Time of night and moonlight structure vertical space use by insectivorous bats in a Neotropical rainforest: an acoustic monitoring study

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Abstract

Background.

Previous research has shown diverse vertical space use by various taxa, highlighting the importance of forest vertical structure. Yet, we know little about vertical space use of tropical forests, and we often fail to explore how this three-dimensional space use changes over time.

Methods.

Here we use canopy tower systems in French Guiana and passive acoustic monitoring to measure Neotropical bat activity above and below the forest canopy throughout nine nights. We use a Bayesian generalized linear mixed effect model and kernel density estimates to demonstrate patterns in space-use over time.

Results.

We found that different bats use both canopy and understory space differently and that these patterns change throughout the night. Overall, bats were more active above the canopy (including *Cormura brevirostris*, *Molossus molossus*, *Peropteryx kappleri*, and *Peropteryx macrotis*), but multiple species or acoustic complexes were more active in the understory (such as *Centronycteris maximiliani*, *Myotis riparius*, *Pteronotus alitonus*, and *Pteronotus rubiginosus*). We also found that most bats showed temporally-changing preferences in hourly activity. Some species were less active (*e.g. P. kappleri* and *P. macrotis*), whereas others were more active (*Pteronotus gymnonotus*, *C. brevirostris*, and *M. molossus*) on nights with higher moon illuminance.

Conclusions.

This work highlights the need to consider diel cycles in studies of space use, as animals use different habitats during different periods of the day.

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Introduction

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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). Understanding space use over time is vital if we hope to accurately assess habitat use and quality (Bernard, 2001; Müller et al., 2013; Appel et al., 2019). 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. The ability for powered flight allows them to easily access the various strata of the forest, and previous studies have shown that Neotropical species vary in their use of three-dimensional space (Kalko & Handley, 2001; Pereira, Marques & Palmeirim, 2010; Rex et al., 2011; Marques, Ramos Pereira & Palmeirim, 2016). However, most of these studies have used mist-nets, which are more likely to capture bats in the Family Phyllostomidae (Kalko & Handley, 2001; Pereira, Marques & Palmeirim, 2010; Rex et al., 2011). Given that most bats in Neotropical rainforests are not phyllostomid bats, but rather aerial insectivores from other Families, there is a gap in vertical stratification knowledge within these forests (Marques, Ramos Pereira & Palmeirim, 2016; Silva et al., 2020). Aerial insectivorous bats rely on echolocation to orient, navigate, and forage on the wing for arthropod prey (Schnitzler, Moss & Denzinger, 2003). Echolocation calls of aerial insectivorous species are generally distinct to the species level, which allows bats to be relatively easily monitored. Passive acoustic monitors are rapidly becoming low-cost and open-source, and advances in automatic detection of biotic signals (i.e. echolocation calls) have greatly increased analytical throughput (Gibb et al., 2019; López-Baucells et al., 2019).

Passive monitoring of rainforest bats during the dry season in Brazil suggests that bat activity and species diversity is higher in the canopy, relative to mid- or below-canopy (Marques, Ramos Pereira & Palmeirim, 2016). In Marques et al. (2016), only one species (*Myotis riparius*) did not prefer to forage above the canopy. This may be due to the species' aversion to moonlight (Appel et al., 2019), which would likely be exacerbated above the canopy. The result that all other bats prefer to forage above the canopy 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 the abundance of arthropod prey, and thus bats foraging above the canopy, would vary throughout the night. Indeed, some tropical insectivorous bat species adjust their activity during the night to take advantage of more favorable periods to forage, such as to avoid rain or moonlight (Appel et al., 2019).

Little is known about temporal patterns of vertical space use of aerial insectivorous bats, and surprisingly little is known about bats in the Guiana Shield. Here we use passive acoustic monitors to survey vertical space use by Neotropical bats in French Guiana to fill this knowledge gap. Since only one of the bat species (*Myotis riparius*) we detected in this study has previously been found to prefer forest understory (Marques, Ramos Pereira & Palmeirim, 2016), we expected to see similar results to previous work, where most bats prefer the forest canopy. Yet, if we are to make generalizable inference, it is important to validate past results in different areas across different times of year, such as we attempt to do here. Additionally, we aim to explore how bats use this vertical space over the course of a night, which may highlight that different strata of the rainforest are important during different times.

Methods

Setup

We worked at the Saut Pararé Nourages research station (4°2’30” N, 52°40’30” W), French Guiana from the evening of 10 April 2018, to the morning of 19 April 2018 in the wet season. The area contains a dense, nearly undisturbed old-growth rainforest, dominated by Burseraceae trees, with a maximum forest canopy of approximately 40 m high (Joetzjer et al., 2017). This location has a humid climate (3000 mm of precipitation per year) with a short dry season from mid-August to mid-November with less than 100 mm of rainfall (Joetzjer et al., 2017). Mean monthly air temperature in this location ranges from 25.5 °C in January to 27.5 °C in October (Obregon et al., 2011). This station has two forest canopy towers that are part of the COPAS infrastructure (Gottsberger & Döring, 1995; Gottsberger, 2017). The towers are 180m apart, and

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were 45 high (Gottsberger, 2017), placing them above the nearby forest canopy which was approximately 40 m high or less (Joetzjer et al., 2017).

