# Temperature, rainfall, and moonlight intensity effects on activity of tropical insectivorous bats

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# Temperature, rainfall, and moonlight intensity effects on activity of tropical insectivorous bats

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The extrinsic factors that most influence animal activity are weather and light conditions, which can be assessed at hourly, monthly, and even lunar-cycle timescales. We evaluated the responses of tropical aerial-insectivorous bats to temperature, rainfall, and moonlight intensity within and among nights. Temperature positively affected the activity of two species (*Cormura brevirostris* and *Saccopteryx bilineata*). Moonlight reduced *Myotis riparius* activity and increased the activity of *Pteronotus rubiginosus* and *S. leptura*. Rainfall can promote an irregular activity peak during the night compared to nights without rainfall, but the bats in our study were not active for a longer time after a rainfall event. Our findings indicate that moonlight and temperature are the variables with the highest impact on the activity of tropical insectivorous bat species and that some species are sensitive to small variations in rainfall among and within nights.

Os fatores extrinsícos que mais afetam a atividade dos animais são o clima e a luminosidade, que podem ser avaliados em escalas horárias, mensais e em ciclos lunares. Avaliamos as respostas dos morcegos insetívoros aéreos tropicais aos efeitos da temperatura, chuva e luminosidade lunar entre noites e dentro de uma mesma noite. A temperatura afetou positivamente a atividade de duas espécies (*Cormura brevirostris* e *Saccopteryx bilineata*). A luminosidade lunar reduz a atividade de *Myotis riparius* e aumenta as atividades de *Pteronotus rubiginosus* e *S. leptura*. A chuva pode promover um pico irregular de atividade ao longo da noite em comparação com noites sem chuva, mas os morcegos na nossa área de estudo não ficaram ativos por mais tempo após uma chuva. Os resultados indicam que a luminosidade lunar e a temperatura são as variáveis que mais afetam a atividade das espécies de morcegos insetívoros aéreos e algumas espécies são sensíveis a pequenas variações de chuva entre noites e dentro de uma mesma noite.

Key words: acoustic monitoring, activity pattern, Amazon, Chiroptera, lunar cycle, rainfall, temperature

Animals commonly adjust their activity to extrinsic factors such as weather and light conditions (Davies et al. 2012). By studying the effects of such factors over a period of time, we can evaluate temporal variation in animal activity, thereby improving our understanding of their ecology and behavioral patterns (Aschoff et al. 1982). The effects of weather and light conditions can be assessed at different timescales (e.g., hourly, monthly, according to the lunar cycle, or seasonally), resulting in different responses of animal activity (Erkert 1982; Mccann et al. 2017). The weather conditions that most commonly affect diurnal animal activity are temperature, humidity, and rainfall (Vickery and Bider 1981; Asmus et al. 2018). However, moonlight also strongly affects foraging behavior in some nocturnal animals (Prugh and Golden 2014; English et al. 2017; Underhill and Höbel 2018).

Moonlight increases the activity of nocturnal animals that use vision to forage. Bright nights increase prey visibility and, consequently, increase foraging success of predators. Animals that are simultaneously prey and predators face the crucial trade-off between increasing foraging success and the risk of predation (Lang et al. 2006; Clarke 2014; Blubaugh et al. 2017; Musila et al. 2019). For instance, tropical rodents use ambient light to detect insects, being more active during periods of full moon; however, since they are common prey of owls, they have to use their higher visual acuity during those nights to detect the owls (Maestri and Marinho 2014; Rubolini et al. 2014). In contrast, the foraging activity of some bat species that primarily use other senses (e.g., olfaction or echolocation) decreases on bright nights to avoid visually oriented predators (Pech-Canche et al. 2010; Saldaña-Vázquez and Munguía-Rosas 2013).

Temperature, humidity, and rainfall are less predictable than lunar cycles and usually vary within the same day and between days, substantially affecting the activity of numerous animal species (Hayes 1997; Adams and Hayes 2008). Ambient temperature has a profound effect on energy expenditure to maintain body heat in warm-blooded animals. Therefore, low temperature usually results in decreased activity of many species in both tropical and temperate latitudes (Giné et al. 2015; Klüg-Baerwald et al. 2017). The effects of humidity vary among species; some animals, such as bats, are less active at relatively low humidity levels to avoid the atmospheric attenuation to their echolocation calls, but nocturnal birds increase foraging activity because prey availability is generally higher (Digby et al. 2014; Chaverri and Quirós 2017). Rainfall negatively affects thermoregulation, especially of small mammals such as bats, rodents, and marsupials, by wetting their fur and also because flight is impeded during strong rainfall events (Brandt and Lambin 2005; Snell-Rood 2012).

The effects of moonlight, temperature, relative humidity, and rainfall have been studied mostly using relatively long time intervals (e.g., seasonally—Pearce-Higgins et al. 2015; Pettit and O'Keefe 2017). However, daily or nocturnal variations can also have marked effects on animal foraging activity (Milne et al. 2005). Some species can adjust their activity to rapid changes in these factors to take advantage of the most favorable conditions (e.g., torpor—Smit et al. 2011). For example, heavy rain at the beginning of the night can cease the activity of some bat species (Kunz 1973; Weinbeer and Meyer 2006). The effects of weather conditions and moonlight over hourly intervals have rarely been studied due to difficulties in registering the activity of most species during short intervals of time (Sánchez-Ferrer et al. 2016; Davimes et al. 2017). However, due to the rapid technological advances in noninvasive and remote-sensing sampling methods, it is now possible to monitor the activity of some species by registering acoustic calls, photographs, or even skin temperature at short time intervals (Froidevaux et al. 2014; Attias et al. 2018).

