

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/309955209>

Aerial insectivorous bat activity in relation to moonlight intensity

Article · November 2016

DOI: 10.1016/j.mambio.2016.11.005

CITATIONS

0

READS

1,278

4 authors:



[Giulliana Appel](#)

Instituto Nacional de Pesquisas da Amazônia

3 PUBLICATIONS 2 CITATIONS

[SEE PROFILE](#)



[Adria Lopez-Baucells](#)

University of Lisbon

35 PUBLICATIONS 80 CITATIONS

[SEE PROFILE](#)



[William E. Magnusson](#)

Instituto Nacional de Pesquisas da Amazônia

398 PUBLICATIONS 5,898 CITATIONS

[SEE PROFILE](#)



[Paulo Bobrowiec](#)

Instituto Nacional de Pesquisas da Amazônia

31 PUBLICATIONS 121 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Programa de Pesquisa em Biodiversidade – PPBio [View project](#)



Bird and bat assemblages in Madagascar's humanized landscapes [View project](#)

All content following this page was uploaded by [Adria Lopez-Baucells](#) on 13 March 2017.

The user has requested enhancement of the downloaded file. All in-text references [underlined in blue](#) are added to the original document and are linked to publications on ResearchGate, letting you access and read them immediately.



Original investigation

Aerial insectivorous bat activity in relation to moonlight intensity

Giulliana Appel^{a,*}, Adrià López-Baucells^{b,c}, William Ernest Magnusson^d,
Paulo Estefano D. Bobrowiec^{d,*}

^a Programa de Pós-graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, CP 2223, Manaus, AM, 69080-971, Brazil

^b Centre for Ecology, Evolution and Environmental Changes, Faculty of Science, University of Lisbon, Edifício C2, 5º Piso, Campo Grande, 1749-016 Lisboa, Portugal

^c Granollers Museum of Natural Sciences, Bat Research Group, c/ Palaudàries, 102 - Jardins Antoni Jonch Cuspinera, Granollers 08402, Catalonia, Spain

^d Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, CP 2223, Manaus, AM, 69080-971, Brazil

ARTICLE INFO

Article history:

Received 23 June 2016

Accepted 9 November 2016

Handled by Danilo Russo

Available online 11 November 2016

Keywords:

Foraging strategy

Chiroptera

Moon

Rainforest

Hourly activity

ABSTRACT

It is commonly assumed that aerial insectivorous bats in the tropics respond to moonlight intensity by decreasing their foraging activity during bright nights due either to an increase in predation risk, or to a reduction in insect availability.

The effect of moonlight on bat activity can be measured both between nights and within a single night. However, few studies have simultaneously used both approaches, and most authors generally compare bat activity with lunar phases. Our main aim was to evaluate how 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 the Moontool program nightly throughout a 53-day sampling period. Only one species (*Myotis riparius*) responded negatively to moonlight, while two species (*Pteronotus parnellii* and *Saccopteryx leptura*) increased their foraging activity in moonlight. For *Cormura brevirostris* and *S. bilineata*, moonlight intensity did not affect activity level. 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 adaptive. Thus, bat response to the effect of moonlight intensity is more apparent between nights than within a single night and may depend on species-specific traits, such as flight speed, flexibility in habitat use and body size.

© 2016 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Introduction

Species activity patterns can be defined as the consistent repetition of certain behaviors over time (Erkert, 1982). These 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-day variation according to daylight hours (Tarlow et al., 2003).

On the other hand, nocturnal species tend 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 investment (Digby et al., 2014; York et al., 2014). Activity of visually-oriented predators increases during bright nights, probably due to 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 so as to avoid predators (Fenton et al., 1977; Kramer et al., 2001). This differential response to moonlight is essentially 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 min later each night across the monthly cycle which results in different times of moonrise and moonset (Hibbard, 1925). Some nights start without moon, but the moon may rise hours after sun-

* Corresponding authors.

