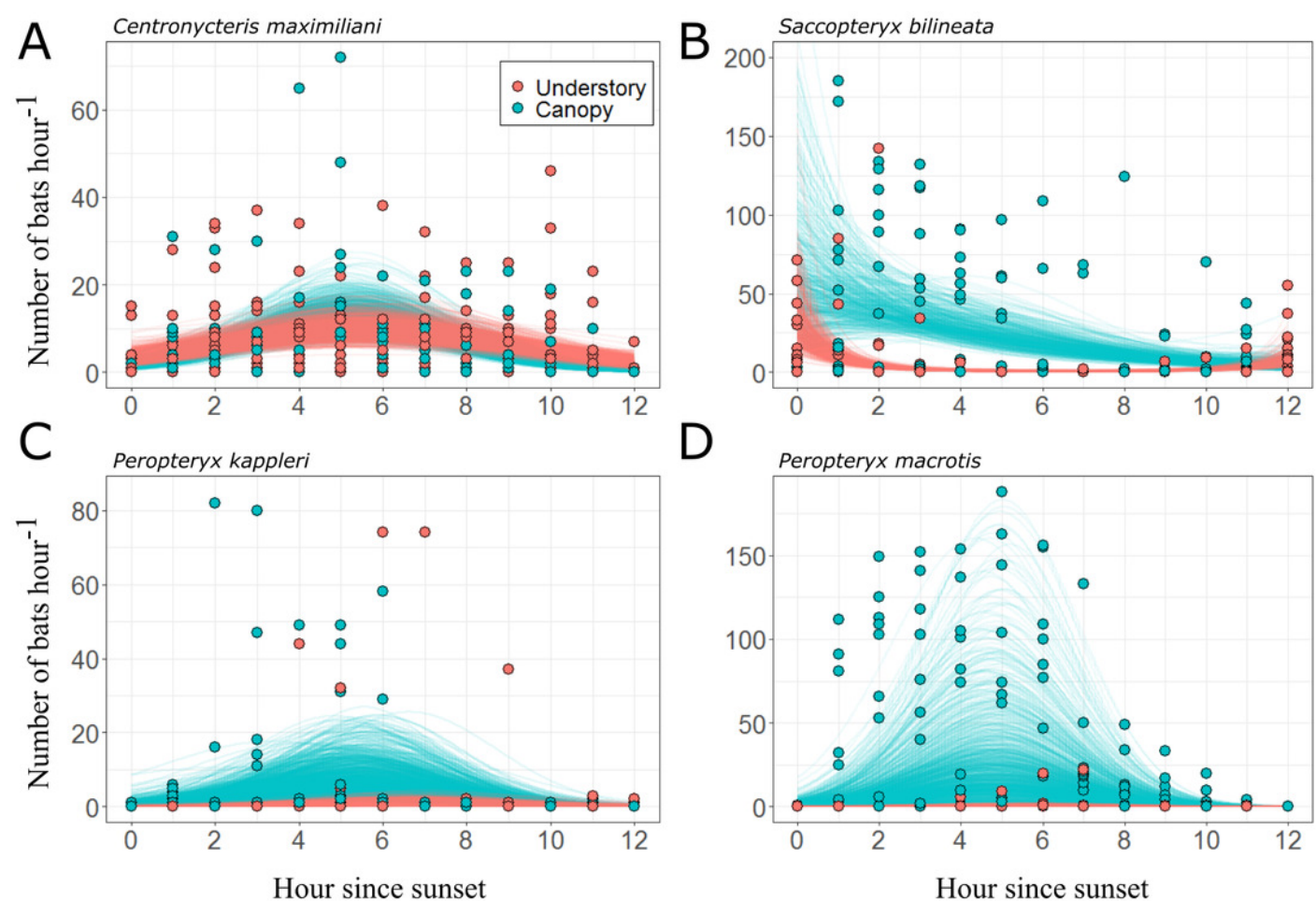


Table 1 (on next page)

Passive acoustic monitoring observations over nine nights within the understory and canopy at the COPAS facility in French Guiana.

Diclidurus sp. may include *Diclidurus albus*, *D. scutatus*, and/or *D. ingens*. *Lasiurus* sp. may include *Lasiurus ega*, *L. castaneus*, *L. egregius*, and/or *L. atratus*. *Molossidae* group A may include *Molossus sinaloe*, *M. rufus*, *M. currentium*, *Promops centralis*, *Cynomops planirostris*, and/or *C. parvus*. *Molossidae* group B may include *Cynomops greenhalii*, *C. abrasus*, *Eumops auripendulus*, *E. glaucinus*, *E. dabbenei*, *E. hansae*, *E. maurus*, *Nyctinomops laticaudatus*, and/or *Tadarida brasiliensis*.

Acoustic group	Understory	Canopy	Total
<i>Peropteryx trinitatis</i>	0	1	1
<i>Pteronotus sp.</i>	0	1	1
<i>Saccopteryx gymnura</i>	1	0	1
<i>Diclidurus sp.</i>	2	3	5
<i>Molossus molossus</i>	0	20	20
<i>Pteronotus gymnonotus</i>	2	19	21
<i>Pteronotus rubiginosus</i>	20	15	35
<i>Lasiurus blossevilli / Rhogeessa Io</i>	0	37	37
<i>Lasiurus sp.</i>	69	3	72
<i>Phyllostomidae</i>	13	84	97
<i>Myotis riparius</i>	203	2	205
<i>Myotis simus/nigricans</i>	143	88	231
<i>Molossidae group B</i>	55	198	253
<i>Molossidae group A</i>	57	214	271
<i>Pteronotus alitonus</i>	362	4	366
<i>Cormura brevirostris</i>	10	379	389
<i>Saccopteryx leptura</i>	397	671	1068
<i>Peropteryx kappleri</i>	280	1264	1544
<i>Centronotus maximiliani</i>	1270	944	2214
<i>Saccopteryx bilineata</i>	1018	3512	4530
<i>Peropteryx macrotis</i>	70	4692	4762