For bats, the upsurge in use of ultrasound recorders and acoustic-analysis software allows the passive and autonomous continuous monitoring of many species throughout the night (Britzke et al. 2013). The total number of search-phase calls is directly associated with foraging activity (Fenton 2013; Adams et al. 2015) and is therefore a direct measure of bat activity levels or relative abundance (Oliveira et al. 2015; Torrent et al. 2018). Bats are small endothermic mammals, and their activity behavior is strongly associated with weather conditions and moonlight intensity (Ciechanowski et al. 2007; Burles et al. 2009; Appel et al. 2017). For aerial-insectivorous bats, environmental temperature is crucial because they need to maintain a stable body temperature and because it largely influences insect activity (Agosta et al. 2005; Barros et al. 2014). Humidity and rainfall also interfere with atmospheric propagation of echolocation, and heavy rain can influence the thermoregulation of bats, thereby hindering foraging activity and directly affecting flight ability (Voigt et al. 2011; Russo and Voigt 2016). Effects of moonlight intensity are species-specific and can be related to the species' flight speed and prey availability (Lang et al. 2006; Appel et al. 2017; Roeleke et al. 2018). In general, lunar phobia is more evident in tropical bat species than in temperate species and more commonly found in species that forage over the water and forest canopy and are therefore more exposed to predators (Saldaña-Vázquez and Munguía-Rosas 2013).

The influences of environmental cues on bat activity have been documented for numerous temperate aerial-insectivorous bat species (Geluso and Geluso 2012; Farneda et al. 2015; Pettit and O'Keefe 2017), but rarely for tropical insectivorous species (Meyer et al. 2004; Barros et al. 2014; Appel et al. 2017; Dias-Silva et al. 2018). Furthermore, most studies in the tropics have evaluated only one environmental factor or entirely removed periods with unfavorable conditions, such as rainy nights (Appel et al. 2017; Dias-Silva et al. 2018). In this study, we examined how activity of aerial-insectivorous bats responds to air temperature (factor negatively correlated with humidity), rainfall, and moonlight intensity among nights and how hourly activity of bats responds to rainfall within a night. We only examined the influence of rainfall on hourly activity. Other factors such as temperature have low variation (a few degrees) during the same night. Therefore, our main research questions and predictions were as follows:

1) Does bat activity respond to temperature, rainfall, or moonlight intensity between nights? We predicted that bat activity would be positively associated with air temperature and negatively with rainfall among nights. We also predicted that responses to moonlight intensity would be species-specific.
2) Does bat activity respond to weather conditions (temperature, rainfall) differently between dark and bright nights? We expected that the bat species with higher activity on dark nights would be less affected by temperature and rainfall on dark than on bright nights. We also predicted that bat species with higher activity on bright nights would be less influenced by weather conditions on bright nights than on dark nights.
3) Do the duration time and hour of the activity peak within a night change after rainfall? Bats show peaks of activity throughout the night, and most species are active shortly after sunset because more insects are available soon after sunset. Rainfall during the peak period could require the bats to increase their activity at other times. We therefore predicted that the hour of the activity peak would be later

after a rainfall event and that bats would be active longer after rainfall to compensate for the loss in foraging activity. For nights without rainfall, we predicted that bats would forage for a shorter time, with activity concentrated immediately after sunset.

## Materials and Methods

*Study area.*—The study was conducted at the Reserva Florestal Adolpho Ducke (2°58′S, 59°55′W; hereafter Ducke Reserve), a protected area of 10,000 ha in central Amazonia, Brazil. The site supports mainly terra firme rainforest with different vegetation structures, based on the relief and soil composition (Hopkins 1999). The climate in this region is characterized by a dry season that usually occurs between June and November and a rainy season between December and May (Oliveira et al. 2008). The average temperature was 26.7°C, and the average annual precipitation was 2,400 mm, with a maximum of 299 mm in February and a minimum of 93 mm in June, in the period from 1965 to 1994 (Ferreira et al. 2012). During the rainy period of 2013, the average temperature of the Ducke Reserve was 24.7°C and the average precipitation was 2,093 mm.

The reserve has a trail system that forms a 64-km$^2$ grid (5 × 5 km), with nine trails oriented north–south and nine trails east–west. We used a subsection of the trail system with six trails oriented north–south and six trails east–west, covering an area of 25 km$^2$. The trail system was established according to the RAPELD method (RAP component: rapid biodiversity survey; PELD component: studies of long-term ecological research—Magnusson et al. 2005). Ducke Reserve is part of the Brazilian Long-Term Ecological Research Program of the Brazilian National Research Council (PELD–CNPq) and a site of the National Program for Biodiversity Research (PPBio—Magnusson et al. 2005, 2014). Each plot is 250 m long, with an irregular shape that minimizes within-plot topographic variation and consequently minimizes variations in soil properties, drainage, and plant-species composition (Magnusson et al. 2005). We sampled 10 plots in riparian and 10 in nonriparian areas within the grid (Fig. 1), with a distance of 0.56–8.1 km between plots.

*Bat acoustic survey.*—We used automatic recording detectors (Song Meter SM2Bat+), coupled to omnidirectional ultrasonic SMX-US microphones (Wildlife Acoustics, Maynard, Massachusetts), to register aerial-insectivorous bat activity. The SM2Bat+ units were configured to passively register bat activity in real time, with a 16-bit full spectrum resolution, 1-s pre-trigger, 0.1-s post-trigger, High Pass Filter set at fs/32 (12 kHz), and trigger level of 18 SNR. The recorders were programmed to monitor bat activity between 1800 and 0600 h. The recorders were placed at the center of each plot and the microphones at a height of 1.5 m. In riparian plots, we installed 3-m cables to position the microphones over the center of the stream. Each plot was monitored from four to six consecutive nights during the 2013 rainy season (January to May), and the detectors were not necessarily set to record in both plots at