E-mail addresses: giuappel@outlook.com, giu.appel@gmail.com (G. Appel), paulobobro@gmail.com (P.E.D. Bobrowiec).

set. Some nights have little 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 and O’Keefe, 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 forage at night (Speakman, 1995). The term ‘lunar phobia’ proposed by Morrison (1978) suggests that some 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 in predation risk (Esbérard, 2007; Lima and O’Keefe, 2013), and/or due to lower activity of some prey groups (Lang et al., 2006). However, some bat species have been found to not decrease their activity when moonlight increases (Kuenzi and Morrison, 2003; Karlsson et al., 2006). For instance, frugivorous and nectarivorous species are more active on bright nights, when they seem to be more efficient at detecting fruits and flowers (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 seem to be less susceptible to predators and thus can forage more safely on bright nights (Holland et al., 2011). Also, bat species that use multiple habitats, such as forest interiors, forest edges, and open areas, fly through great variation in vegetation cover intensity (Mancina, 2008). Species that forage in different habitats are more tolerant of illumination changes and are therefore may be less affected by variation in moonlight intensity (Rydell, 1991; Breviglieri, 2011).

Several studies have evaluated the relationship between moonlight intensity and bat activity (Karlsson et al., 2006; Santos-Moreno et al., 2010). A recent review suggested that the lunar phobia response is more common in tropical bats than in temperate species, because of the high diversity of predators and the high proportion of slow-flying bat species in tropical zones (Saldaña-Vázquez and Munguía-Rosas, 2013). However, most studies in the tropics have concentrated on fruit bats; how moonlight affects aerial activity of tropical insectivorous bats remains essentially unknown (Saldaña-Vázquez and Munguía-Rosas, 2013). Furthermore, with the exception of Mello et al. (2013), 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 generated by reflectance from 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 and predictions were:

- (1) Does aerial-insectivorous bat activity change according to variations in moonlight intensity between nights? Assuming bats 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 more homogeneous, without peaks, while on bright nights, activity will have only one peak in the early evening.
- (3) Since moonlight intensity is never constant throughout a single night, is bat activity influenced by the timing of moonrise/moonset within a single night? During those nights when the moon rose late we expected bat activity to decrease as the

night proceeded. Moreover, on nights that began bright and ended dark (when the after moon was sets for the entire night), we predicted that bat activity would be higher in the dark period. We also expected total bat activity to be higher during dark nights in which the moon was rarely above the horizon than during nights when the moon was visible for most of the night.

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 Amazonia, Brazil. The reserve covers an area of 10,000 ha of *terra firme* continuous rainforest and is integrated in the Brazilian Long-term Ecological Research Program of the Brazilian National Research Council (Programa de Pesquisas Ecológicas de Longa Duração – PELD/CNPq) and the national Program for Biodiversity Research (PPBio). The climate is humid tropical with two seasons: rainy (November–May), and dry (June–October) (Oliveira et al., 2008). The average annual temperature in the 1990s was 26 °C and precipitation varied between 1750 and 2500 mm (Ribeiro et al., 1999). The reserve has a trail system that forms a 25 km² grid (5 × 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 highly-suited for studies of long-term ecological research (PELD component) (Magnusson et al., 2005, 2014). The grid gives access to 72 permanent plots distributed evenly to each 1 km (Fig. 1). Each plot is 250 m long and follows the relief contour in order to minimize the effects of soil structure and drainage (Magnusson et al., 2005). We sampled 10 permanent plots, separated between 1 and 6 km (Fig. 1).

Bat activity

To record insectivorous-bat foraging activity, we used 11 automatic 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-h recording period per night. Each plot was sampled from four to six consecutive nights, resulting in a total of 53 sampling nights and 636 h of recording during the 2013 rainy season (January–May).

Bat activity was quantified using bat-passes as a unit sample. A bat pass was considered as any 5 s recording where two or more search-phase pulses characteristics of a certain bat species were identified (Oliveira et al., 2015). 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 (López-Baucells et al., 2016), located 60 km north of Ducke Reserve, and also comparing them with available data from the literature (Barataud et al., 2013; Briones-Salas et al., 2013; Jung et al., 2007, 2014). Only search-call pulses with >20 Db intensity greater than background noise were considered. Feeding buzzes and social calls were not included in the analysis. Bat activity was

