**INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA - INPA**

**PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA**

# ATIVIDADE DE MORCEGOS INSETÍVOROS AÉREOS EM RELAÇÃO A DIFERENTES ESCALAS TEMPORAIS DE LUMINOSIDADE LUNAR

**GIULLIANA APPEL**

Manaus, Amazonas

Junho de 2016

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# Atividade de morcegos insetívoros aéreos em relação a diferentes escalas temporais de luminosidade lunar

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**Sinopse:**

Foi avaliado como a luminosidade da lua influencia na atividade de morcegos insetívoros aéreos na Reserva Adolpho Ducke, Amazônia Central em diferentes escalas temporais. A resposta dos morcegos a luminosidade da lua é mais evidente em escala temporal longa, entre noites com variação de luminosidade lunar. Em escala temporal curta, dentro de uma mesma noite, a atividade dos morcegos é maior no início da noite independente da exposição da lua.

**Palavras-chave**: Chiroptera, Atividade horária, Fobia lunar, Estratégia de Forrageio, Risco de predação, Energia, Floresta de terra firme - Amazônia, Reserva Ducke.

Dedico a minha dissertação a minha família

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**RESUMO**

É globalmente aceito que os morcegos insetívoros aéreos respondem a luminosidade lunar com a diminuição de atividade em noites claras pelo aumento do risco de predação e pela menor disponibilidade de determinados insetos. O efeito da luminosidade pode ser avaliado entre noites e dentro de uma mesma noite, no entanto poucos estudos envolvem os dois enfoques sincronicamente e a maioria dos autores usam fases lunares como preditor da atividade de morcegos. Nosso objetivo foi avaliar como a luminosidade lunar influencia na atividade dos morcegos insetívoros aéreos em diferentes escalas temporais: entre noites (noites claras, noites escuras e com grande variação de luz) e dentro de uma mesma noite. Para estimar a atividade de cinco espécies de morcegos insetívoros aéreos usamos estações de gravação autônomas de ultrassom e usamos dados de percentagem de intensidade de luminosidade lunar retirados do programa Moontool. A atividade das cinco espécies foi calculada por noite para as 53 noites amostradas e foi calculada a atividade por hora para noites escuras e claras e dentro de uma mesma noite. A atividade apenas de uma espécie de morcego (*Myotis riparius*) diminuiu por causa da luminosidade lunar entre noites, enquanto a atividade de *Pteronotus parnellii* e *Saccopteryx leptura*) aumentaram de atividade e outras duas não responderam (*Cormura brevirostris* e *S. bilineata*). A atividade das espécies foi maior no início da noite independente da exposição da lua, evidenciando que a reposição energética no forrageio após a saída do abrigo é essencial. A resposta dos morcegos aos efeitos da luminosidade lunar é mais aparente em escala temporal longa e pode ser dependente a fatores intrínsecos de cada espécie como velocidade do voo, flexibilidade no uso de habitat e tamanho do corpo.

**Aerial insectivorous bats activity in relation to different time scales of moonlight intensity**

## ABSTRACT

It is commonly assumed that aerial insectivorous bats might respond to moonlight intensity by decreasing their foraging activity during bright nights due to the inherent predation risk increase of due to the lower insect availability. The effect of moonlight can be measured among nights and within a night. However, only few studies synchronously involve both approaches and most authors essentially compare bat activity with lunar phases. Our main aim was to evaluate how the moonlight influences aerial insectivorous bat activity at different time scales: between nights (bright and dark nights and wide range of moonlight intensity) and within the same night. Bat activity from five species was calculated using autonomous ultrasound recording stations and moonlight intensity percentages retrieved from Moontool program. Bat activity was calculated per species per night during a 53-day sampling period. Bat activity was also assessed hourly in a gradient of different moonlight intensity nights. Only one species (*Myotis riparius*) positively responded to moonlight, while two species (*Pteronotus parnellii* e *Saccopteryx leptura*) increased their foraging activity and other two did not respond (*Cormura brevirostris* and *S. bilineata*). Bat activity was for all the species greater at the beginning of the night independently of the moon presence, indicating that foraging just after the sunset is essential. The response of bats to the effects of moonlight intensity is more apparent between nights than within a single night and might depend on particular traits of each species such as flight speed, flexibility in habitat use and body size.

**SUMÁRIO**

## APRESENTAÇÃO

O padrão de atividade temporal em animais pode ser avaliado em diferentes escalas de tempo. Estações do ano refletem uma escala de tempo longa, enquanto ciclos circadianos estão relacionados a uma escala temporal curta. A mudança de atividade dos animais no tempo é dirigida principalmente pela oscilação da duração da luz e/ou temperatura (Refinetti & Menaker 1992; Foster & Kreitzmann 2004; Koukkari & Sothern 2006). A duração da luz em um período de 24 horas é o fator ambiental mais forte para sincronizar o comportamento, reprodução e a fisiologia entre as estações e dentro do mesmo dia (Halle & Stenseth 2000; Dawson et al. 2000; Tarlow et al. 2003).

Em uma escala de tempo curta, as espécies noturnas regulam a atividade em função do tempo de duração do dia e da luminosidade lunar que varia entre noites e dentro de uma mesma noite (Enright 1970; Smit et al. 2011). A luz do sol refletida pela lua afeta processos fisiológicos, reprodutivos, comportamentais e o forrageio dos animais noturnos (Zimecki 2006; York et al. 2013; Digby et al. 2014). O forrageio dos predadores noturnos visualmente orientados aumenta em noites mais claras, por causa da maior percepção e facilidade de capturar as presas (Prugh & Golden 2014; Navarro-Castilla et al. 2014). Por outro lado, presas noturnas diminuem a atividade em noites claras como uma maneira de evitar a predação (Price et al. 1984; Fenton et al. 1977, Kramer & Birney 2001). A resposta dos animais noturnos à luminosidade lunar gera uma demanda conflitante entre o risco de predação e a necessidade de encontrar alimento (Erkert 1982; Kronfeld-Schor et al. 2013; Penteriani et al. 2013).

A luminosidade lunar também varia dentro de uma mesma noite. A lua nasce cerca de 50 minutos mais tarde a cada noite o que resulta em horários diferentes do nascer e pôr da lua (Hibbard 1925). Algumas noites podem iniciar sem luminosidade lunar ou a lua pode se pôr após algumas horas de exposição no início da noite, no entanto outras não apresentam variação da luminosidade lunar, podendo ser completamente escuras ou claras. Existem evidências que o tempo de exposição da lua em uma mesma noite afeta a atividade horária e o pico de atividade de forrageio de espécies noturnas de aves, morcegos, roedores, lagartos e peixes (Stutz 1974; Alkon & Saltz 1988; Wolfe & Summerlin 1989; Smit et al. 2011; Rubolini et al. 2014). Apesar da importância da incidência luminosa sobre a atividade noturna em espécies animais, poucos estudos têm avaliado simultaneamente diferentes escalas temporais da luminosidade lunar sobre a atividade dos animais (Milne et al. 2005; Nash 2007; Mello et al. 2013).

Morcegos são animais com atividade de forrageio essencialmente noturna (Erkert 1982; Speakman 1995). O termo fobia lunar proposto por Morrison (1978) sugere que guildas e espécies de morcegos diminuem a atividade em noites claras de lua cheia (Speakman 2000; Elangovan & Marimuthu 2001; Meyer et al. 2004). A baixa atividade em noites claras é impulsionada por hipóteses relacionadas ao maior risco de predação pelo aumento da visibilidade dos predadores (Morrison 1978; Elangovan & Marimuthu 2001; Esberárd et al. 2007) e menor atividade de alguns insetos como da ordem Orthoptera consumidos por morcegos insetívoros catadores e aéreos (Lang et al. 2005). Contudo, algumas espécies não respondem a mudanças da luminosidade lunar (Gannon & Willig 1997; Karlsson et al. 2002; Kuenzi & Morrison 2003), enquanto outras aumentam a atividade em noites claras, como é o caso de algumas espécies de frugívoros que aumentam a eficiência na detecção de frutos e flores (Riek et al. 2010; Gutierrez et al. 2014). A resposta à intensidade luminosa lunar depende da estratégia de forrageio das espécies e o tipo de ambiente que forrageiam. Espécies que voam rápido são menos suscetíveis a predadores e podem forragear em noites claras (Holland et al. 2011). Morcegos que comutam entre o interior da floresta e áreas de borda e abertas experimentam grande variação da cobertura de vegetação. Essas espécies são mais tolerantes a mudanças da luminosidade e por isso tendem a ser pouco afetadas pela intensidade da luz lunar (Rydell 1991; Jung & Kalko 2010; Breviglieri 2011).