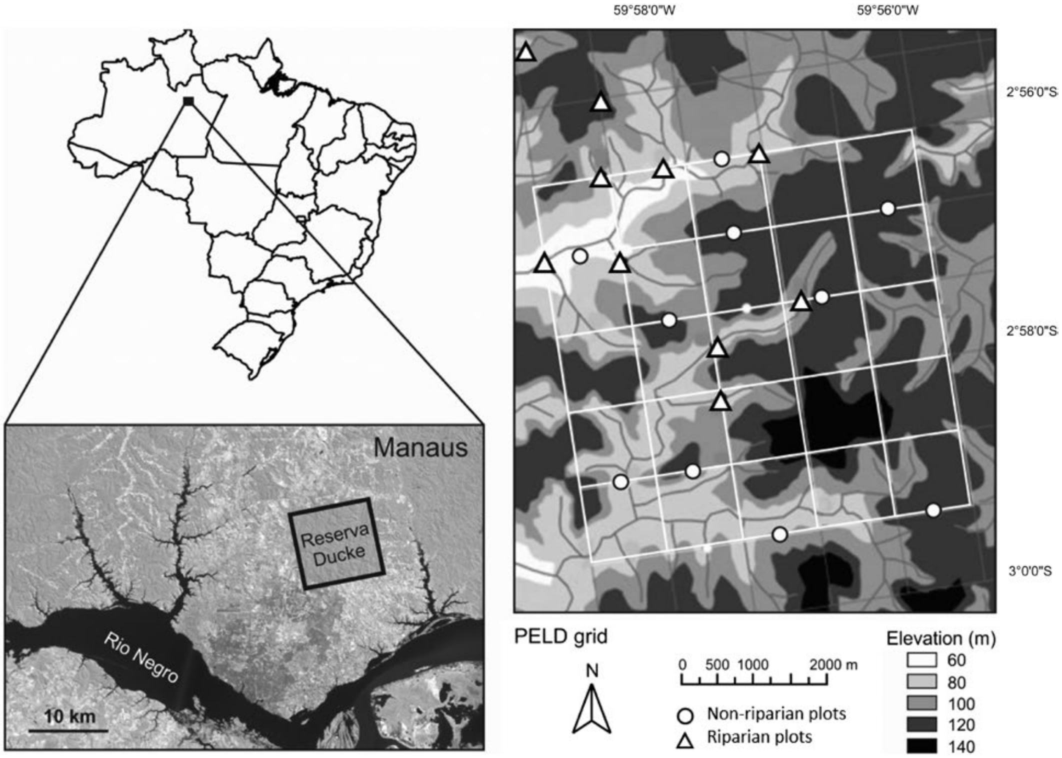

**Fig. 1.**—Ducke Reserve, north of Manaus, Amazonas, Brazil. Distribution of sampled plots in the PELD grid, including topography and streams. The circles represent the non-riparian plots and the triangles correspond to the riparian plots.

the same time. The recording effort resulted in 104 nights and 1,248 effective recording hours.

Bat activity was considered as the number of bat passes per hour and night. A bat pass was defined as a 5-s recording that contained at last two search-phase calls characteristic of a bat species (Oliveira et al. 2015; Appel et al. 2017). Thus, all bat recordings were segmented into files of 5 s and visualized in the Kaleidoscope program 3.1.1 (Wildlife Acoustics). All bat passes were manually identified to species level or sonotypes when it was not possible to confidently identify a particular species (Torrent et al. 2018). The classification was based on the library of Amazonian bat ultrasounds (López-Baucells et al. 2018) and on call characteristics available in the literature (Jung et al. 2007, 2014; Barataud et al. 2013; Briones-Salas et al. 2013; Arias-Aguilar et al. 2018). We did not include feeding buzzes and social calls in the analysis because of small sample sizes and difficulties in their classification; we only considered search-phase calls easily distinguishable from background noise.

*Bat-species identification.*—We identified 15,321 bat passes from 17 aerial-insectivorous bat species and five acoustic complexes. The limited range of species detection by recorders (< 50 m around recorder) can introduce bias into estimates of species activity. We minimized any potential detection-related biases by focusing on species that are well sampled with SM2 recordings. We determined a minimum of 12 plots (60% of sampled plots) and a minimum of 20 nights as the cutoff, sufficient sampling to run the analysis (see Supplementary Data SD1). The results include the following species: mustached bat, *Pteronotus rubiginosus* (named as *P. parnellii* in Oliveira et al. 2015 and Appel et al. 2017, but revised by López-Baucells et al. 2017 and Pavan et al. 2018); thumbless bat, *Furipterus horrens*; shaggy bat, *Centronycteris maximiliani*; chestnut sac-winged bat, *Cormura brevirostris*; greater sac-winged bat, *Saccopteryx bilineata*; lesser sac-winged bat, *Saccopteryx leptura*; and riparian myotis, *Myotis riparius*.

*Moonlight intensity and weather conditions.*—We used the Moontool 2.0 software to estimate moonlight intensity (adapted by Meeus 1991). The software calculates luminance based on the portion of the lunar disc that reflects sunlight and considers the position of the Earth in relation to the sun, showing the time of moonrise and moonset. To test the effect of dark and bright nights, we classify the type of night (dark or bright) using the threshold of 0–30% of moonlight intensity as dark nights and 70–100% as bright nights as proposed by Appel et al. (2017).

Canopy openness and presence of clouds can influence negatively the penetration of moonlight, and therefore its intensity, inside a forest, with consequent effects upon bat activity. We obtained data on canopy openness for three riparian and four nonriparian plots sampled in this study (Research Program on Biodiversity 2012). The information indicated low variation in the percentage of canopy openness between sampled plots (mean ± *SD* min–max; 7.63% ± 1.07, 6.13–9.17%). Because of the low variation among plots, we assume that moonlight penetrates into the forest similarly among the plots sampled; therefore, the influence of canopy openness on bat activity was similar. Presence of clouds was assessed by the accumulated rainfall data from the Climatological Station. Rainfall data for this case were used for detection of cloudy nights, since it was not possible to monitor cloud cover across the study period. Nights were considered "cloudy" when rainfall ranged from 0.1 to 10 mm/h, generally classified as weak to moderate rain. To test if the occurrence of clouds affected bat activity, an analysis of covariance (ANCOVA) was used with cloudy nights as a covariate (categorical variable) and the moonlight intensity percentage as a predictor (continuous variable). For all studied bat species, cloud cover did not affect bat activity and therefore was not used in subsequent models (see Supplementary Data SD2).

To evaluate weather conditions, we used data on accumulated rainfall, relative humidity, and air temperature from the Ducke Reserve Meteorological Station. These data were collected every 30 min between January and May 2013 by the technical team of the Coordination of Climate and Water Resources Research (CPCR) of the National Institute of Amazonian Research (INPA). We used the means of air temperature, relative humidity, and accumulated rainfall for each hour. Air temperature (°C) and relative humidity (%) were measured by a HMP45C instrument (Campbell Scientific, São Paulo, Brazil). Data on accumulated rainfall in millimeters were obtained from a rain gauge that recorded this information automatically.