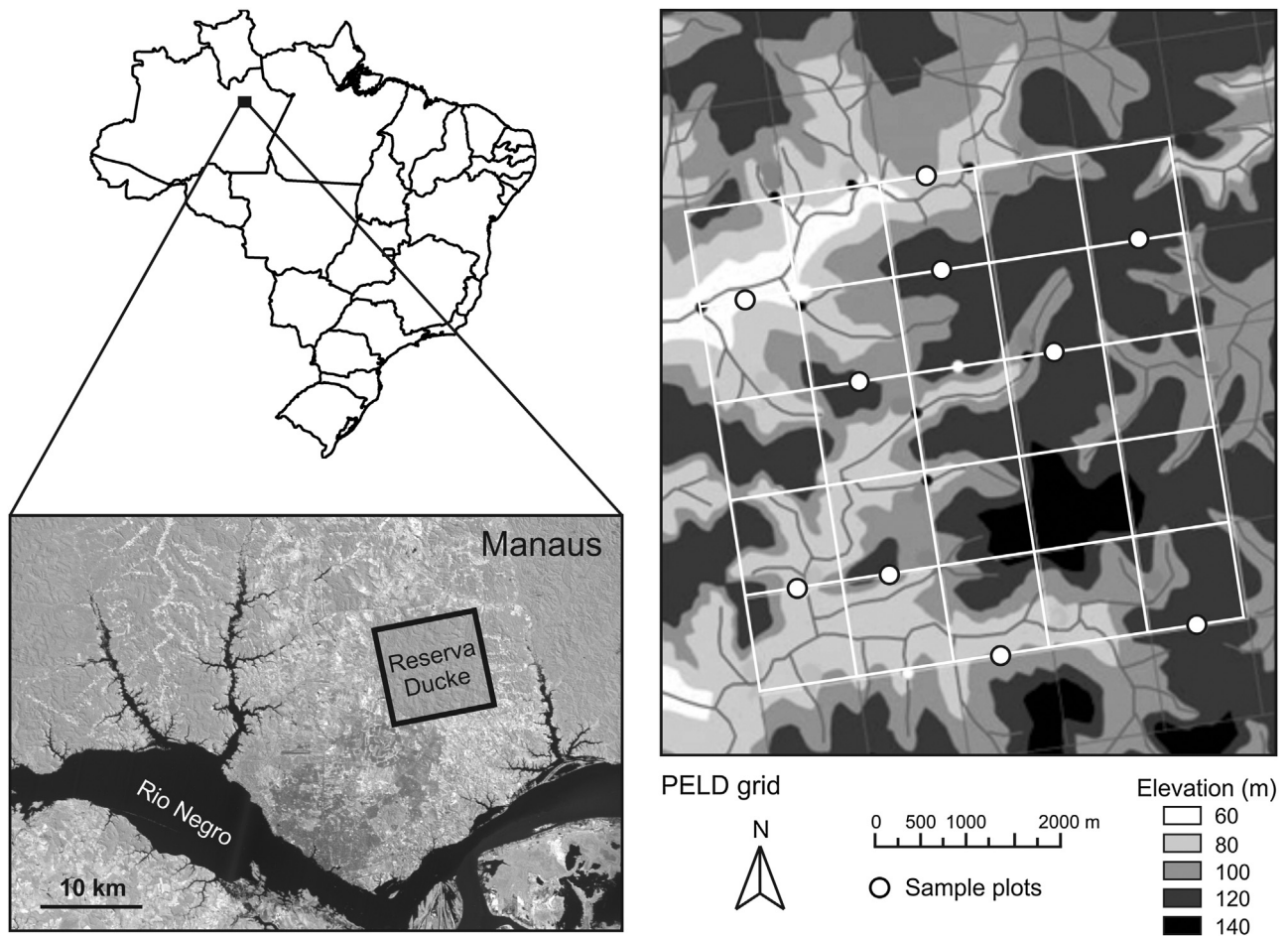


Fig. 1. Ducke Reserve, north of Manaus, Amazonas, Brazil. Distribution of study plots in the RAPELD grid, including topography and streams.