Acoustic sampling

We conducted paired sampling on top of and below the canopy towers, to get a measure of bat activity above the forest canopy and within the forest understory, respectively. At each sample site, we deployed a passive acoustic monitoring unit (Song Meter SM3) with an omnidirectional ultrasonic microphone (SMU; Wildlife Acoustics, Massachusetts, USA). To reduce echoes in recordings, microphones on canopy towers were attached to the ends of 2 m poles, which in turn were attached to the COPAS platform. Thus the above-canopy microphones were 45 m off the ground. The passive acoustic monitoring units in the forest understory were placed in relatively open, non-dense flyways that had little vegetation. The microphones were also attached to the ends 2 m poles as above, which were in turn attached to the trunks of trees, 1.5 m off the ground, far from any vegetation to reduce echoes. The absolute detection range of the microphones is dependent on many factors including sonar emission intensity, ambient background sound levels and the frequency of the signal (Agranat, 2014). Conservative detection estimates are between 8-30m for a sonar emission of 100-120 dB, a peak frequency of 30-50 kHz, and a 20 dB background sound level, with no interfering vegetation (Agranat, 2014). Further, the vegetation of the forest canopy formed a barrier to the transmission of the short ultrasonic wavelengths of bat echolocation between the recorders. Thus it was exceedingly unlikely that both acoustic monitors simultaneously detected bats both above and below the canopy We left passive acoustic monitors in the field for the duration of the study, and they were programmed to automatically turn on at sunset and off at sunrise (12 hours per night x 9 nights x 4 locations = 432 monitored 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.

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Sonar sequence identification

Bat recordings were batch processed with Sonobatch automatic scrubbing software to exclude files that did not contain bat calls (Szewczak, 2015). We then visualized the remaining 16,123 sequences with Kaleidoscope Software (version 4.3.2; Wildlife Acoustics, Massachussetts, 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 (López-Baucells, 2018; Torrent et al., 2018). Our data included a total of 13 species and eight acoustic complexes, with a total of 21 sonotypes from the families Emballonuridae, Molossidae, Mormoopidae, Phyllostomidae and Vespertilionidae (Table 1). We defined bat activity as the number of bat passes per hour each 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).

Moonligh data

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Moon illuminance was calculated using custom windows command line code, *sunmoon* program (Jeff Conrad *unpublished software*). The methods are similar to those of Janiczek and DeYoung (1987). Sun and Moon positions are determined using the more accurate formulas of Van Flandern and Pulkkinen (1979).

Ethics statement

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Statistical analysis

Data were explored following the protocol of Zuur, Ieno & Elphick (2010). We built a generalized linear (mixed) effects model within a Bayesian framework with MCMC in Stan within the R programming language (R Core Team, 2017) package `rstanarm` and function `stan_glmer.nb` (Gabry & Goodrich, 2016). MCMC is essentially a simulation technique to obtain the distribution of each parameter in a model (Zuur & Ieno, 2016). All model settings were `rstanarm` defaults (see supplementary code or Gabry & Goodrich, 2016). For example, priors were weakly informed normal distributions ($\mu = 0$, $\sigma = 2.5$), the number of chains = 4, and the number of iterations = 2000, with 1000 warmup iterations. We visually checked model residuals (Zuur & Ieno, 2016) and trace plots, and all chains mixed well (see S1). We inspected predictors for collinearity by using Variance Inflation Factors (VIF) with the function `check_collinearity` from the package `performace` (Lüdecke et al., 2019), and all VIF < 2 (see S1). There were no divergent transitions in simulated parameter trajectories, suggesting the posterior was well-explored, nor issues with convergence (all rhat values were very close to 1; see S1 and S2). We did not thin chains (Link & Eaton, 2012).

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We analyzed the response data, which were counts of bat passes, with a negative binomial distribution and log link function. In this model (see S2), we removed all bat species (or acoustic complexes) that contained 5 or fewer observations, since these data are not robust enough for inference, but included all other bat species/complexes. Thus, we set a random intercept for all included bat species, with random slope for hour after sunset (0-12), vertical strata (canopy vs understory), for the interaction between the two, and for moon illuminance – *i.e.* each of these four terms was allowed to vary by bat species. These four terms (hour after sunset, vertical strata, the interaction between the two, and moon illuminance) were also fit as fixed effects to make inferences on 'all bats' overall. We included site as a random intercept, to avoid pseudoreplication (Zuur & Ieno, 2016), although we did not have at least five levels (Harrison et al., 2018). Moon illuminance was centered by the mean and scaled by two standard deviations to both improve the computability of the model and to make this directly comparable to categorical (*e.g.* above vs below the canopy) predictors (Gelman, 2008).We included horizontal moon illumination (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 study (either due to moonlight or day of the year).

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Eliminado: Moon illuminance was calculated using custom windows command line code, *sunmoon* program (Jeff Conrad *unpublished software*). The methods are similar to those of Janiczek and DeYoung (1987). Sun and Moon positions are determined using the more accurate formulas of Van Flandern and Pulkkinen (1979).(Kyba, Conrad & Shatwell, 2020)following (Kyba, Conrad & Shatwell, 2020))

To further elucidate patterns of bat activity over the course of the night, we separately analyzed the 11 most common bat species or acoustic complexes (See Table 1 for list) with kernel density estimators of bat activity by hour after sunset, by vertical strata (canopy vs understory). We did not build kernel density estimates for other species, as the number of counts for those species was low, and we did not feel comfortable making inferences on minimal data.