*Data analysis.*—To test how the activity of each bat species responded to moonlight intensity and weather conditions, we used generalized linear mixed models (GLMMs) with the "lme4" R package (Bolker et al. 2009; Bates et al. 2016). To control overdispersion of the data, we used a quasi-Poisson distribution for six species; because of zero-inflated data, we fitted our models for one species (*F. horrens*) with the negative binomial distribution. Temperature was correlated with relative humidity (Pearson correlation = −0.77), and we opted to use only temperature and rainfall as predictor variables in all analyses. The response variable (total number of bat passes per night – $P$) was transformed to $\log(P + 1)$ to enhance linearity. Predictor variables were standardized to a mean of 0 and a *SD* of 1 to facilitate comparison of their relative effects. To account for the temporal autocorrelation in the data and to account for the differences of the nonriparian and riparian plots, we included type of plot (nonriparian or riparian plot) as random variable in the GLMMs. We also calculated the independent contribution of each variable in the model, using hierarchical partitioning (HP) with the "hier.part" R package (Nally and Walsh 2004). We used a total of 104 sampling nights in this analysis.

We tested the influence of weather conditions on bat activity between the types of night (dark and bright) through an ANCOVA, using GLMMs. The response variable was bat activity (log-transformed), the predictor variables were rainfall or temperature, the covariate variable was the type of night, and we included type of plot (nonriparian or riparian plot) as a random variable. We used ANCOVA for each species, with rainfall, temperature, and the interaction between rainfall, temperature, and the covariate (type of night). If the interaction between rainfall or temperature and the covariate (type of night) was significant, this indicated that bat activity was affected by the weather conditions differently between dark and bright nights. We used 29 dark and 38 bright nights in this analysis.

To test the effect of rainfall on the activity peak, we used analysis of variance (ANOVA) with post hoc Tukey's tests to compare bat activity among 12 h of records for nights without rainfall and for nights with rainfall during the interval of peak activity. We defined the activity peak as the highest activity in the whole night and visualized the peak using percentiles of activity in the "quantile" R package (Adams et al. 2015). For most species, the activity peak was between 1800 and 2200 h, and therefore, we considered the occurrence of rainfall as a minimum of 2 h between 1800 and 2200 h ($n$ = 25 nights). In particular for *P. rubiginosus*, hourly activity peaked in the middle of the night, and for this species, we considered the occurrence of rainfall when there was a minimum of 2 h between 2100 and 0200 h ($n$ = 10 nights). We considered accumulated rainfall between 0.3 and 10 mm/h as weak to moderate (World Metereological Organization 2008), which can inhibit bat activity (Erkert 1982; Ciechanowski et al. 2007). Heavier rainfalls occurred on only three nights in our study period; because of low numbers of heavy rainfalls, they were not included for this analysis. To test if the duration of bat activity was higher after a rainfall event, we used Student's $t$-test to compare the durations of bat activity (in minutes after sunset) after rainfall to the same time interval (x-y hours) on nights without rainfall (control). For example, if the rain occurred between 1800 and 2200 h (5 h of rain), we summed the minutes with bat activity during 5 h after the rainfall (2300 to 0500) and compared this with the duration of bat activity of the same interval (2300 to 0500) on nights without rainfall.

## RESULTS

*Effects of weather conditions and moonlight intensity on bat activity among nights.*—Of the seven species studied, the activity of five species was affected by temperature, rainfall, or moonlight intensity, but the variable that most contributed to HP values was moonlight intensity (Table 1). *Pteronotus rubiginosus* and *S. leptura* were positively associated with moonlight intensity, and *M. riparius* responded negatively to moonlight. Temperature positively affected *C. brevirostris* and *S. bilineata*. *Centronycteris maximiliani* and *F. horrens* were not influenced by any of the tested factors (Table 1).

*Effects of weather conditions on bat activity during dark and bright nights.*—The activity of *M. riparius* was higher on dark nights, while *S. leptura* and *P. rubiginosus* had higher activity on bright nights (Table 2). The interaction between rainfall and type of night for *P. rubiginosus* showed that this species increased its activity during rainfall on bright nights and decreased activity during rainfall on dark nights (Table 2). The interaction between temperature and type of night was not significant for any bat species activity (Table 2).

*Effects of rainfall on hourly activity of bats.*—The activity of *C. brevirostris* and *S. leptura* was more irregular on nights with rainfall, especially during the hours in which rainfall occurred (Table 3). On nights without rainfall, *C. brevirostris* and *S. leptura* had activity peaks during the first 60 min after sunset, but rainfall during this period caused them to be more active during the whole night (Fig. 2). *Pteronotus rubiginosus* did not show activity peaks on nights with rainfall different from those on nights without rainfall (Table 3; Fig. 2). *Furipterus horrens*, *S. bilineata*, and *M. riparius* did not alter their period of peak activity regardless of rain (Table 3).

The duration of activity after a rainfall event changed for *P. rubiginosus* and *S. leptura* (Table 4). *Saccopteryx leptura* was active for longer after a rainfall event compared to nights without rainfall (after rain = 21.6 min ± 34.11; same interval without rain = 4.8 min ± 16.61). On the other hand, *P. rubiginosus* decreased activity time after the rain (after rain = 18 min ± 28.9; same interval without rain = 50.84 min ± 68.58). The other five species showed no changes in activity duration between the interval after a rainfall event compared to a night without rain.