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

To evaluate the influence of moonlight on aerial-insectivorous bat activity (Question 1), we used the percentage of lunar luminosity generated by Moontool 2.0 software, 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 nights that had at least four hours with moonlight and four hours without moonlight (with moonsets and moonrises between 22:00 and 2:00 h respectively). Additionally, completely dark (no moon) and bright nights (moon above horizon all night) were included as controls. Moonrise and moonset hours were retrieved from the Brazilian Astronomic Almanac (Campos, 2013).

Cloudy nights and closed-canopy vegetation 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 Ducke Reserve. 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 min intervals between January and May 2013. Nights were considered ‘cloudy’ when rainfall ranged from 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 analyses (Table S1). We used the percentage of canopy openness to infer the amount of moonlight that can penetrate into the forest. Canopy openness was obtained between November and January 2011 from seven permanent plots sampled in the present study and indicated a low variation in the percentage of canopy openness between plots (mean \pm DP, min-max; $7.63\% \pm 1.07$, 6.13%–9.17%). Because of the low variation between the plots, we assume that the effect on bat activity of moonlight penetration into the forest was similar in the plots we studied.

Bat species

Among the 19 aerial insectivorous-bat species recorded for the Ducke Reserve, 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 met these criteria. The species, in decreasing order of bat-passes, were: *Pteronotus parnellii* (3156), *Saccopteryx bilineata* (2390), *Myotis riparius* (1730), *Cormura brevirostris* (1236), and *Saccopteryx leptura* (564) (Table S2).

Aerial-insectivorous bats show substantial difference in habitat use; *Pteronotus parnellii* is known to forage in cluttered habitats (Emrich et al., 2014; Marinello and Bernard, 2014; Oliveira et al., 2015), *Saccopteryx bilineata* and *Cormura brevirostris* are found over the whole vertical strata of the forest (Bernard, 2001), *Myotis riparius* forages more in open and edge sites (Barclay, 1991), as does *Saccopteryx leptura*, which also flies in open areas (Gardner, 2007).

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) in 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 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 in 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. 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 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 analyses 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 analyses were undertaken 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).