Throughout the results we report model estimates and 80% and 90% credible intervals (for all in-text estimates see R code). While these choices (including 95%) are always largely arbitrary, we chose these values because 80% and 90% intervals both display a wide interval spanning a high probability range of parameter values, especially with the 80% interval replacing the common Stan default of 50% (McElreath, 2020). We avoid using a 95% credible interval for a number of reasons. Firstly, these can often be misinterpreted as 95% confidence intervals (McElreath, 2020). The latter, in contrast to Bayesian credible intervals, assume that the interval is random and the parameter is fixed, rely on imaginary resampling of data, and are often interpreted as a hypothesis test (McElreath, 2020). 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. As these are not hypothesis tests, these credible intervals give the reader a summary of the posterior distribution, thus reporting multiple credible intervals, rather than just one, help to demonstrate the shape of the posterior distribution (McElreath, 2020).

Results

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There were 12,151 bat passes above the canopy and 3,972 below the canopy. After accounting for repeat sampling of species, hour after sunset, and moon illuminance, generalized linear mixed effects models suggest that bat activity was 9.5 times (90% CI: 4.3 – 21.1) higher above the canopy, relative to the understory (S2). Yet, patterns for individual species (or acoustic complexes) were mixed (Fig. 1; S2). Broad patterns at 80% credible intervals suggest six species/complexes were more active above the canopy (*Cormura brevirostris*, *Molossus molossus*, Molossidae group B, *Peropteryx kappleri*, *Peropteryx macrotis*, and *Lasiurus blossevilli/Rhogeessa Io*), five in the understory (*Centronycteris maximiliani*, *Myotis riparius*, *Myotis simus/nigricans*, *Pteronotus alitonus*, and *Pteronotus rubiginosus*), and six show no difference (Molossidae group A, Phyllostomidae, *Pteronotus gymnonotus*, *Saccopteryx bilineata*, *Saccopteryx leptura*, and *Lasiurus* sp.). Of the strongest trends, *P. macrotis* was 21.8 times more likely to be found above the canopy (90% CI: 6.01 – 84.6), whereas *M. riparius* was a factor of 132.8 more likely to be in the understory (90% CI: 31.2 – 586.6).

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Overall bat activity decreased 22.0% (90% CI: 14.8 – 29.6%) for every hour above 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; S2). The bat complexes (Molossidae A, Molossidae B and *Lasiurus* sp.) 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). Above-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).

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The complexes Molossidae group A & B increased the use of both understory and above the canopy throughout the night.

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C. maximiliani activity showed a peak of activity in the middle of the night. This species was slightly more active in the understory, relative to above the canopy, during early and late parts of the night, whereas they were more active above the canopy during the middle of the night (Fig. 3A). *S. bilineata* had higher activity in the understory at the beginning and end of the night (dusk and dawn), and higher above-canopy activity in the early-middle of the night (Fig. 3B). Both *P. kappleri* and *P. macrotis* were far more active above the canopy (relative to understory) early in the night, but there was a spike in understory activity late in the night (Fig. 3C, D).

There is an 80.9% probability that moonlight had a positive effect on overall bat activity. Similarly, *M. molossus, C. brevirostris, and P. gymnonotus* have high probabilities of positive effects of moonlight on species activity (90.3%, 85.4%, and 87.8% respectively). *C. maximiliani*, *P. kappleri*, and *P. macrotis*, on the other hand, have high probabilities of negative effects of moonlight on bat activity (80.4%, 93.8%, and 89.5% respectively; Fig. 4).

Discussion

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Here we show that Neotropical bats use habitat above the forest canopy and within the forest understory differently throughout the night. We found that bats are overall more active above the canopy, which is consistent with previous work (Marques, Ramos Pereira & Palmeirim, 2016) and that overall bat activity decreases above the canopy throughout the night. We found four species here that were also more common in the canopy (*Cormura brevirostris, Molossus molossus*, *Peropteryx kappleri*, and *Peropteryx macrotis*). Wing aspect ratios (square of the wingspan divided by wing area) are high for three of these species, (*M. molossus, P. kappleri*, and *P. macrotis; C. brevirostris* is not represented in the literature; Marinello & Bernard, 2014), suggesting these bats are fast fliers with low maneuverability, which is thought to be advantageous in open spaces, such as above the canopy (see supplement for exploratory visualization of model estimates by wing aspect ratios and wing loading). Indeed, *P. kappleri*, and *P. macrotis* are known edge / open space foragers (Kalko et al., 2008; Barboza-Marquez et al., 2014). However, we found multiple species that are more active in the understory (compared to one species in Marques, Ramos Pereira & Palmeirim, 2016) including strong preferences for understory habitat for *Pteronotus alitonus*, and weaker preferences in the same direction for *Pternotus rubiginosus*. We also found two somewhat conflicting patterns, which might be explained by a lack of species resolution. *Centronycteris maximiliani* in our study weakly preferred the understory, while members of the same genus (i.e. *Centronycteris sp.*) were more common in the canopy in Marques et al. (2016). However, it isn't clear what species might have been included in *Centronycteris sp.* in their study. Similarly, we found a weak preference for the understory in a myotid acoustic complex (*Myotis simus/nigricans*), while Marques et al. (2016) found a canopy preference for *M. nigricans*, although we caution that this previous pattern is informed by only thirteen observations. Both the current study and Marques et al. (2016), show a clear understory preference for *Myotis riparius*. Other myotid species are thought to prefer to forage in the understory elsewhere in the world (Kennedy, Sillett & Szewczak, 2014; Wellig et al., 2018), suggesting that this characteristic may be a trait of the genus independent of the geographic location.