## DISCUSSION

Our results indicate that some tropical bat species respond to weather conditions and moonlight intensity in a predictable way. Moonlight intensity, followed by temperature, influenced the activity of the aerial-insectivorous bats more than rainfall. We found a general trend of increasing bat activity on warmer nights. Some species tended to increase their activity on bright nights, whereas other species tended to increase activity on

**Table 1.**—Summary of generalized linear mixed models (GLMMs) examining bat activity of each species in terms of moonlight intensity, rainfall, and air temperature, considering type of plot (riparian or nonriparian plot) as a random variable, and all 103 sampling nights in the Ducke Reserve, Brazil. The $R^2$ values represent the variance explained by the model. Hierarchical partitioning (HP) indicated independent effects of each predictor variable on bat activity. * indicates $P \leq 0.05$.

| Species | $R^2$ | Moonlight intensity | | Rainfall | | Temperature | |
|---|---|---|---|---|---|---|---|
| | | Z | HP (%) | Z | HP (%) | Z | HP (%) |
| *Pteronotus rubiginosus* | 0.21 | 3.11* | 70.92 | 0.12 | 0.31 | 1.31 | 28.76 |
| *Furipterus horrens* | 0.03 | 0.81 | 48.56 | −0.69 | 46.82 | 0.10 | 4.60 |
| *Centronycteris maximiliani* | 0.08 | −2.12 | 86.69 | 1.12 | 1.68 | 1.74 | 11.64 |
| *Cormura brevirostris* | 0.04 | 1.63 | 73.94 | −0.70 | 3.25 | 2.19* | 22.79 |
| *Saccopteryx bilineata* | 0.09 | 1.02 | 71.24 | −1.20 | 8.25 | 2.48* | 20.50 |
| *Saccopteryx leptura* | 0.10 | 2.61* | 76.43 | −0.95 | 3.93 | 1.20 | 19.62 |
| *Myotis riparius* | 0.10 | −3.03* | 94.42 | 0.35 | 2.42 | 1.10 | 3.14 |

**Table 2.**—Results of analyses of covariance (ANCOVAs) with temperature or rainfall as predictor variables, type of night and interaction between the predictor variables as covariates, and bat activity as the response variable. The type of night was determined by the amount of moonlight during the night: dark nights are between 0–30% and bright nights are between 70–100% of full moonlight intensity. * indicates $P \leq 0.05$.

| Species | Rainfall | | Temperature | | Type of night (dark or bright) | | Rainfall × type of night | | Temperature × type of night | |
|---|---|---|---|---|---|---|---|---|---|---|
| | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* | *F* | *P* |
| *Pteronotus rubiginosus* | 1.05 | 0.29 | 1.26 | 0.2 | −2.58 | 0.01* | −2.35 | 0.02* | 0.34 | 0.72 |
| *Furipterus horrens* | 1.76 | 0.08 | −0.18 | 0.85 | −0.57 | 0.56 | −1.27 | 0.20 | −0.49 | 0.62 |
| *Centronycteris maximiliani* | 0.64 | 0.51 | 0.87 | 0.38 | 1.43 | 0.15 | −0.31 | 0.75 | −0.97 | 0.33 |
| *Cormura brevirostris* | 1.50 | 0.13 | 0.25 | 0.79 | −1.37 | 0.17 | −0.69 | 0.49 | −0.30 | 0.76 |
| *Saccopteryx bilineata* | 0.31 | 0.75 | 0.83 | 0.40 | −1.76 | 0.08 | −0.83 | 0.40 | −0.05 | 0.95 |
| *Saccopteryx leptura* | 0.30 | 0.75 | 0.19 | 0.84 | −2.66 | 0.01* | −0.73 | 0.46 | −0.07 | 0.94 |
| *Myotis riparius* | 0.31 | 0.08 | 1.89 | 0.06 | 3.20 | 0.002* | −1.57 | 0.12 | −1.95 | 0.055 |

dark nights. The effect of rainfall was mostly evident on the activity peak; bats tended to have peaks at other times on nights with rain. Bats generally did not compensate the duration of activity after a rainfall event (e.g., *P. rubiginosus* increased activity and *S. leptura* reduced activity after rainfall compared to nights without rainfall).

The addition of temperature and rainfall to our models did not change the results in relation to moonlight intensity, as reported in our previous study (Appel et al. 2017). Species whose activity increased with moonlight intensity might have adopted strategies to take advantage of bright nights to avoid predators or find food (Arndt et al. 2018; Roeleke et al. 2018). *Pteronotus rubiginosus* and *S. leptura* are forest species that increased their activity on bright nights, but use more cluttered vegetation areas to forage, probably to avoid being detected by predators (Jung and Kalko 2011). Predator avoidance is stronger in slow-flying species, and *M. riparius* is a slow-flying species that increases its activity on dark nights, as reported for other *Myotis* species (Azam et al. 2015). However, species such as *S. bilineata* and *C. brevirostris*, which did not change their activity in response to moonlight intensity, have been reported to forage closer to vegetation during full moon than during new moon (Jung and Kalko 2011). Canopy cover reduces the amount of light inside the forest and may prevent the bats from being detected by predators (Breviglieri 2011; Halat et al. 2018; Roeleke et al. 2018).

Air temperature is an important variable that positively influences bat activity (Russ et al. 2003). This relationship is particularly evident for temperate species, who use hibernation as a strategy to minimize energy expenditure, often associated with lack of insect availability (Stawski et al. 2014; Klüg-Baerwald et al. 2017). In our study, only a few species responded to air temperature, possibly because the temperature varied little among the nights, and they can maintain a stable body temperature when air temperature does not drop to extremely low values (Erkert 2000). The higher activity of some species during warmer nights may be a response to prey availability (O'Donnell 2000; Fukui et al. 2006). High temperature increases the flight activity of many tropical insects, especially species of Lepidoptera, Diptera, and Hymenoptera (Taylor 1963; Stangler et al. 2014). A positive effect of temperature on bat activity has also been suggested for other tropical aerial-insectivorous bat families, such as Molossidae, Vespertilionidae, and Emballonuridae (Meyer et al. 2004; Barros et al. 2014; Dias-silva et al. 2018). However, the relationships between insect prey and bat predators in the tropics are poorly understood and need further investigation (Lima and O'Keefe 2013).

Reproductive status can also influence the response of female bats to air temperature (Racey and Entwistle 2000). Pregnant and lactating females are more sensitive to heat loss and decrease their activity in low temperatures to reduce energy expenditure and water loss (Kunz et al. 1995; Chruszcz and Barclay 2002). Female *C. brevirostris*, *S. leptura*, and *S. bilineata* are usually pregnant during the rainy season (Bradbury and Vehrencamp 1976; Yancey et al. 1998a, 1998b), which is also the case in the Ducke Reserve. Although it is not possible to differentiate males from females or to assess female reproductive status from ultrasound recordings, the higher activity on warmer nights may be linked to the reproductive status of females.