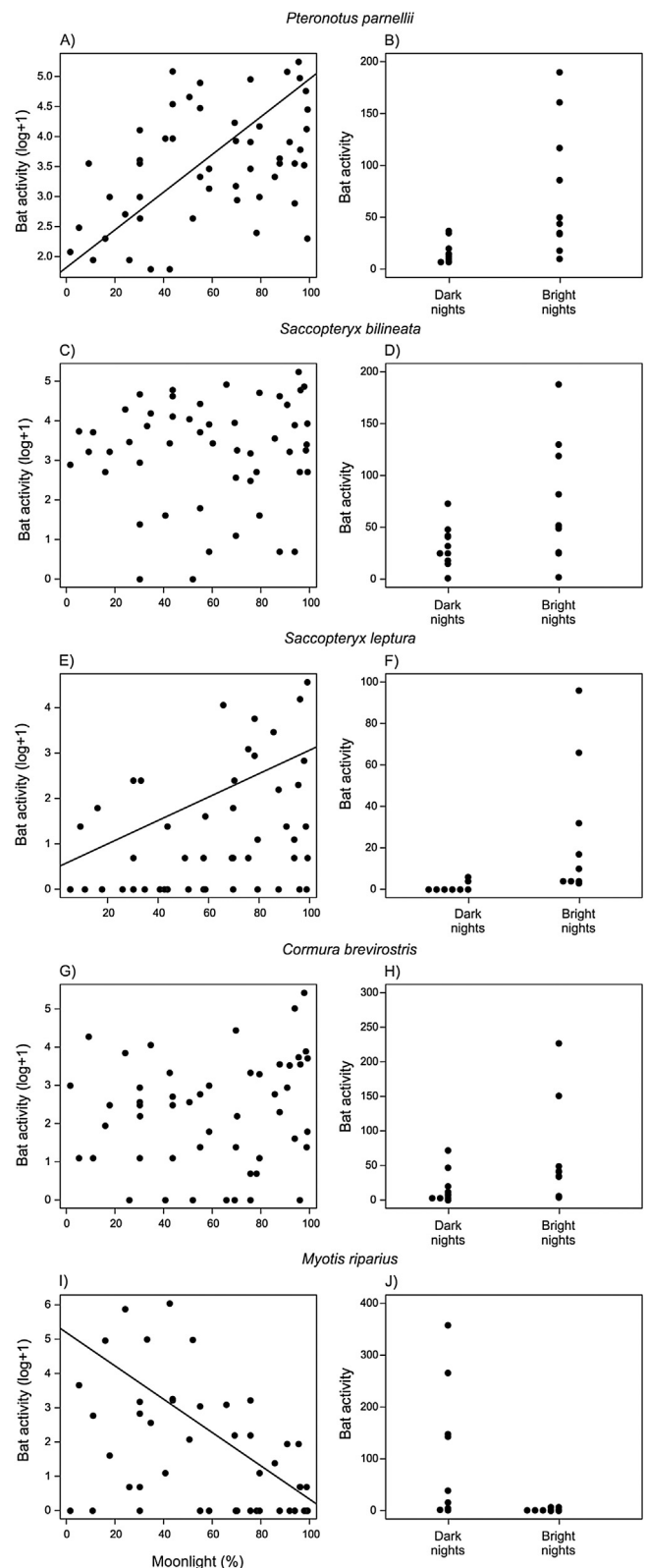


Fig. 2. Relation between aerial activity of five species of insectivorous bats (log-transformed) with the moonlight intensity (%) (A, C, E, G, and I) and difference in bat activity between dark and bright nights (B, D, F, H, and J). Dark nights were considered those with moonlight intensity between 0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

Table 1

Results of Generalized Linear Mixed Models (GLMM) testing the relationships between bat activity and moonlight intensity. Results of Student's *t*-test with the difference in activity between dark and bright nights. Significant values ($P \leq 0.05$) are in bold.

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

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 min after sunset, regardless of moonlight intensity. *Saccopteryx leptura* was the only species with activity restricted to the first 60 min of the night (Table 2).

During 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. brevirostris* occurred a few minutes after sunset, for *M. riparius* around 60 min after, and for *P. parnellii* 120 min 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 min 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 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 (Fig. 4).

When we compared nights with variation in 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

Our results indicate that moonlight intensity influences the foraging activity of the five species of aerial insectivorous bats at different temporal scales. Lunar phobia cannot be generalized to all insectivorous-bat species as this particular behavior only occurred 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 the first study to test lunar phobia at different temporal scales in tropical aerial insectivorous bats.

Contrary to our expectations, two species were more active on moonlit nights. It is well-known that moonlight intensity influences the activity of nocturnal insects (Meyer et al., 2004; Lang et al., 2006). Species of Diptera, Lepidoptera, Coleoptera, and Hemiptera have been recorded flying greater distances on bright nights (Bidleingmayer, 1964; Rydell, 1992; Lorenz 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), and *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* might be strongly influenced by prey availability, which might increase substantially on bright nights.

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 ($P \leq 0.05$) values accompanied with the letter “a” are the highest values.

	Minutes after sunset	<i>Pteronotus parnellii</i>	<i>Saccopteryx bilineata</i>	<i>Saccopteryx leptura</i>	<i>Cormura brevirostris</i>	<i>Myotis riparius</i>
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	