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For many bats, there were no clear differences in activity between above-canopy and understory habitat (e.g., *Saccopteryx bilineata, S. leptura, Lasiurus* sp., and *Pteronotus gymnonotus*). These patterns may occur for multiple reasons. *Lasiurus* sp., for example, might include multiple species (see Table 1 caption). If some species are more common above the canopy, and others below the canopy, these patterns might be cancelled when analyzed together as an acoustic complex. These patterns instead might occur because bats are just as active in the both vertical strata. Bernard (2001), for example, found the same lack of vertical stratification pattern as we did for *S. 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, we found that these two species were more active in the understory early and late in the night, while they were more active above the canopy in the early-middle of the night (Fig. 3B and S1). 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. *S. bilineata* has relatively high wing aspect ratios (Marinello & Bernard, 2014), which is thought to be advantageous for fast flight and confer low maneuverability, yet they spend considerable time below the canopy. This might be because they are opportunistic foragers (Jung & Kalko, 2011) that are foraging for different types of insects at different times (Rydell, Entwistle & Racey, 1996). However, this is speculation, and a deeper understanding of the natural histories of many

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of these taxa, along with more morphological data, are necessary for us to pin down exactly what these patterns mean.

Although previous work indicates that bat activity tends to decline with increasing moonlight illumination (Prugh & Golden, 2014), here we find a high probability that our sample of Neotropical bats generally show the opposite pattern, increasing bat activity with increasing moon illumination. At the individual species level, *M. molossus, P. gymnonotus,* and *C. brevirostris* all show increasing trends with higher levels of moonlight illumination, and all three of these species are more common above the canopy where they are more likely to be exposed directly to moonlight. It is not clear why these bats would prefer moonlight, but it is possible that certain prey are more likely to fly above the canopy on brighter nights (Roeleke et al., 2018; Kolkert et al., 2020) or that bats are more able to detect predators with vision in moonlight. *C. brevirostris* did not significantly alter activity in moonlight in previous studies (Appel et al., 2017), although in one study they trended in the same direction (positively) as found here (Appel et al., 2019). *C. maximiliani*, on the other hand, decreased activity in increased moonlight in our study, and is more common below the canopy, where moonlight often fails to penetrate. *P. kappleri, and P. macrotis* also both show decreasing activity trends with increasing moonlight, yet they are both more active above the canopy, where moonlight likely plays a larger sensory role. Many species have estimates that substantially overlap no effect. Notable examples are *P. rubiginosus, S. leptura,* and *M. riparius*, which all changed activity in relation to moonlight in previous studies (Appel et al., 2017, 2019). *M. riparius*, is a slow-flying bat with a low wing aspect ratio, that likely makes it vulnerable to predation in open spaces, an interpretation shared by authors of previous work that found this bat to avoid moonlight (Appel et al., 2017; Vásquez, Grez & Pedro, 2020). Thus, it is odd that this species is not affected by moonlight here. *P. rubiginosus* and *S. leptura* both increased activity in moonlight in previous work (Appel et al., 2019), but also show no changes here. All three of these species prefer the understory (more strongly in *M. riparius* and more weakly in *S. leptura*), which might suggest that the forest is quite dense at our sites, filtering out most of the moonlight. Such an effect has been shown with respect to artificial light from street lamps (Straka et al., 2019). However, as mentioned above *C. maximiliani* was less active in bright nights and also preferred the understory, so the idea that moonlight is filtered out by the canopy is certainly not conclusive.

This study was conducted during the wet season in French Guiana and Marques et al. (2016) occurred during the dry season in Brazil; both studies were short duration (9 and 20 days respectively) and unlikely to offer substantial inference for understanding seasonal effects. Further, many other differences between the French Guiana and Brazilian forests likely obfuscate any speculation about seasonality. Future research should push to understand vertical stratification over much longer periods of time to understand the effects of seasonality. In addition, a focus on bat prey will likely aid in understanding these patterns. 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). 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). Thus, seasonal cycles likely have important consequences for patterns of vertical stratification. 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 likely 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.

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Conclusions

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We used passive acoustic monitoring to explore how Neotropical bats use space over time. While bats generally were more active above the forest canopy, we show that individual groups of bats use space differently over the course of a night, and some prefer the understory. Given that most bats were more commonly detected above the canopy, it is possible that we might form erroneous conclusions about the quality of that habitat, or make poor management decisions, if we fail to survey habitat in three dimensions, and for the entire duration of a night. 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.

Acknowledgements:

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Data Availability

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The following information was supplied regarding data availability: ….