Embora diversos estudos têm avaliado a relação da luminosidade lunar com a atividade de morcegos (Usman et al. 1980; Rydell et al., 1996; Karlsson et al. 2002; Santos-Moreno et al. 2010; Holland et al. 2011), poucos têm considerado morcegos insetívoros aéreos das regiões tropicais. Além disso, a maioria dos estudos têm associado a atividade dos morcegos com as fases da lua (Hecker & Brigham 1999; Elangovan & Marimuthu 2001; Meyer et al. 2004; Cichocki et al. 2015). A variação da intensidade da luminosidade lunar é grande dentro de uma mesma fase e fases lunares diferentes também sobrepõem parte da intensidade de luz refletida pela lua (Fenton et al. 1977; Reith 1982; Meyer et al. 2004; Santos-Moreno et al. 2010). No presente estudo nós investigamos o padrão de atividade noturna de morcegos insetívoros aéreos em uma área de 25 km² de floresta contínua na Amazônia Central. Nós avaliamos como a atividade das espécies de morcegos insetívoros aéreos responde a variação de luminosidade lunar em diferentes escalas temporais: entre noites (noites claras, noites escuras e com grande variação de luz) e dentro de uma mesma noite. Especificamente, nossas perguntas são:

(1) O padrão de atividade dos insetívoros aéreos muda com a luminosidade da lua entre noites? Nós esperamos que a atividade dos morcegos seja relacionada negativamente com a luminosidade lunar entre noites.

(2) A atividade horária dos morcegos varia entre noites escuras e claras? Nós esperamos que em noites mais escuras a atividade seja homogênea, sem picos de atividade ou com vários picos ao longo da noite, enquanto que em noites claras, a atividade dos morcegos tenha apenas um pico no início da noite.

(3) Devido a lua se pôr durante a noite e mudar a luminosidade lunar, a atividade dos morcegos está relacionada com a presença da lua ao longo da noite? Nós prevemos que em noites que iniciam sem a lua (quando a lua nasce no meio da noite) a atividade diminuirá com a entrada da lua ao longo da noite. Por outro lado, em noites que iniciam muito claras e terminam escuras (quando a lua se põe ao longo da noite), a atividade dos morcegos será maior no período escuro. Noites totalmente escuras prevemos uma maior atividade das espécies de morcegos comparados a noites totalmente claras.

## OBJETIVO

Avaliar como a luminosidade lunar influencia na atividade de morcegos insetívoros aéreos em uma área da Amazônia Central em diferentes escalas temporais.

### Objetivos específicos

1. Avaliar como a atividade dos morcegos insetívoros aéreos varia com a intensidade luminosa lunar entre noites
2. Avaliar como os horários de pico de atividade dos morcegos insetívoros aéreos variam entre noites escuras e claras
3. Avaliar como a atividade dos morcegos insetívoros aéreos é influenciada pelos períodos de presença da lua (claro) e ausência da lua (escuro) ao longo da noite

## Capítulo I.

Appel, G; Pereira, López-Baucells, A.; Magnusson, W. E; Bobrowiec, P. E. D; **Activity of aerial insectivorous bats in relation to different time scales of moonlight intensity.** Manuscrito submetido para revista *Mammalian Biology*.

# Aerial insectivorous bats activity in relation to different time scales of moonlight intensity

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**Abstract**

It is commonly assumed that aerial insectivorous bats might respond to moonlight intensity by decreasing their foraging activity during bright nights due either to the inherent increase in predation risk, ordue to a lowering insect availability. The effect of moonlight on bat activity can be measured both between nights and within a single night. However, only few studies have synchronously used both approaches, and most authors generally compare bat activity with lunar phases. Our main aim was to evaluate how the moonlight influences aerial insectivorous bat activity at different time scales: between nights and within the same night. Activity of five bat species was measured using autonomous ultrasound recording stations and moonlight intensity percentages retrieved from Moontool program, per night during a 53-day sampling period, and also hourly between dark and bright nights. Only one species (*Myotis riparius*) positively responded to moonlight, while two species (*Pteronotus parnellii* and *Saccopteryx leptura*) increased their foraging activity in moonlight, while in two others moonlight intensity made no difference to activity levels (*Cormura brevirostris* and *S. bilineata*). Bat activity was greater for all species at the beginning of the night, independent of the presence of the moon, indicating that foraging just after the sunset is essential. Thus, bat response to the effect of moonlight intensity is more apparent between nights than within a single night and might depend on particular traits of each species such as flight speed, flexibility in habitat use and body size.

**Keywords:** foraging strategy, Chiroptera, moon, rain forest, hourly activity.

## Introduction

Species activity patterns can be defined as the consistent repetition of certain behaviors over time (Erkert, 1982; Zimecki, 2006), and most can be evaluated at different temporal scales. Annual seasonality can be generally linked with long time scales, while circadian cycles are more related to behaviors that occur over short time scales. It has been demonstrated that temporal variation in several forms of animal activity is mainly driven by light intensity and temperature oscillation (Refinetti and Menaker, 1992). Most animals essentially synchronize their behavior, reproduction and physiology between the seasons, and within-a-day variation according to daylight hours (Tarlow et al., 2003).

On the other hand, nocturnal species tends to regulate their activity as a function of moonlight intensity, which varies both between nights and within the same night (Smith et al., 2011). Moonlight intensity affects both physiological, reproductive and behavioral processes, including foraging time investment (Digby et al., 2014; York et al., 2014). Activity of visually-oriented predators increases during bright nights, probably due to the enhanced perception and thus increased chances of prey capture (Navarro-Castilla and Barja, 2014; Prugh and Golden, 2014). Correspondingly, and as a direct consequence, nocturnal prey species are more likely to decrease their activity during bright nights in order to avoid predators (Fenton et al., 1977; Kramer et al., 2001). This differential response to moonlight is basically driven by the trade-off between predation risk and the demands of foraging (Haeussler and Erkert, 1978; Penteriani et al., 2013).

Moonlight intensity also varies within the same night. The moon rises 50 minutes later each night which results in different times of moonrise and moonset (Hibbard, 1925). While some nights can start without moon, in others the moon can rise a few hours after sunset. Some nights have no variation of moonlight, and the night can be either completely dark or bright. There is clear evidence that moonrise affects the peak foraging activity of many nocturnal species, including species of birds, bats, and rodents (Wolfe et al., 1989; Smit et al., 2011; Lima et al., 2013). Despite the importance of moonlight intensity for determining animal foraging activity, few studies have evaluated its effect simultaneously at different temporal scales (Milne et al., 2005; Mello et al., 2013).

Bats are primarily nocturnal foraging mammals (Speakman, 1995). The term ‘lunar phobia’ proposed by Morrison (1978) suggests that some guilds and bat species might decrease their activity during full moon nights (Speakman et al., 2000; Elangovan and Marimuthu, 2001). The decrease in insectivorous bat activity during bright nights might be driven by the increase of predation risk (Esbérard, 2007; Lima and O’Keefe, 2013), and/or due to lower activity of some prey insect groups (Lang et al., 2006). However, some bat species have been found to not decrease their activity when moonlight increases (Kuenzi et al., 2003; Karlsson et al., 2006). For instance, frugivorous species are more active on bright nights, when they seem to be more efficient at detecting fruit and flower (Riek et al., 2010; Gutierrez et al., 2014). The response to moonlight might depend on the species foraging strategy and habitat use (Jones and Rydell, 1994; Jung and Kalko, 2010). Fast-flying species seems to be less susceptible to predators and thus, they can forage more safely on bright nights (Holland et al., 2011). Also, bats flying in forest interiors, forest edges and open areas pass through great variation of vegetation cover intensity (Mancina, 2008). Such species are more tolerant of illumination changes and are therefore less affected by the  variation in moonlight intensity (Rydell, 1991; Breviglieri, 2011).