Rain events decrease bat activity (Ciechanowski et al. 2007; Pettit and O'Keefe 2017), but in our study, the amount of rainfall was not sufficient to lead to different levels of bat activity among nights. The rainfall volume analyzed in our study is considered low to moderate (< 10 mm/h) and was not enough to inhibit bat activity. Rainfall also did not sufficiently reduce air temperature to influence bat activity (nights with rain: 23.4°C ± 0.66; nights without rain: 23.3°C ± 1.23). Since weak rain does not reduce insect availability in the forest, foraging in light rainfall may not be disadvantageous for bats (Erkert 1982; Belwood and Fullard 1984). Some studies reported that only strong rainfall suppresses bat activity by affecting the echolocation accuracy and increasing the inherent flight energy costs (Fenton et al. 1977; Voigt et al. 2011; Geluso and Geluso 2012).

Only *P. rubiginosus* activity differed between dark and bright nights in relation to rainfall. Light rainfall did not influence the activity of *P. rubiginosus* on bright nights, but activity decreased on dark rainy nights. Insect availability on dark and rainy nights is lower in some orders of insects that *P. rubiginosus* eats (e.g., Diptera), and therefore, the negative effect of rainfall on their availability may compromise bat foraging success under dark, rainy conditions (Fenton et al. 1977; Voigt et al. 2011; Rolfe and Kurta 2012; Gonsalves et al. 2013).

Some bat species changed their peak activity time on nights with light rainfall. On nights without rain, peak activity was

**Table 3.**—Hourly bat activity on nights without rainfall and on nights with rainfall during typical peak activity times for the species. Values represent the total number of bat passes (mean ± *SD*). Gray boxes represent times when rainfall occurred in the night (0.3–10 mm). Means of minutes after sunset that share the same letter are not significantly different from each other (Tukey's HSD, $P \leq 0.05$).

|  | Minutes after sunset | *Pteronotus rubiginosus* | *Furipterus horrens* | *Centronycteris maximiliani* | *Cormura brevirostris* | *Saccopteryx bilineata* | *Saccopteryx leptura* | *Myotis riparius* |
|---|---|---|---|---|---|---|---|---|
| Nights without rainfall | 0 | 0 (0 ± 0)ab | 3 (0.12 ± 0.43)a | 5 (0.2 ± 0.65)a | 397 (15.88 ± 35.83)a | 475 (19 ± 23.70)a | 297 (11.88 ± 21.64)a | 69 (2.76 ± 12.56)a |
|  | 60 | 14 (0.56 ± 1.08)a | 0 (0 ± 0)a | 50 (2 ± 7.01)a | 16 (0.64 ± 1.43)b | 83 (3.32 ± 6.92)b | 1 (0.2 ± 0.04)b | 79 (3.16 ± 15.38)a |
|  | 120 | 146 (5.84 ± 9.36)a | 0 (0 ± 0)a | 9 (0.36 ± 1.07)a | 2 (0.08 ± 0.4)b | 16 (0.64 ± 2.11)b | 2 (0.08 ± 0.27)b | 2 (0.08 ± 0.4)a |
|  | 180 | 99 (3.96 ± 5.20)a | 1 (0.04 ± 0.2)a | 9 (0.36 ± 0.95)a | 3 (0.12 ± 0.6)b | 5 (0.2 ± 0.81) | 0 (0 ± 0)b | 2 (0.08 ± 0.27)a |