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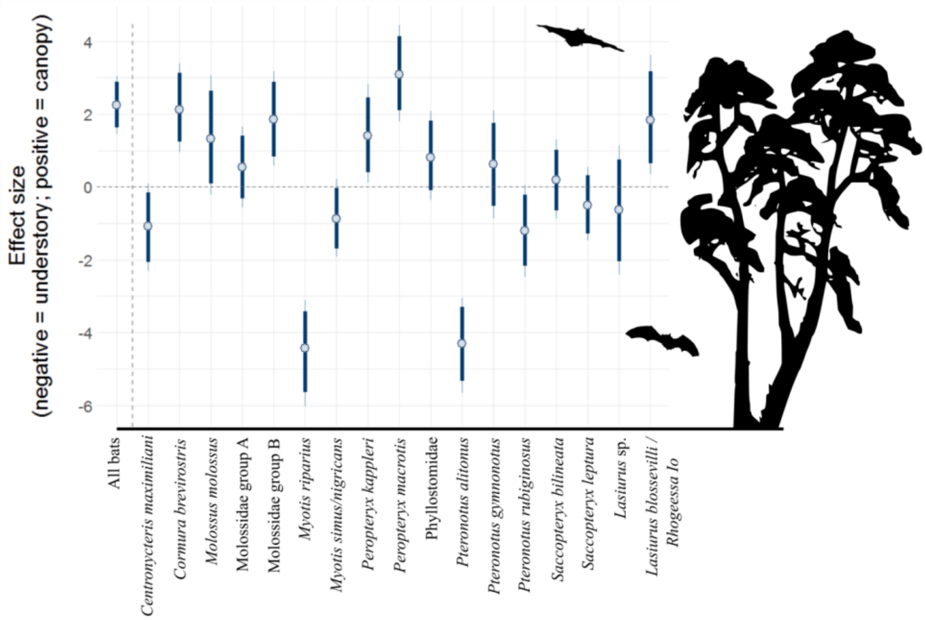

Figure 1: Model coefficient estimates for activity in vertical strata, by bat species/complex. Positive values on y axis indicate that bats were more active in the canopy, whereas negative values indicate that bats were more active near the forest floor. Bold lines are 80% credible intervals, whereas thin lines are 90% CI. See Table 1 caption for acoustic complex species breakdown

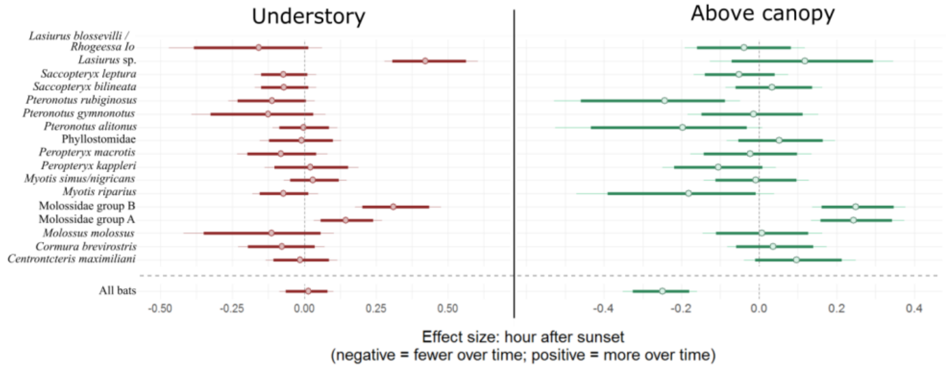

Figure 2: Model coefficient estimates for activity over the course of the night by bat species. Estimates on left are for understory activity, whereas those on right are for canopy activity. Positive values on x axis indicate that bats were more active as time passed within a night, whereas negative values indicate that bats were more active earlier in the night. Bold lines are 80% credible intervals, whereas thin lines are 90% CI. See Table 1 caption for acoustic complex species breakdown

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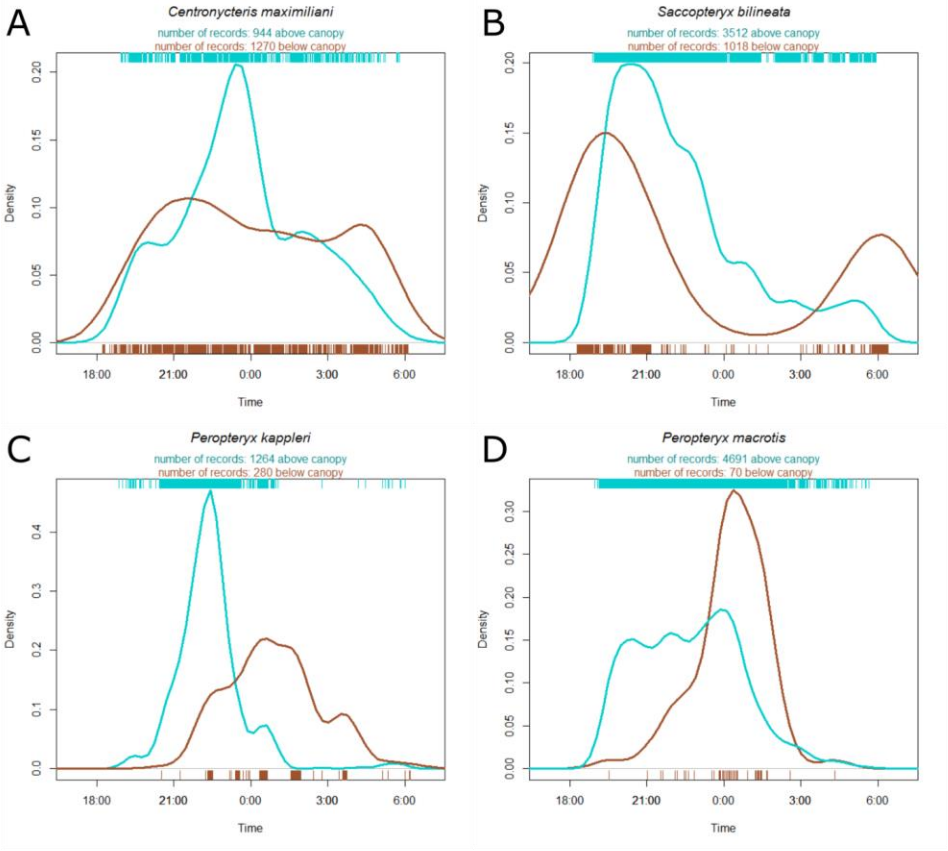

Figure 3: Kernel density estimate of activity of four most common species recorded at the Nouragues Research Station in French Guiana, plotted by time. hash marks at the bottom and top of the plot indicate raw data by understory (brown) and above canopy (blue), respectively. Species names and individual record numbers for both vertical strata are indicated above the plots. See supplement for further species plots.