Several studies have evaluated the relation between moonlight intensity and bat activity (Karlsson et al., 2006; Santos-Moreno et al., 2010), but the majority of these studies have taken place in temperate habitats. Consequently, how moonlight affects aerial activity of tropical insectivorous bats remains essentially unknown (Saldaña-Vázquez and Munguía-Rosas, 2013). Furthermore, most studies have considered moon phases, but have neglected moonlight variation within the same night (Meyer et al., 2004; Cichocki et al., 2015). Variation in moonlight intensity is considerable within the same moon phase and different moon phases also partly overlap in the intensity of illumination reflected by the moon. In the present study we investigated the pattern of nocturnal activity of aerial insectivorous bats within a continuous forest in Central Amazonia. We evaluated how aerial insectivorous bat species respond to moonlight variation at different temporal scales: between nights (dark nights, bright nights and wide range of moonlight intensity), and within the same night. Specifically, our questions were:

(1) Does aerial insectivorous bat activity change accordingly to the moonlight intensity between nights? Assuming they show lunar phobia, we expected bat activity to be negatively associated with moonlight intensity.

(2) Does hourly bat activity vary between dark and bright nights? We predicted that bat activity during dark nights would be homogeneous, without peaks, while on bright nights, activity will have only one peak in the early evening.

(3) Because the intensity of moonlight is not always constant throughout a single night, is bat activity influenced by the timing of moonrise/moonset within the same night? We expected bat activity to decrease throughout the night during those nights in which the moon only rises late at night. Moreover, on nights that start bright and end dark (when the moon sets throughout the night), we predicted that the activity of bats

would be higher in the dark period. We also expected total bat activity to be higher during completely dark nights than during totally bright nights.

## Methods

### *Study Site*

This study was conducted in the Reserva Florestal Adolpho Ducke (2°58' S, 59 °55' W), located on the northern edge of Manaus city, Central Amazonian Brazil. The reserve covers an area of 10,000 ha of lowland continuous rainforest and is integrated to the Brazilian Long-term Ecological Research Program of the Brazilian National Research Council (Programa de Pesquisas Ecológicas de Longa Duração - PELD/CNPq). The climate is humid tropical with two seasons: rainy (November-May), and dry (June-October) (Oliveira et al., 2008). The average annual temperature is 26 °C and precipitation varies between 1750 to 2500 mm (Ribeiro et al., 1999). The reserve has a trail system that forms a 25 $km^2$ grid (5 x 5 km) with 6 trails oriented North-South and 6 trails oriented East-West (Fig. 1). The system was established according to the RAPELD method that allows rapid survey of biological communities (RAP component) and is ideal for studies of long-term ecological research (ELD component) (Magnusson et al., 2005, 2014). The grid give access to 30 permanent plots distributed evenly to each 1 km (Fig. 1). Each plot is 250 m length and follows the relief contour in order to minimize the effects of the soil structure and drainage (Magnusson et al., 2005) We sampled 10 permanent plots, separated between1 and 6 km (Fig. 1).

### *Bat Activity*

To record insectivorous bat foraging activity, we used autonomous recording detectors (Song Meter SM2Bat) with an omnidirectional ultrasonic SMX-US microphone (Wildlife Acoustics, Maynard, Massachusetts, USA). The detectors were installed at the center of each plot and the microphones set at a height of 1.5 m. The detectors were programmed to passively record bat activity in real time with a full spectrum resolution of 16-bit with 1-s pre-trigger and 0.1-s post-trigger, High Pass Filter set at fs/32 (12 kHz) and Trigger Level 18SNR. The SM2Bat units were set to record bats between 18:00 and 06:00 h, resulting in a 12-hour recording period per night. Each plot was sampled from four to six consecutive nights, resulting in a total of 53 sampling nights and 636 hours of recording during the 2013 rainy season (January to May).

Bat activity was quantified using bat-passes as a unit sample. A bat pass was considered as any 5” recording where two or more search-phase pulses characteristics of a certain bat species were identified. All recordings were thus divided in segments of 5-s duration and visualized using the Kaleidoscope program 3.1.1. (Wildlife Acoustics, Maynard, Massachusetts, USA). Bat species were manually identified by comparing the structure and frequency parameters of the pulses with a reference library of bat ultrasounds recorded in the Biological Dynamics of Forest Fragments Project (DBFFP), located 60 km North of Reserve Ducke, and also comparing them with available data from literature (Barataud et al., 2013; Briones-Salas et al., 2013; Jung et al., 2007, 2014). Only search-call pulses with >20 Db of sound intensity of difference with noise background were taken into account. Feeding buzzes and social calls were not included in the analysis. Bat activity was thus estimated as number of bat-passes per night per plot. Hourly activity was quantified by the number of bat-passes per hour in each night per plot.

*Moonlight intensity*

In order to evaluate the influence of moonlight upon aerial insectivorous bat activity (Question 1), we used the percentage of lunar luminosity generated by Moontool 2.0 software (Walker, 2016), adapted from Meeus (1991). The calculation of moonlight intensity is based on the portion of the lunar disc reflecting sunlight, and takes into account the position of the Earth in relation to the sun, including the geographical position of the sampling site.

To assess how bat activity was affected hourly between dark and bright nights (Question 2), we considered dark nights to be those with 0-30% of moonlight intensity and bright nights those with 70-100%. Ten dark nights and 10 bright nights were included in the analysis.

To understand how the presence of the moon affects bat activity during the same night (Question 3), we analyzed both those nights that had at least four hours with moonlight and four hours without moonlight (with moonsets and moonrises between 22:00 and 2:00h respectively). Additionally, completely dark and bright nights were included as controls. Moonrise and moonset times were retrieved from the Brazilian Astronomic Almanac (Campos, 2013).

Cloudy nights can reduce luminosity inside a forest, with potential collateral effects upon bat activity. Occurrence of clouds was assessed by the accumulated rainfall data from the permanent Climatological Station in Reserve Ducke. Rainfall data was used as a surrogate to detect cloudy nights, since it was not possible to monitor the cloud-cover across the whole study period. Rainfall data comprised measures at 30' intervals between January and May 2013. Nights were considered 'cloudy' when rainfall ranged 0.1 to 10 mm per hour, generally classified as weak to moderate rain. Nights with more than 10 mm rainfall per hour corresponded to nights with heavy rain and thus were removed from the analysis (Racey and Swift, 1987; Carvalho et al., 2011). In order to test whether the presence of clouds affected bat activity, an analysis of covariance (ANCOVA) was used with cloudy nights as a covariate (categorical variable) and the percentage of moonlight intensity as a predictor (continuous variable). For all bat species, the presence of clouds did not influence bat activity and thus, this predictor was not included in subsequent analyzes (Table S1).

*Bat species*

Among the 19 aerial insectivorous bats species recorded for the Reserve Ducke, species with more than 10 bat-passes per night and occurring in at least 10 dark and bright nights were selected for analysis. Only five species matched these criteria. The species, in decreasing order of bat-passes, were: *Pteronotus parnellii* (3,156), *Saccopteryx bilineata* (2,390), *Myotis riparius* (1,730), *Cormura brevirostris* (1,236) and *Saccopteryx leptura* (564) (Table S2).

*Data analysis*

In order to test the influence of moonlight on bat activity between nights (Question 1), we used Generalized Linear Mixed Models (GLMM) with a Poisson distribution controlled for overdispersion (Zuur et al., 2009), performed using the 'lme4' package (Bates et al., 2016). The number of bat-passes per night in each plot was used as the response variable (log-transformed) and the moonlight intensity as the predictor variable. Because 4-5 consecutive nights of recording per plot might generate temporal autocorrelation in the data, the plot was considered as the random variable. We compared total bat activity between dark and bright nights using a Student's t-test. Dark nights were those with moonlight intensity between 0 and 30% (n = 10 nights) and bright nights between 70 and 100% (n = 10).