|  | 240 | 93 (3.72 ± 5.74)a | 0 (0 ± 0)a | 16 (0.64 ± 1.93)a | 7 (0.28 ± 0.97)b | 1 (0.04 ± 0.2)b | 0 (0 ± 0)b | 3 (0.12 ± 0.43)a |
|  | 300 | 89 (3.56 ± 5.06)a | 1 (0.04 ± 0.2)a | 12 (0.48 ± 1.68)a | 4 (0.16 ± 0.62)b | 0 (0 ± 0)b | 0 (0 ± 0)b | 7 (0.28 ± 1.02)a |
|  | 360 | 110 (4.4 ± 6.51)a | 0 (0 ± 0)a | 5 (0.2 ± 0.64)a | 0 (0 ± 0)b | 2 (0.08 ± 0.4)b | 0 (0 ± 0)b | 7 (0.28 ± 0.84)a |
|  | 420 | 92 (3.68 ± 5.45)a | 0 (0 ± 0)a | 16 (0.64 ± 1.82)a | 0 (0 ± 0)b | 0 (0 ± 0)b | 0 (0 ± 0)b | 7 (0.28 ± 0.79)a |
|  | 480 | 82 (3.28 ± 7.30)a | 0 (0 ± 0)a | 20 (0.8 ± 1.93)a | 0 (0 ± 0)b | 4 (0.16 ± 0.8)b | 0 (0 ± 0)b | 13 (0.52 ± 2.00)a |
|  | 540 | 43 (1.72 ± 4.65)a | 0 (0 ± 0)a | 5 (0.2 ± 0.81)a | 17 (0.68 ± 2.46)b | 27 (1.08 ± 4.27)b | 0 (0 ± 0)b | 29 (1.16 ± 4.11)a |
|  | 600 | 12 (0.48 ± 0.87)ab | 0 (0 ± 0)a | 4 (0.16 ± 0.8)a | 5 (0.2 ± 0.57)b | 5 (0.2 ± 1)b | 0 (0 ± 0)b | 12 (0.48 ± 2.4)a |
|  | 660 | 8 (0.32 ± 0.85)ab | 1 (0.04 ± 0.2)a | 18 (0.72 ± 3.03)a | 102 (4.08 ± 9.67)b | 112 (4.48 ± 6.83)b | 6 (0.24 ± 1.01)b | 21 (0.84 ± 1.99)a |
| Nights with rainfall during peak species activities | 0 | 0 (0 ± 0)a | 4 (0.16 ± 0.37)a | 40 (1.6 ± 5.45)a | 444 (17.76 ± 37.57)a | 624 (24.96 ± 30.80)a | 397 (15.88 ± 53.38)a | 107 (4.28 ± 17.71)a |
|  | 60 | 10 (1 ± 2)a | 3 (0.12 ± 0.43)a | 21 (0.84 ± 1.88)a | 91 (3.64 ± 10.11)b | 187 (7.48 ± 14.12)b | 30 (1.2 ± 2.32)ab | 273 (10.92 ± 51.35)a |
|  | 120 | 25 (2.5 ± 4.88)a | 13 (0.52 ± 2.21)a | 15 (0.6 ± 1.65)a | 91 (3.64 ± 8.57)b | 18 (0.72 ± 1.36)b | 4 (0.16 ± 0.62)b | 37 (1.48 ± 4.69)a |
|  | 180 | 27 (2.7 ± 5.14)a | 1 (0.04 ± 0.2)a | 21 (0.84 ± 2.15)a | 134 (5.36 ± 18.88)ab | 102 (4.08 ± 17.29)b | 78 (3.12 ± 15.18)ab | 13 (0.52 ± 1.47)a |
|  | 240 | 55 (5.5 ± 8.48)a | 0 (0 ± 0)a | 19 (0.76 ± 2.87)a | 24 (0.96 ± 3.51)b | 1 (0.04 ± 0.2)b | 0 (0 ± 0)b | 1 (0.04 ± 0.2)a |
|  | 300 | 57 (5.7 ± 13.20)a | 2 (0.08 ± 0.4)a | 11 (0.44 ± 1.41)a | 3 (0.12 ± 0.43)b | 13 (0.52 ± 2.4)b | 0 (0 ± 0)b | 16 (0.64 ± 1.38)a |
|  | 360 | 13 (1.3 ± 2.35)a | 2 (0.08 ± 0.27)a | 5 (0.2 ± 0.5)a | 116 (4.64 ± 21.14)ab | 14 (0.56 ± 2.12)b | 3 (0.12 ± 0.6)b | 10 (0.4 ± 1.22)a |
|  | 420 | 12 (1.2 ± 1.68)a | 0 (0 ± 0)a | 0 (0 ± 0)a | 9 (0.36 ± 1.25)b | 0 (0 ± 0)b | 0 (0 ± 0)b | 8 (0.32 ± 1.06)a |
|  | 480 | 9 (0.9 ± 1.37)a | 4 (0.16 ± 0.47)a | 1 (0.04 ± 0.2)a | 36 (1.44 ± 7.2)b | 2 (0.08 ± 0.4)b | 0 (0 ± 0)b | 12 (0.48 ± 2.02)a |
|  | 540 | 4 (0.4 ± 0.84)a | 0 (0 ± 0)a | 1 (0.04 ± 0.2)a | 3 (0.12 ± 0.43)b | 2 (0.08 ± 0.4)b | 0 (0 ± 0)b | 5 (0.2 ± 0.57)a |
|  | 600 | 1 (0.1 ± 1.31)a | 0 (0 ± 0)a | 1 (0.04 ± 0.2)a | 3 (0.12 ± 0.43)b | 4 (0.16 ± 0.37)b | 0 (0 ± 0)b | 13 (0.52 ± 1.44)a |
|  | 660 | 0 (0 ± 0)a | 0 (0 ± 0)a | 42 (1.68 ± 7.87)a | 178 (7.12 ± 15.80)ab | 98 (3.92 ± 5.05)b | 13 (0.52 ± 1.04)b | 81 (3.24 ± 12.55)a |