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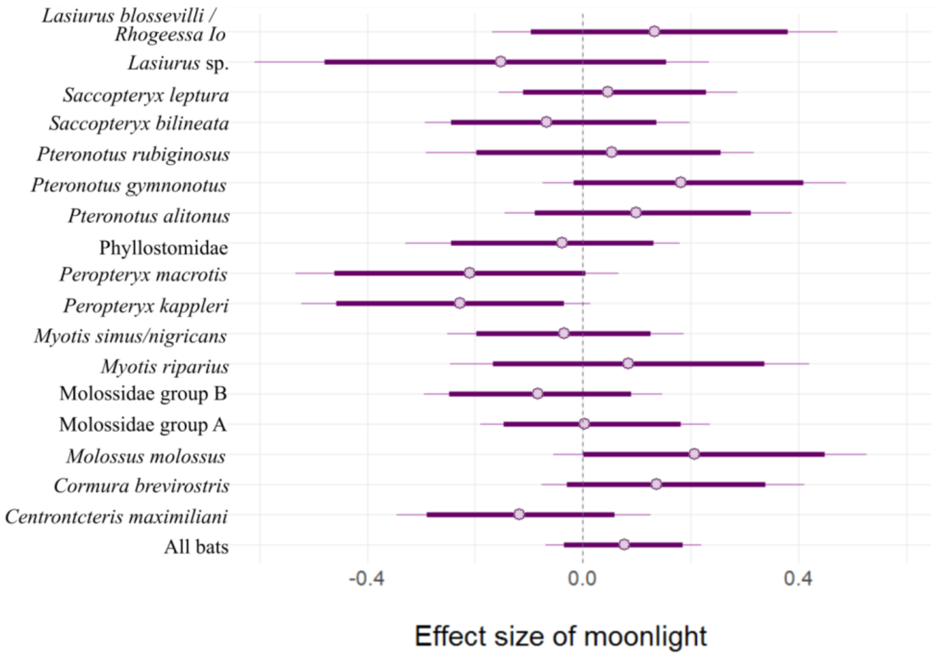

Figure 4: Model coefficient estimates for activity relative to moon illuminance. Estimates on left suggest less activity with increasing moonlight, whereas those on right suggest more activity for increasing moonlight. Bold lines are 80% credible intervals, whereas thin lines are 90% CI. See Table 1 caption for acoustic complex species breakdown

Table 1:

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

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Table 2:

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Output from Bayesian generalized linear mixed-effect model (negative binomial family; log-link function). SE = standard error, N Eff = number of effective samples in MCMC, and Rhat (A.K.A. the Gelman-Rubin statistic) is a measure of how chains might be reaching different conclusions. Here, all values are very close to 1, which indicates good model convergence. The first five ‘Variables’ are fixed effects, whereas all variables wrapped in ‘b[ ]’ are random effects. “Int.” = intercept, “Above” = above canopy (relative to below the canopy; i.e. the intercept), “Hour” is the hour since sunset, and everything to the right of the “|” are indicating that the effects vary by bat species / acoustic complexes and are keyed as follows: cenmax = *Centronycteris maximiliani*, corbre = *Corumura brevirostris*, molmol = *Molossus molossus*, Mol.A = Molossidae group A (see Table 1), Mol.B = Molossidae group B (see Table 1), myorip = *Myotis riparius*, myo.sp = *Myotis simus/nigricans*, perkap = *Peropteryx kappleri*, permac = *Peropteryx macrotis*, phyllo = Phyllostomidae, pteali = *Pteronotus alitonus*, ptegym = *Pteronotus gymnonotus*, pterub = *Pteronotus rubiginosus*, sacbil = *Saccopteryx bilineata*, saclep = *Saccopteryx leptura*, las.sp = *Lasiurus* sp. (see Table 1), lasblo/rhoio = *Lasiurus blossevilli / Rhogeessa Io.*