In order to test hourly variation on bat activity between dark and bright nights (Question 2), percentiles of activity were established using the ‘quantile’ stats package (Hyndman and Fan, 1996). We used the average species activity from 20 nights (10 bright nights and 10 dark nights), to calculate three percentiles (50th, 80th, 99th). Following Adams et al. (2015), activity peaks were defined as those periods where bat activity reached the 99th percentile. Complementarily, the timing of activity peaks for the five species were compared using an Analysis of Variance (ANOVA) with a *post hoc* Tukey test.

In order to test the influence of moonlight on bat activity within the same night (Question 3), we used a paired t-test to compare bat activity between the beginning and at the end of the night. We performed an ANOVA with Tukey *post hoc* test to compare the total activity between the four night types. The combination of these two analyzes is essential to assess whether bat activity within the same night is influenced by moonlight or determined by the emergence time of the bats. If the activity was only influenced by the presence of moonlight, we would expect bat activity to be related to moonlight intensity (dark or bright) at the beginning or end of the night, regardless of the time. If the activity was mostly influenced by the time, bat activity would be consistently higher in a particular part of the night (beginning or end), regardless of moonlight intensity. All analyzes were performed in R version 3.2.2 (R Core Team, 2015).

## Results

*Effects of moonlight intensity on bat activity*

*Pteronotus parnellii* (Fig. 2A) foraging activity was positively related to moonlight intensity, with activity levels on average 4.5 times higher on bright nights than on the dark nights (Fig. 2B, Table 1). The same pattern was found for *S. leptura* (Fig. 2C), where activity levels were 10.08 times higher on bright nights (Fig. 2D, Table 1). In contrast, *M. riparius* activity levels (Fig. 2I) decreased with moonlight intensity, with activity being 46.6 times higher on dark nights (Fig. 2J; Table 1). Levels of *S. bilineata* and *C. brevirostris* foraging activity did not differ between bright and dark nights (Fig. 2E-H; Table 1).

*Effects of moonlight intensity on bat hourly activity*

Patterns of activity during the night varied between bat species and between bright and dark nights (Table 2). Except for *P. parnellii*, all species concentrated their activity at the beginning and end of the night, decreasing their activity between 120 and 540 minutes after sunset, regardless of moonlight intensity. *Saccopteryx leptura* was the only species with activity restricted to the first 60 minutes of the night (Table 2).

During the dark nights, all species only had a single peak of activity at the beginning of the night (Fig. 3; Table 2). Activity peaks for *S. bilineata, S. leptura* and *C. brevirostri*s occurred a few minutes after sunset, for *M. riparius* around 60 minutes after, and for *P. parnellii* 120 minutes after sunset (Fig. 3; Table 2). During bright nights, activity peaks also occurred at the beginning of the night, but *S. bilineata*, *C. brevirostris* and *M. riparius* had a second peak at the end of the night, 660 minutes after the sunset (Fig. 3; Table 2). For *P. parnellii*, activity was constant throughout the night (Fig. 3; Table 2).

*The influence of the timing of moonrise-moonset on bat activity*

As predicted, during the nights that started without moonlight (Table 3), bat activity was higher at the beginning of the night, except for *M. riparius*. However, contrary to our expectations, for nights that began bright and ended dark (Table 3), bat activity was also higher at the beginning of the night, during the bright period (except for *C. brevirostris* and *M. riparius*). When bat activity was compared between entirely dark and bright nights (Table 3), activity was higher in the early evening only for *S. bilineata* and *S. leptura* on entirely bright nights.

When we compared nights with variation of the presence of moonlight and nights without such variation, we found that activity in *P. parnellii* was higher on entirely bright nights, while for *M. riparius* it was higher on completely dark nights (Table 4). *Saccopteryx leptura*, *S. bilineata* and *C. brevirostris* did not differ in their activity levels between nights with variation in moonlight and nights without variation (Table 4).

## Discussion

According to our results, moonlight intensity influences the foraging activity of the five species of aerial insectivorous bats at different temporal scales. Lunar phobia cannot be generalized to the activity of all the insectivorous bats species as this particular behavior only appeared in some species under some specific situations. As suggested by (Morrison, 1978) with the "lunar phobia hypothesis", moonlight intensity variation might have an unpredictable effect on bat activity, usually increasing on dark nights. This is to our knowledge the first study to test lunar phobia at different temporal scales in aerial insectivorous bats.

Contrary to our expectations, two species were positively affected by moonlight intensity between nights. It is well-known that moonlight intensity-influences the activity of nocturnal insects (Meyer et al., 2004; Lang et al., 2006). Diptera, Lepidoptera, Coleoptera and Hemiptera are all fly greater distances on bright nights (Bidlingmayer, 1964; Rydell, 1992; Lorenzo and Lazzari, 1998; Gonsalves et al., 2013; Jiang 2016). This could make them more vulnerable to aerial predators such as *S. leptura* (whose diet is mainly composed of Coleoptera and Diptera, (Bradbury and Vehrencamp, 1976; Yancey et al., 1998) or *P. parnellii*, a species that usually forages more intensely in places with greater insect availability, even in cluttered sites (Oliveira et al., 2015). This suggests that the foraging strategy of *P. parnellii* is strongly influenced by the prey availability, which might increase substantially on bright nights.

Up to a limit-point, visual perception of predators increases during periods of higher illumination (Prugh and Golden, 2013) allowing members of visually-oriented bat species to capture slow-flying species more easily than fast-flying ones (Ciechanowski et al., 2007; Azam et al., 2015). Inherent bat species characteristics such as flight speed, body size and type of foraging habitat may compromise the abilities o individuals of such species to respond to predator pressure. Slow-flying species avoid sites or bright periods of night that have intense light exposure because of the high risk of predation (Rydell et al., 1996; Kuijper et al., 2008). Short and broad wings (low wing loading and low aspect ratio) and low weight are the morphological characteristics of slow-flight species (Norberg and Rayner, 1987). That *M. riparius* has morphology typical of species with slow maneuverable flight could explain why there is a decrease in activity on bright nights. Other species of *Myotis* are known to respond negatively to natural and artificial light, reducing their activity in open areas and on bright nights, as observed by (Stone et al., 2009; Azam et al., 2015), and corroborated by our results for *M. riparius*.

Moonlight can affect bats differently because of their individual and inherent foraging strategies and differential habitat use (Jung and Kalko, 2010). The fact that we did not find any effect of moonlight on *C. brevirostris* and *S. bilineata* foraging activity could be explained by their microhabitat adaptability. Opportunistic species that can use different types of habitat could switch from open areas to more protected habitats depending on environmental conditions. Bats that fly in different forest strata might be able to forage in shadier places during bright nights, reducing exposure to potential predators (Jones and Rydell, 1994; Breviglieri, 2011). For instance, during full moon nights, *C. brevirostris* is known to fly closer to the vegetation around streetlights, presumably to avoid predators (Jung and Kalko, 2010).

*Pteronurus parnellii* can perform long flights between daytime roosts and feeding areas (Goldman et al., 1977; Marinello and Bernard, 2014). This bat species produces typical long constant frequency calls that allows it to forage in highly cluttered habitats (Denzinger and Schnitzler, 2013; Oliveira et al., 2015), such behavior can reduce predation risk during bright nights.

Hourly activity trends of most species differed between dark and bright nights. During dark nights, species had only one peak of activity while on bright nights, we observed two peaks of activity. Insect activity peaks might an important factor driving bat activity peaks. Insects, especially Diptera, are known to have two peaks of activity, one after the sunset and other before sunrise (Rydell et al., 1996). Our results showed that four of the five studied bat species show bimodal activity, possibly affected by insect activity (Meyer et al., 2004; Weinbeer and Meyer, 2006). The bimodal pattern was most evident during bright nights, a pattern also observed in African insectivorous bats (Fenton et al., 1977).