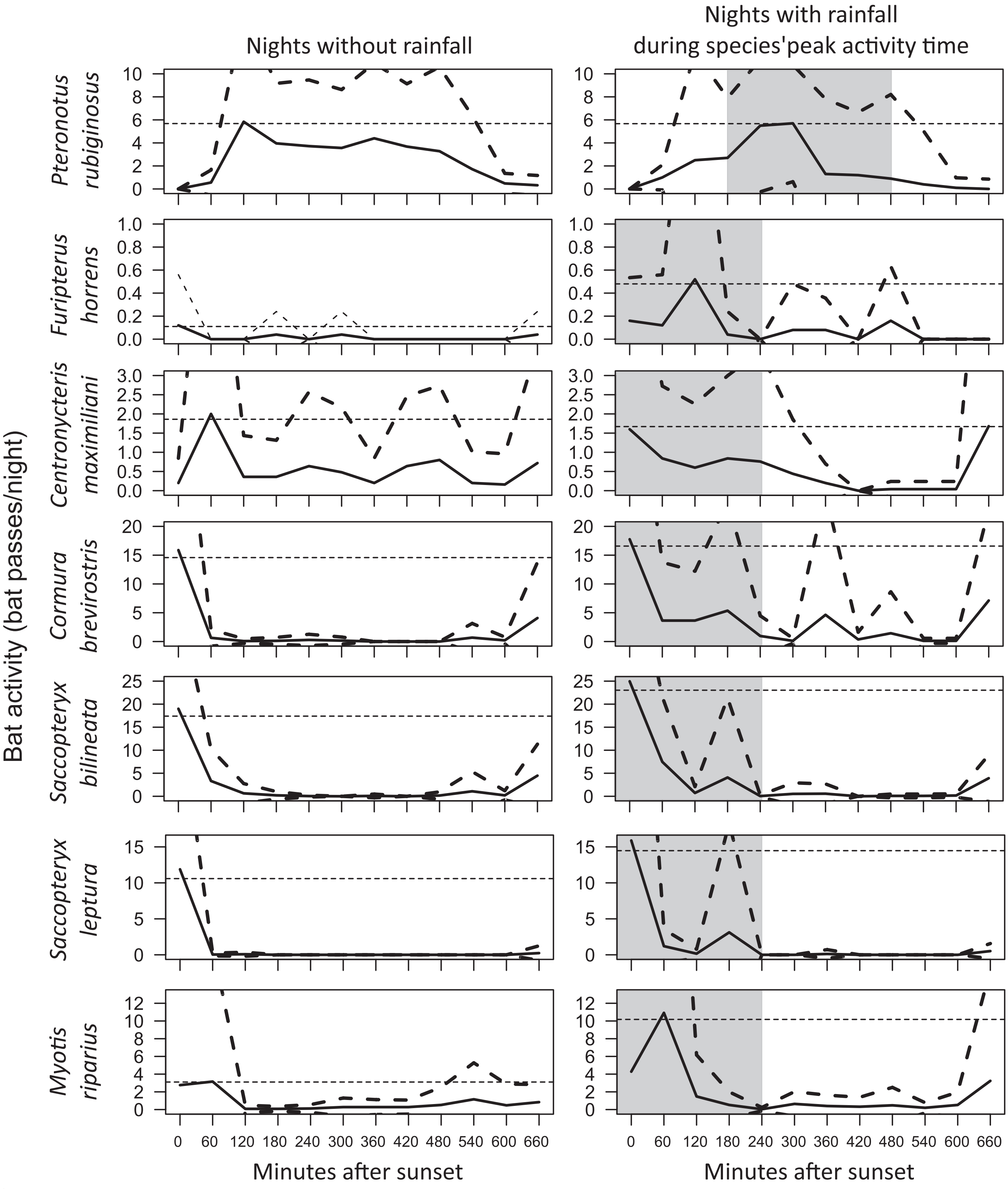

**Fig. 2.**—Hourly activity of seven species of insectivorous bat on nights without rainfall ($n = 25$) and nights with rainfall during species' peak activity time ($n = 18$; for *Pteronotus rubiginosus* $n = 9$). The gray boxes represent the interval of light rainfall during the night (0.3–10 mm). The solid line is the average activity and the dotted line represents the standard deviation of activity. Dotted horizontal lines indicate the 99th percentile, which represents the peak activity of each bat species.

**Table 4.**—Results of Student's *t*-test comparing duration of activity (minutes after sunset) between nights when rainfall occurred at the beginning of the night to nights without rainfall (control). The duration of activity was between 2300 to 0600 h, except for *Pteronotus rubiginosus* when we used the interval 0300 to 0600 h. The nights with rainfall consisted of nights with rainfall events between 1800 to 2300 h. Values represent the minutes of bat activity (mean ± *SD*). * indicates $P \leq 0.05$.

| Species | *t* | Duration of activity (minutes) after a rainfall | Duration of activity (minutes) on nights without rainfall |
|---|---|---|---|
| *Pteronotus rubiginosus* | 1.96* | 18 ± 28.9 | 50.84 ± 68.58 |
| *Furipterus horrens* | 1.03 | 14.4 ± 39.79 | 4.8 ± 24 |
| *Centronycteris maximiliani* | −0.8 | 28.8 ± 57.75 | 45.6 ± 87.08 |
| *Cormura brevirostris* | 1.89 | 72 ± 72.5 | 40.8 ± 48.12 |
| *Saccopteryx bilineata* | 1.2 | 67.2 ± 63.21 | 48 ± 48.98 |
| *Saccopteryx leptura* | 2.21* | 21.6 ± 34.11 | 4.8 ± 16.61 |
| *Myotis riparius* | 0.85 | 74.4 ± 87.08 | 55.2 ± 71.24 |

concentrated in the early evening (Appel et al. 2017), but rain caused the activity peak to be extended during or after rain. This change in foraging behavior probably meets the energetic requirement of bats. Our results indicate that foraging activity was not interrupted by light rain, suggesting that potential insect prey of bats are also active during weak rains (Fenton et al. 1977; DeCoursey and DeCoursey 2014). Because bats begin the night with low energy levels, the costs of maintaining body temperature during rain are likely compensated by rapid energy gain through feeding (Thies et al. 2006; Weinbeer and Meyer 2006).

Contrary to our expectations, the duration of foraging did not increase after the rain stopped and possibly even decreased in *P. rubiginosus*. These results are in accordance with other studies that found that insectivorous bats continue to fly in light rain (Weinbeer and Meyer 2006; DeCoursey and DeCoursey 2014). In contrast, frugivorous bats decrease their activity if it starts raining during the night (Thies et al. 2006). This difference in foraging behavior in relation to rain is probably related to the type of food ingested—insects have more energy by weight unit compared to fruits. Thus, insectivorous bats acquire energy more quickly, compensating for foraging during light rains (Fenton et al. 1977). Frugivorous bats avoid flying in rainy nights to not cool the body and lose energy. *Pteronotus rubiginosus* also decreased activity on rainy nights. This bat feeds mainly on Lepidoptera (Rolfe and Kurta 2012), which should avoid flying during rains, even light ones, because their wings are damaged when wet. Only *S. leptura* was more active after rainfall; this species may spend more time active after rain to compensate for the energetically costly flights during rainfall (O'Donnell 2000; Salvarina et al. 2018).

Rainy seasons in the Amazonian forests are likely to experience rain almost every day; thus, aerial-insectivorous bat species are expected to show adaptability to forage in rainy conditions. We showed that hourly activity varied after rainfall events, which may depend on insect availability during these hours and could be associated with an individual's experience from the previous night. We used data on rainfall collected by the Climatological Station of the Reserve for our analysis, but it is important to evaluate rainfall at a more local scale because rainfall events are not necessarily equal for all studied plots. In addition, canopy cover could affect rainfall intensity inside the forest.

Our findings demonstrate that responses to temperature, rainfall, and moonlight intensity vary among tropical forest aerial-insectivorous bat species. Small changes in air temperature (20.6–25.4°C) were sufficient to influence the forage activity of some aerial-insectivorous bats, while light rain (0.3–10 mm) affected the hourly activity more than the duration of activity of bat species. However, the explanatory power of our models was low ($R^2 < 0.21$), indicating that other variables probably also influence bat activity patterns and foraging behavior. Ecological interactions, such as insect availability and predator presence, can shape the nocturnal and hourly activity of bats, but they are considerably harder to quantify than weather and moonlight variables. Other weather variables as barometric pressure and wind are environmental cues that directly and indirectly may affect bat activity and insect availability. Climatic conditions are unpredictable variables that fluctuate widely between nights and within the same night. The behavioral response of bats to unpredictable climatic conditions is not instantaneous and should be more perceptible and predictable over long (seasonal) timescales.

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## Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Summary of acoustic activity (number of bat passes) of the seven aerial-insectivorous bat species. The values represent total number of bat passes (mean ± *SD*).

Supplementary Data SD2.—Results of analysis of covariance (ANCOVA), with the predictor variable moonlight intensity, the covariate cloud, and the interaction between moonlight intensity and cloud. * indicates $P \leq 0.05$.

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