Comentado [ACAM3]: Include this table as supplement 2

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Variable	Estimate	SE	80% CI	90% CI	N Eff	Rh
Intercept	-1.63	0.56	-2.34 – -0.88	-2.55 – -0.68	1123	1.00
Moon Illuminance	0.08	0.08	-0.03 – 0.19	-0.07 – 0.22	1420	1.002
Hour	0.02	0.05	-0.06 – 0.09	-0.08 – 0.11	897	1.005
Above	2.06	0.51	1.38 – 2.70	1.18 – 2.90	1152	1.006
Hour:Above	-0.28	0.06	-0.35 – -0.21	-0.38 – -0.18	2233	1.001
b[Int. |cenmax]	3.39	0.62	2.61 – 4.19	2.40 – 4.44	1378	1.002
b[Hour |cenmax]	0.00	0.07	-0.09 – 0.10	-0.12 – 0.13	1791	1.002
b[Above |cenmax]	-1.09	0.70	-2.00 – -0.17	-2.29 – 0.05	1759	1.003
b[Moon Illuminance |cenmax]	-0.12	0.14	-0.29 – 0.06	-0.35 – 0.13	2559	1.002
b[Hour:Above |cenmax]	0.06	0.09	-0.05 – 0.19	-0.09 – 0.23	2859	1.001
b[Int. |corbre]	-0.91	0.74	-1.87 – 0.02	-2.14 – 0.29	1650	1.001
b[Hour |corbre]	-0.12	0.10	-0.25 – 0.00	-0.29 – 0.03	2383	1.001
b[Above |corbre]	2.15	0.76	1.23 – 3.16	0.98 – 3.43	1949	1.003
b[Moon Illuminance |corbre]	0.14	0.14	-0.03 – 0.34	-0.08 – 0.41	2209	1.002
b[Hour:Above |corbre]	0.16	0.10	0.03 – 0.30	0.00 – 0.33	2984	1.000
b[Int. |molmol]	-3.25	1.04	-4.65 – -1.98	-5.05 – -1.63	2183	1.001
b[Hour |molmol]	-0.13	0.14	-0.31 – 0.04	-0.38 – 0.08	2947	1.000
b[Above |molmol]	1.53	1.03	0.33 – 2.96	0.00 – 3.40	2412	1.002
b[Moon Illuminance |molmol]	0.21	0.17	0.00 – 0.45	-0.05 – 0.53	3192	1.000

b[Hour:Above |molmol]	0.12	0.13	-0.03 – 0.30	-0.08 – 0.36	2832	1.000
b[Int. |Mol.A]	-0.90	0.64	-1.76 – -0.08	-1.99 – 0.17	1334	1.002
b[Hour |Mol.A]	0.13	0.07	0.04 – 0.23	0.02 – 0.25	1221	1.004
b[Above |Mol.A]	0.66	0.68	-0.24 – 1.53	-0.52 – 1.77	1608	1.004
b[Moon Illuminance |Mol.A]	0.00	0.12	-0.15 – 0.18	-0.19 – 0.24	1576	1.004
b[Hour:Above |Mol.A]	0.12	0.08	0.03 – 0.23	0.00 – 0.27	2286	1.001
b[Int. |Mol.B]	-2.21	0.78	-3.26 – -1.23	-3.60 – -0.93	1688	1.001
b[Hour |Mol.B]	0.28	0.09	0.17 – 0.40	0.14 – 0.44	1722	1.001
b[Above |Mol.B]	1.72	0.82	0.73 – 2.80	0.45 – 3.13	1884	1.001
b[Moon Illuminance |Mol.B]	-0.08	0.13	-0.25 – 0.09	-0.29 – 0.15	2153	1.002
b[Hour:Above |Mol.B]	0.00	0.09	-0.12 – 0.12	-0.16 – 0.15	2841	1.000
b[Int. |myorip]	2.06	0.58	1.32 – 2.81	1.13 – 3.03	1317	1.002
b[Hour |myorip]	-0.08	0.06	-0.16 – 0.00	-0.19 – 0.03	1220	1.003
b[Above |myorip]	-4.66	0.88	-5.88 – -3.56	-6.26 – -3.29	2414	1.002
b[Moon Illuminance |myorip]	0.08	0.19	-0.17 – 0.34	-0.25 – 0.42	3426	1.002
b[Hour:Above |myorip]	-0.16	0.15	-0.36 – 0.03	-0.45 – 0.08	3753	1.000
b[Int. |myo.sp]	1.10	0.57	0.35 – 1.85	0.14 – 2.08	1237	1.003
b[Hour |myo.sp]	0.03	0.06	-0.05 – 0.12	-0.07 – 0.14	1134	1.004
b[Above |myo.sp]	-1.05	0.65	-1.88 – -0.20	-2.14 – 0.03	1590	1.004
b[Moon Illuminance |myo.sp]	-0.04	0.12	-0.20 – 0.13	-0.25 – 0.19	3227	1.000
b[Hour:Above |myo.sp]	-0.03	0.08	-0.14 – 0.07	-0.17 – 0.11	2964	1.001
b[Int. |perkap]	1.43	0.74	0.49 – 2.39	0.25 – 2.67	1587	1.001
b[Hour |perkap]	0.03	0.09	-0.09 – 0.15	-0.12 – 0.19	1763	1.003
b[Above |perkap]	1.51	0.75	0.58 – 2.51	0.32 – 2.81	1630	1.002
b[Moon Illuminance |perkap]	-0.23	0.16	-0.46 – -0.04	-0.52 – 0.01	2413	1.000
b[Hour:Above |perkap]	-0.12	0.10	-0.25 – 0.01	-0.30 – 0.04	2575	1.001
b[Int. |permac]	0.64	0.73	-0.28 – 1.54	-0.53 – 1.79	1470	1.002
b[Hour |permac]	-0.05	0.09	-0.17 – 0.06	-0.20 – 0.10	2101	1.001
b[Above |permac]	3.39	0.77	2.44 – 4.42	2.19 – 4.73	1828	1.003
b[Moon Illuminance |permac]	-0.21	0.18	-0.46 – 0.00	-0.53 – 0.07	2826	1.000
b[Hour:Above |permac]	0.03	0.10	-0.11 – 0.17	-0.15 – 0.21	3553	1.000
b[Int. |phyllo]	-1.34	0.69	-2.26 – -0.40	-2.54 – -0.15	1608	1.003
b[Hour |phyllo]	0.00	0.08	-0.10 – 0.11	-0.13 – 0.15	1830	1.001
b[Above |phyllo]	1.09	0.72	0.14 – 2.05	-0.12 – 2.35	1711	1.004
b[Moon Illuminance |phyllo]	-0.04	0.14	-0.24 – 0.13	-0.33 – 0.18	3216	1.000
b[Hour:Above |phyllo]	0.06	0.09	-0.06 – 0.18	-0.09 – 0.22	3452	0.999
b[Int. |pteali]	2.14	0.59	1.39 – 2.89	1.20 – 3.14	1260	1.003
b[Hour |pteali]	-0.01	0.06	-0.10 – 0.07	-0.12 – 0.10	1265	1.003
b[Above |pteali]	-4.51	0.84	-5.59 – -3.48	-5.87 – -3.21	2370	1.001
b[Moon Illuminance |pteali]	0.10	0.15	-0.09 – 0.31	-0.14 – 0.39	3755	1.001
b[Hour:Above |pteali]	-0.20	0.15	-0.43 – -0.03	-0.51 – 0.02	3441	1.001
b[Int. |ptegym]	-2.30	0.91	-3.47 – -1.14	-3.80 – -0.85	2051	1.001
b[Hour |ptegym]	-0.13	0.13	-0.31 – 0.02	-0.36 – 0.06	3316	0.999
b[Above |ptegym]	0.82	0.86	-0.27 – 1.99	-0.58 – 2.35	2513	1.002