Within a same night, the activity of most of the studied species was higher at the beginning of the night on both bright and dark nights. The need to feed during the first few minutes of the night could be the reason for this first activity peak (Erkert, 2000). Limiting the foraging time to the first minutes after sunset allows bats to attain high foraging efficiencies (O'Donnell, 2000; Speakman et al., 2000). Lower predation pressure at the beginning of the night also encourages bats to emerge from their roosts and optimize the cost-benefit ratio of foraging.

Unlike previous studies (i.e. Herd, 1983), we did not record *P. parnellii* initiating activity a few minutes after the sunset. Activity in *P. parnellii* may be limited by lepidopteran availability, one of the main diet items (Rolfe and Kurta, 2012; Salinas-Ramos et al., 2015), which is more active in the middle of the night (Goldman et al., 1977; Speakman et al., 2000). Such behavior is known for other species of aerial insectivorous bats that feed on lepidopterans, such as *Lasiurus borealis*, *L. cinereus*, and large molossids (Rydell et al., 1995; Hickey et al., 1996). Matching bat foraging activity with highest insect availabilities might optimize foraging success (Rydell et al., 1996; Meyer et al., 2004).

Our study is one of the few to have used moonlight intensity instead of the phases of the moon as a predictor variable (Esbérard, 2007; Mello et al., 2013). Moonlight intensity can greatly vary within the same lunar phase, and different lunar phases can also overlap in moonlight intensity. During the new moon, for example, the intensity of moonlight varies from zero to 35%, while in the waning phase it varies from 3% to 55%. This corresponds to ten nights of moonlight intensity overlapping between new moon and waning phase. In our study, the bat species did not respond to the moon phase, except for the increased activity of *M. riparius* during new moon nights (Table S3). Thus categorization of moonlight intensity on moon phases can lead to misinterpretations regarding the association between activity of nocturnal species and availability of light.

Bat species response to moonlight intensity was species-specific and highly dependent on the temporal scale considered. The effect of the moonlight intensity was more evident at a longer, between nights, time scale. Within a single night, bat activity was higher in the evening regardless of the presence or absence of moonlight. Thus, bat activity response to moonlight is not immediate, and could be more directly associated to an individual's experience of the previous night. Inherent species traits such as flight speed, body size, flexibility in using different habitats, and predation pressure may influence specific responses to moonlight. These factors need to be addressed in future studies in order to understand how the variation in moonlight intensity affects the nocturnal activities of bats. Because bat species respond differently to change in moonlight intensity, we recommend that studies on population and community structure of aerial insectivorous bats should be performed along the entire lunar cycle in order to include the periods of high activity of bat species.

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## Figure Captions

**Fig. 1.** Ducke Reserve in the North of Manaus, Amazonas, Brazil. Distribution of study plots in RAPELD grid, including topography and streams.

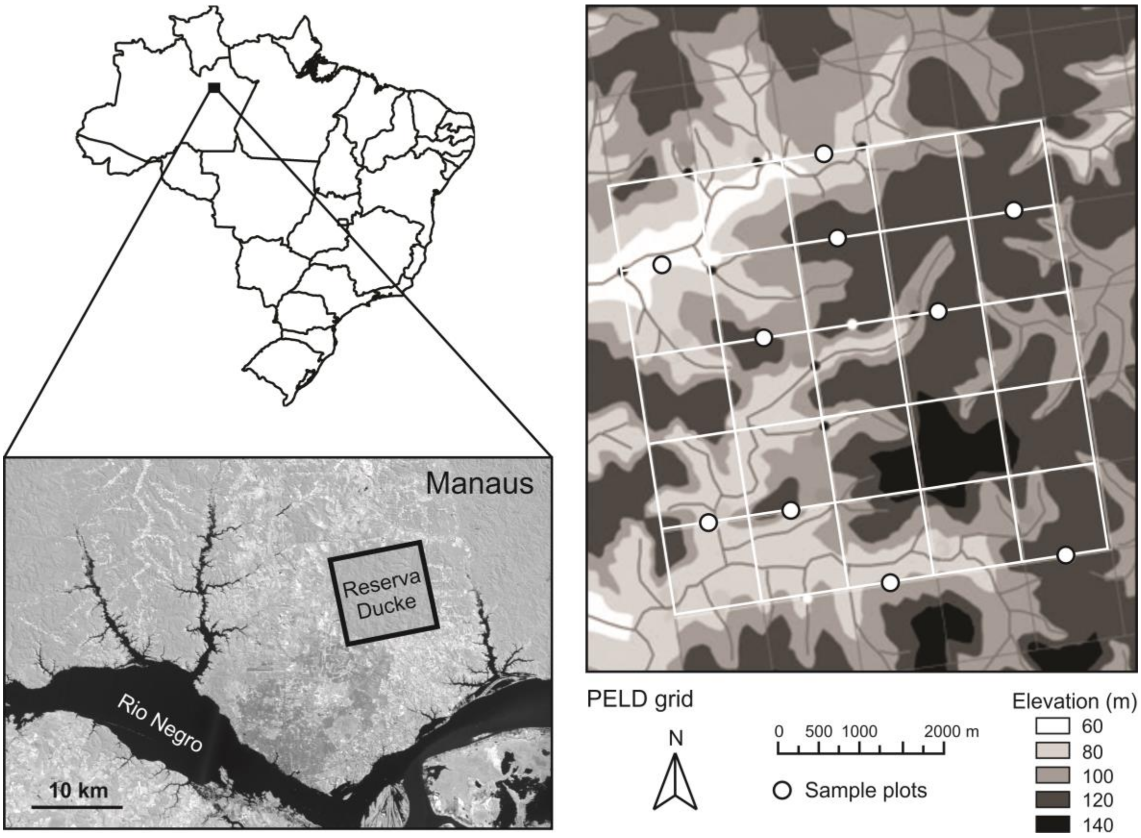
**Fig. 2.** Relation between aerial activity of five species of insectivorous bat (log-transformed) with the moonlight intensity (%) (A, C, E, G and I) and difference in bat activity between dark and bright nights (B, D, F, H and J). Dark nights were considered those with moonlight intensity between 0 and 30%, bright nights those above 70%.

**Fig. 3.** Hourly aerial activity of five species of insectivorous bat on dark nights (N = 10) and bright nights (N = 10). Dark nights were considered between 0 and 30% and bright nights those above 70%. The solid line is the average hourly activity and the dotted line represents the standard deviation of hourly activity. Dotted horizontal lines mean the percentiles (99th, 80th, and 50th).

**Fig. 4.** Nightly aerial activity of five species of insectivorous bat recorded on different types of nights: nights that start dark and end bright (N = 13), nights that start bright and end dark (N = 9), nights entirely bright (N = 18) and nights entirely dark (N = 8).

# Figures

**Figure 1**



679 **Figure 2**

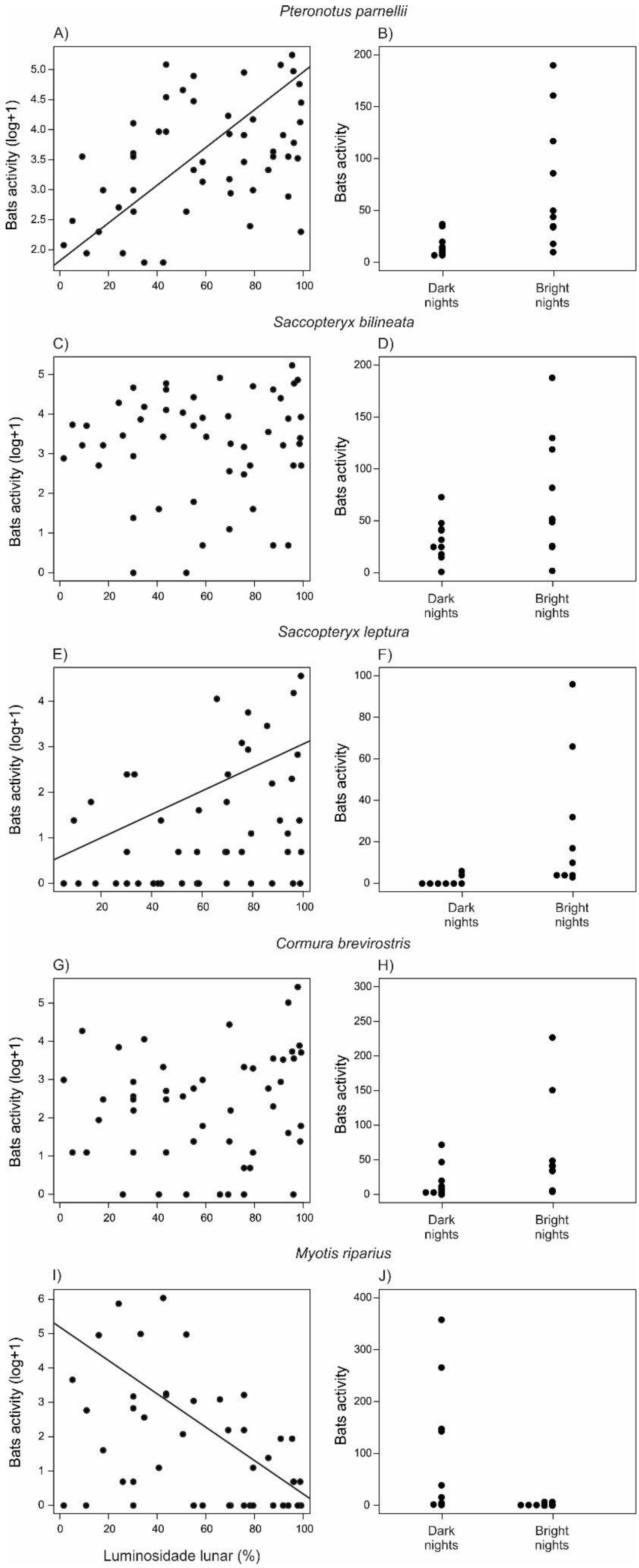



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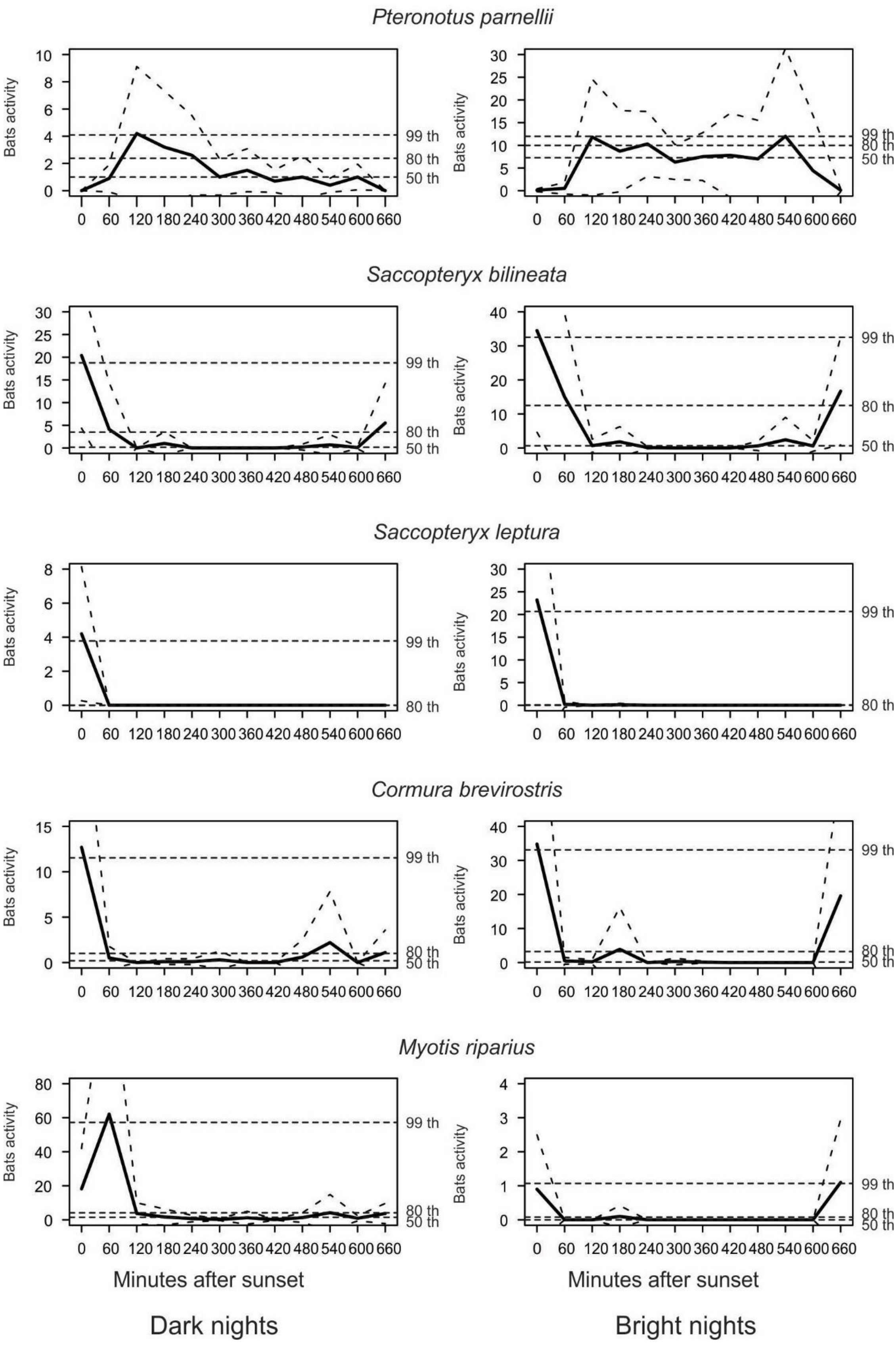
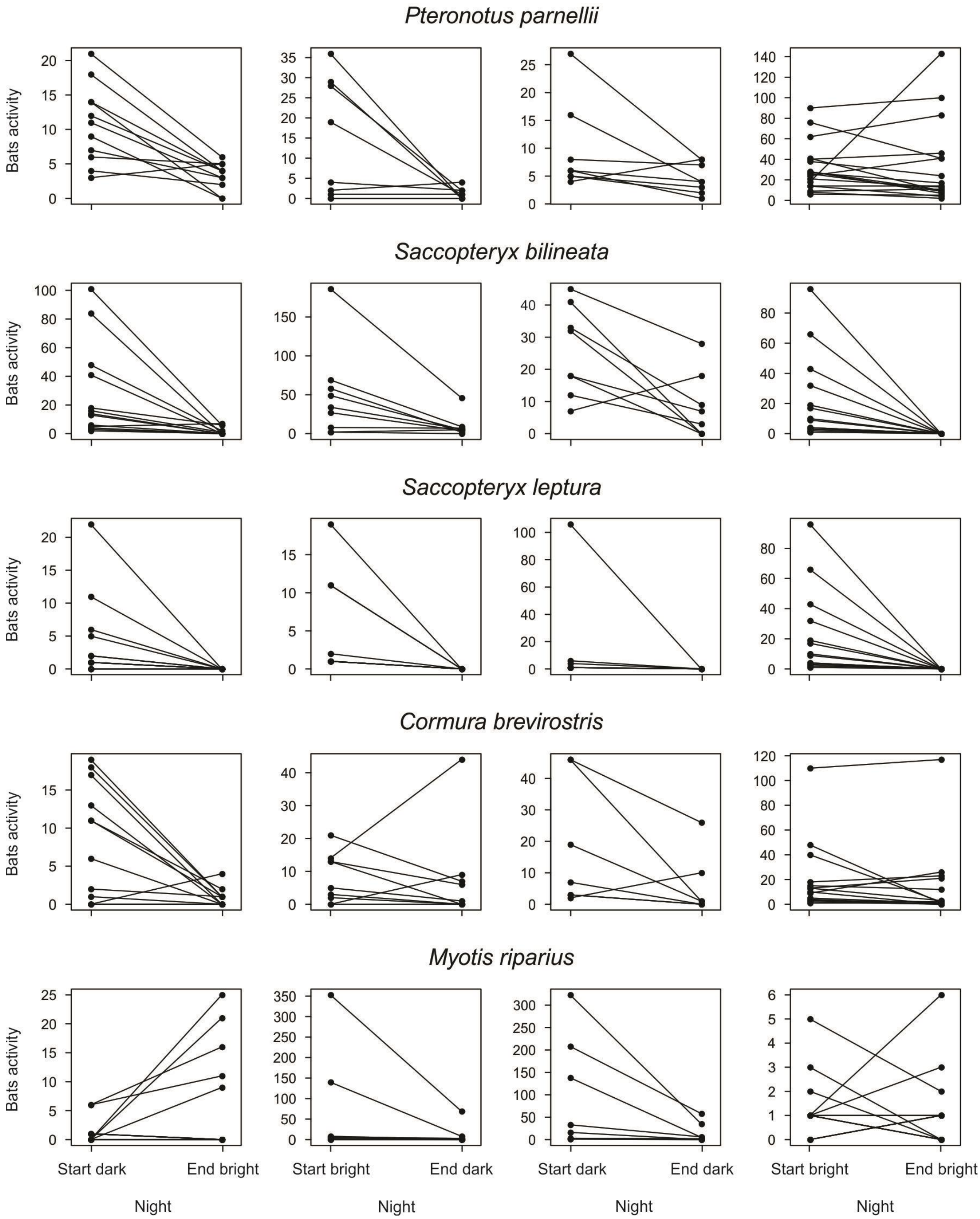
**Figure 3**