b[Moon Illuminance |ptegym]	0.18	0.16	-0.02 – 0.41	-0.07 – 0.49	3286	1.000
b[Hour:Above |ptegym]	0.11	0.12	-0.03 – 0.28	-0.07 – 0.34	3350	0.999
b[Int. |pterub]	-0.15	0.71	-1.03 – 0.76	-1.27 – 1.04	1586	1.002
b[Hour |pterub]	-0.11	0.09	-0.24 – 0.00	-0.27 – 0.04	2181	1.001
b[Above |pterub]	-1.17	0.75	-2.14 – -0.20	-2.43 – 0.10	1997	1.001
b[Moon Illuminance |pterub]	0.05	0.17	-0.20 – 0.26	-0.29 – 0.32	2431	1.001
b[Hour:Above |pterub]	-0.13	0.13	-0.33 – 0.01	-0.41 – 0.06	3623	1.000
b[Int. |sacbil]	3.65	0.59	2.91 – 4.42	2.70 – 4.63	1264	1.003
b[Hour |sacbil]	-0.07	0.07	-0.16 – 0.01	-0.18 – 0.04	1226	1.003
b[Above |sacbil]	-0.02	0.65	-0.89 – 0.87	-1.16 – 1.12	1544	1.003
b[Moon Illuminance |sacbil]	-0.07	0.15	-0.24 – 0.14	-0.29 – 0.20	2204	1.002
b[Hour:Above |sacbil]	0.09	0.08	-0.01 – 0.20	-0.04 – 0.24	3023	1.000
b[Int. |saclep]	2.72	0.56	1.97 – 3.45	1.77 – 3.66	1153	1.003
b[Hour |saclep]	-0.08	0.06	-0.16 – 0.00	-0.18 – 0.03	988	1.004
b[Above |saclep]	-0.70	0.63	-1.52 – 0.15	-1.72 – 0.40	1466	1.004
b[Moon Illuminance |saclep]	0.05	0.13	-0.11 – 0.23	-0.16 – 0.29	2378	1.002
b[Hour:Above |saclep]	0.02	0.07	-0.07 – 0.12	-0.10 – 0.15	2698	1.000
b[Int. |las.sp]	-3.75	0.95	-5.04 – -2.57	-5.49 – -2.28	1848	1.001
b[Hour |las.sp]	0.44	0.10	0.33 – 0.57	0.30 – 0.62	1679	1.001
b[Above |las.sp]	-0.72	1.03	-2.07 – 0.59	-2.48 – 0.99	2085	1.000
b[Moon Illuminance |las.sp]	-0.15	0.24	-0.48 – 0.15	-0.61 – 0.23	2816	1.000
b[Hour:Above |las.sp]	-0.20	0.13	-0.39 – -0.04	-0.44 – 0.00	2655	1.000
b[Int. |lasblo/rhoio]	-2.99	1.03	-4.44 – -1.73	-4.88 – -1.42	2489	1.002
b[Hour |lasblo/rhoio]	-0.14	0.13	-0.33 – 0.03	-0.40 – 0.07	3231	1.001
b[Above |lasblo/rhoio]	2.12	1.03	0.95 – 3.54	0.62 – 3.99	2944	1.002
b[Moon Illuminance |lasblo/rhoio]	0.13	0.17	-0.10 – 0.38	-0.17 – 0.47	3482	1.000
b[Hour:Above |lasblo/rhoio]	0.11	0.13	-0.05 – 0.29	-0.09 – 0.35	3116	0.999
b[Int. |Tower=green]	0.21	0.19	-0.04 – 0.48	-0.15 – 0.59	3696	1.00
b[Int. |Tower=red]	-0.22	0.19	-0.51 – 0.01	-0.63 – 0.11	3631	1.000

Tabla con formato