Pteronotus parnellii
Saccopteryx bilineata
Saccopteryx leptura
Cormura brevirostris
Myotis riparius
Bats activity
99 th
80 th
50 th
0 60 120 180 240 300 360 420 480 540 600 660
Minutes after sunset
Dark nights
Bright nights

**Figure 4**


Pteronotus parnellii
Saccopteryx bilineata
Saccopteryx leptura
Cormura brevirostris
Myotis riparius
Bats activity
Start dark
End bright
Start bright
End dark
Start dark
End dark
Start bright
End bright
Night

# Tables

**Table 1.** Results of Generalized Linear Mixed Models (GLMM) testing the relation between bat activity and moonlight intensity. Results of Student's t-test with the difference in activity between dark and bright nights. Significant values: *P* <0.05, *P* <0.01 and *P* <0.001 are in bold.

| Species | Moonlight intensity | | | Dark × bright nights | | |
|---|---|---|---|---|---|---|
| | $R^2$ | *z* | *P* | *t* | d.f | *P* |
| *Pteronotus parnellii* | 0.03 | 3.19 | **0.001** | 2.90 | 10 | **0.01** |
| *Saccopteryx bilineata* | 0.05 | -0.50 | 0.61 | 2.09 | 11 | 0.06 |
| *Saccopteryx leptura* | 0.12 | 6.81 | **<0.001** | 2.24 | 8 | **0.05** |
| *Cormura brevirostris* | 0.01 | -1.17 | 0.24 | 1.73 | 11 | 0.11 |
| *Myotis riparius* | 0.01 | -5.56 | **<0.001** | -2.37 | 9 | **0.04** |

**Table 2.** Hourly bat activity in dark and bright nights. Values represent total number of bat-passes (mean ± standard deviation). Activity values followed by the same letter are statistically similar (*P* <0.05) values accompanied with the letter a are the highest values.

| | Minutes after sunset | *Pteronotus parnellii* | *Saccopteryx bilineata* | *Saccopteryx leptura* | *Cormura brevirostris* | *Myotis riparius* |
|---|---|---|---|---|---|---|
| Dark nights | 0 | 0 (0 ± 0) c | 204 (20.4 ± 16.04) a | 21 (2.1 ± 3.78) a | 127 (12.7 ± 17.39) a | 182 (18.2 ± 23.67) b |
| | 60 | 9 (0.9 ± 0.99) c | 41 (4.1 ± 10.27) b | 0 (0 ± 0) b | 5 (0.5 ± 1.26) b | 621 (62.1 ± 96.18) a |
| | 120 | 42 (4.2 ± 4.91) ab | 0 (0 ± 0) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 37 (3.7 ± 6.27) b |
| | 180 | 32 (3.2 ± 4.30) b | 10 (1 ± 2.53) b | 0 (0 ± 0) b | 1 (0.1 ± 0.31) b | 17 (1.7 ± 4.71) b |
| | 240 | 26 (2.6 ± 2.91) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 1 (0.1 ± 0.31) b | 7 (0.7 ± 1.88) b |
| | 300 | 10 (1.0 ± 1.33) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 3 (0.3 ± 0.94) b | 2 (0.2 ± 0.63) b |
| | 360 | 15 (1.5 ± 1.58) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 12 (1.2 ± 3.79) b |
| | 420 | 7 (0.7 ± 0.82) c | 0 (0 ± 0) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 1 (0.1 ± 0.31) b |
| | 480 | 10 (1.0 ± 1.56) b | 2 (0.2 ± 0.63) b | 0 (0 ± 0) b | 6 (0.6 ± 1.89) b | 13 (1.3 ± 2.83) b |
| | 540 | 4 (0.4 ± 0.51) c | 7 (0.7 ± 2.21) b | 0 (0 ± 0) b | 22 (2.2 ± 5.63) b | 42 (4.2 ± 10.64) b |
| | 600 | 10 (1.0 ± 0.94) b | 1 (0.1 ± 0.31) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 9 (0.9 ± 1.52) b |

| | | | | | | |
|---|---|---|---|---|---|---|
| | 660 | 0 (0 ± 0) c | 55 (5.5 ± 8.72) b | 0 (0 ± 0) b | 11 (1.1 ± 2.46) b | 37 (3.7 ± 5.92) b |
| Bright nights | 0 | 4 (0.4 ± 1.26) a | 345 (34.5 ± 29.87) a | 232 (23.2 ± 32.51) a | 348 (34.8 ± 51.62) a | 9 (0.9 ± 1.59) ab |
| | 60 | 63 (6.3 ± 13.37) a | 150 (1.5 ± 24.62) b | 2 (0.2 ± 0.63) b | 5 (0.5 ± 0.97) b | 0 (0 ± 0) b |
| | 120 | 89 (8.9 ± 7.68) a | 7 (0.7 ± 1.88) b | 0 (0 ± 0) b | 2 (0.2 ± 0.63) b | 0 (0 ± 0) b |
| | 180 | 85 (8.5 ± 9.04) a | 18 (1.8 ± 4.46) b | 1 (0.1 ± 0.31) | 39 (3.9 ± 12.33) b | 1 (0.1 ± 0.31) b |
| | 240 | 65 (6.5 ± 7.82) a | 1 (0.1 ± 0.31) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 0 (0 ± 0) b |
| | 300 | 65 (6.5 ± 3.37) a | 0 (0 ± 0) b | 0 (0 ± 0) b | 3 (0.3 ± 0.94) b | 0 (0 ± 0) b |
| | 360 | 77 (7.7 ± 5.12) a | 0 (0 ± 0) b | 0 (0 ± 0) b | 1 (0.1 ± 0.31) b | 0 (0 ± 0) b |
| | 420 | 93 (9.3 ± 9.88) a | 0 (0 ± 0) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 0 (0 ± 0) b |
| | 480 | 69 (6.9 ± 8.93) a | 6 (0.6 ± 1.34) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 0 (0 ± 0) b |
| | 540 | 94 (9.4 ± 19.44) a | 24 (2.4 ± 6.56) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 0 (0 ± 0) b |
| | 600 | 41 (4.1 ± 12.26) a | 6 (0.6 ± 1.66) b | 0 (0 ± 0) b | 0 (0 ± 0) b | 0 (0 ± 0) b |
| | 660 | 0 (0 ± 0) a | 167 (16.7 ± 15.82) ab | 0 (0 ± 0) b | 196 (19.6 ± 35.77) ab | 11 (1.1 ± 1.82) a |

**Table 3.** Paired t-test results comparing bat activity between the beginning and end of the night. Bright correspond the period of the presence of moonlight and the dark period of absence of moonlight. During the nights labelled bright, moonset occurred between 22:00 and 2:00 am, and nights called dark, moonrise occurred between 22:00 and 2:00 am. Significant values: *P* <0.5, *P* <0.01 and *P* <0.001 are in bold.

| Species | Periods of the night | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Dark-Bright | | | Bright-Dark | | | Dark-Dark | | | Bright-Bright | | |
| | *t* | g.l | *P* | *t* | g.l | *P* | *t* | g.l | *P* | *t* | g.l | *P* |
| *Pteronotus parnellii* | -3.74 | 12 | **0.002** | -2.40 | 8 | **0.04** | -1.96 | 7 | 0.09 | -0.06 | 17 | 0.95 |
| *Saccopteryx bilineata* | -2.90 | 12 | **0.01** | -2.62 | 8 | **0.03** | -3.16 | 7 | **0.01** | -2.72 | 17 | **0.01** |
| *Saccopteryx leptura* | -2.30 | 12 | **0.03** | -2.39 | 8 | **0.04** | -1.15 | 6 | 0.29 | -2.90 | 13 | **0.01** |
| *Cormura brevirostris* | -3.27 | 11 | **0.007** | -0.08 | 17 | 0.93 | -1.93 | 6 | 0.1 | -1.32 | 14 | 0.2 |
| *Myotis riparius* | 0.33 | 10 | 0.74 | -1.41 | 8 | 0.19 | -2.09 | 7 | 0.07 | 0.12 | 12 | 0.8 |

**Table 4.** Activity of the five species of insectivorous bats recorded in the Reserve Ducke, in Manaus, in nights four different lunar illumination schedules (Dark-Bright, Bright-Dark, Dark-Dark and Bright-Bright). The bright periods correspond to presence of moonlight and dark periods correspond to absence of moonlight that night. The values represent total calls (mean ± standard deviation). Activity values with the same letter a are statistically similar ($P$ <0.05) values accompanied with the letter a are the highest values.

| Start-end night | N of nights | *Pteronotus parnellii* | *Saccopteryx bilineata* | *Saccopteryx leptura* | *Cormura brevirostris* | *Myotis riparius* |
|---|---|---|---|---|---|---|
| Dark-Bright | 13 | 280 (21.53 ± 19.47) b | 377 (29.00 ± 33.16) a | 52 (4.00 ± 6.25) a | 69 (14.84 ± 22.27) a | 98 (7.53 ± 9.93) b |
| Bright-Dark | 9 | 129 (14.33 ± 14.42) b | 519 (57.67 ± 70.12) a | 48 (5.33 ± 6.67) a | 115 (15.33 ± 18.34) a | 178 (19.77 ± 48.22) b |
| Dark-Dark | 8 | 114 (14.25 ± 9.49) b | 1039 (33.83 ± 18.58) a | 120 (17.17 ± 26.60) a | 518 (20.50 ± 25.75) a | 830 (103.75 ± 138.80) a |
| Bright-Bright | 18 | 1149 (63.83 ± 54.27) a | 271 (57.72 ± 52.86) a | 309 (15.00 ± 36.83) a | 158 (27.94 ± 52.51) a | 33 (1.83 ± 2.17) b |

# Supplementary material

**Table S1.** Results of ANCOVA, with the predictor variable moonlight intensity, the covariate cloud and interaction between moonlight intensity and cloud. Significant values: *P* <0.5, *P* <0.01 and *P* <0.001 are in bold.

| Species | Moonlight intensity | | | Cloud | | | Moonlight intensity*Cloud | | |
|---|---|---|---|---|---|---|---|---|---|
| | *F* | g.l | *P* | *F* | g.l | *P* | *F* | g.l | *P* |
| *Pteronotus parnellii* | 12.14 | 1 | **0.001** | 0.01 | 1 | 0.91 | 1.04 | 1 | 0.31 |
| *Saccopteryx bilineata* | 0.29 | 1 | 0.59 | 1.63 | 1 | 0.20 | 0.02 | 1 | 0.88 |
| *Saccopteryx leptura* | 6.85 | 1 | **0.01** | 0.003 | 1 | 0.70 | 0.02 | 1 | 0.88 |
| *Cormura brevirostris* | 0.88 | 1 | 0.35 | 0.88 | 1 | 0.35 | 0 | 1 | 0.99 |
| *Myotis riparius* | 3.86 | 1 | **0.05** | 0.14 | 1 | 0.70 | 0.49 | 1 | 0.48 |

**Table S2.** Summary of acoustic activity (number of bat-passes) of the five aerial insectivorous bats species. The values represent total number of bat-passes (mean ± standard deviation).

| | *Pteronotus parnellii* | *Saccopteryx bilineata* | *Saccopteryx leptura* | *Cormura brevirostris* | *Myotis riparius* |
|---|---|---|---|---|---|
| N of recording nights | 53 | 53 | 33 | 48 | 37 |
| N of calls | 3156 (51.29 ± 74.46) | 2390 (45.09 ± 42.81) | 564 (10.64 ± 22.75) | 1236 (23.32 ± 38.92) | 1730 (46.75 ± 100.64) |
| N of calls on dark nights | 165 (16.50 ± 11.04) | 320 (32.0 ± 20.17) | 21 (2.10 ± 3.78) | 176 (17.60 ± 23.56) | 980 (98.0 ± 127.28) |
| N of calls on bright nights | 765 (76.50 ± 60.50) | 724 (72.40 ± 57.46) | 235 (23.50 ± 32.05) | 594 (59.40 ± 72.35) | 21 (2.10 ± 2.64) |

**Table S3.** Bat activity in each lunar phase. Values represent total number of bat-passes (mean ± standard deviation). Activity values with the same letter are statistically similar (*P* <0.05), values accompanied with the letter a are the highest values.

| Lunar Phases | Nº of nights | *Pteronotus parnellii* | *Saccopteryx bilineata* | *Saccopteryx leptura* | *Cormura brevirostris* | *Myotis riparius* |
|---|---|---|---|---|---|---|
| New | 13 | 230 (47.69 ± 14.81) a | 422 (32.46 ± 21.49) a | 123 (9.46 ± 29.19) a | 262 (20.15 ± 24.08) a | 1298 (99.84 ± 142.09) a |
| Crescent | 14 | 967 (69.07 ± 56.94) a | 788 (43.77 ± 47.73) a | 307 (21.92 ± 28.58) a | 270 (19.28 ± 17.41) a | 44 (3.14 ± 3.20) b |
| Full | 18 | 994 (55.22 ± 42.72) a | 412 (68.66 ± 48.62) a | 56 (3.11 ± 5.32) a | 629 (39.94 ± 60.96) a | 81 (4.50 ± 9.03) b |
| Waning | 6 | 425 (70.83 ± 51.24) a | 723 (50.2 ± 48.17) a | 20 (3.33 ± 4.17) a | 74 (12.33 ± 24.08) a | 68 (11.33 ± 12.42) b |

## CONCLUSÃO

A resposta dos morcegos a variação da luminosidade lunar é um comportamento espécie-específico e varia em relação à escala temporal analisada. O efeito da luminosidade lunar foi mais evidente em uma escala temporal longa entre noites. Em uma escala temporal curta dentro de uma mesma noite, a atividade dos morcegos foi maior no início da noite independente da presença ou ausência da lua.

Fatores intrínsecos das espécies como velocidade do voo, tamanho do corpo e flexibilidade no uso de habitats podem influenciam na resposta dos morcegos a luminosidade lunar. Estes fatores precisam ser abordados em estudos futuros para entendermos como a variação da intensidade luminosa afeta a atividades noturna dos morcegos. Devido às espécies de morcegos responderem de forma diferente a variação da intensidade luminosa da lua, recomendamos que para estudos populacionais e da estrutura de comunidades de morcegos insetívoros aéreos todo o ciclo lunar deve ser amostrado, a fim de incluir os períodos de alta atividade das espécies.