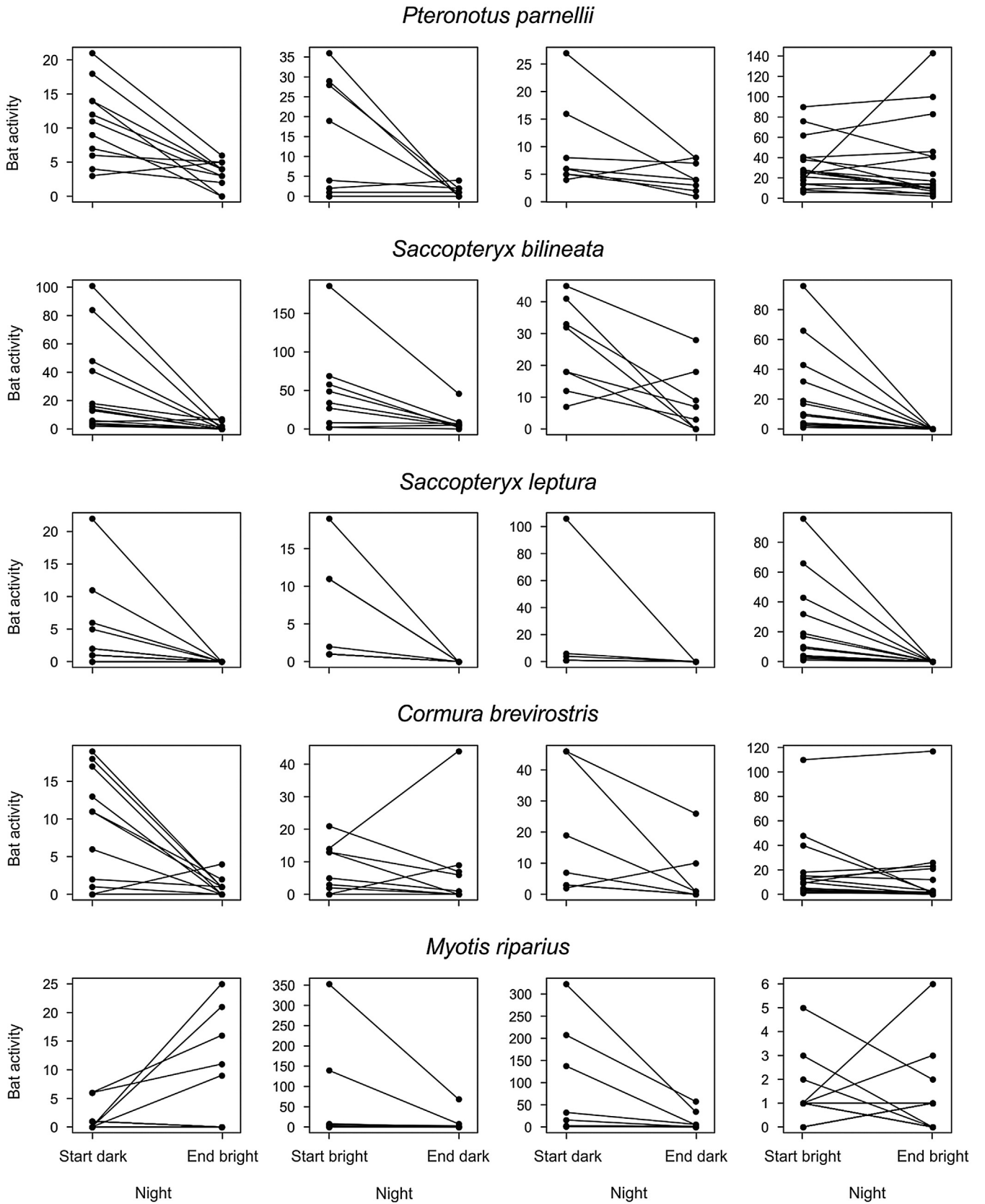


Fig. 4. Nightly aerial activity of five species of insectivorous bats recorded on different types of nights: nights that start dark and end bright (N = 13), nights that start bright and end dark (N = 9), nights entirely bright (N = 18) and nights entirely dark (N = 8).

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 ($P \leq 0.05$) are in bold.

Species	Periods of the night											
	Dark-Bright			Bright-Dark			Dark-Dark			Bright-Bright		
	<i>t</i>	g.l	<i>P</i>	<i>t</i>	g.l	<i>P</i>	<i>t</i>	g.l	<i>P</i>	<i>t</i>	g.l	<i>P</i>
<i>Pteronotus parnellii</i>	-3.74	12	0.002	-2.40	8	0.04	-1.96	7	0.09	-0.06	17	0.95
<i>Saccopteryx bilineata</i>	-2.90	12	0.01	-2.62	8	0.03	-3.16	7	0.01	-2.72	17	0.01
<i>Saccopteryx leptura</i>	-2.30	12	0.03	-2.39	8	0.04	-1.15	6	0.29	-2.90	13	0.01
<i>Cormura brevirostris</i>	-3.27	11	0.007	-0.08	17	0.93	-1.93	6	0.1	-1.32	14	0.2
<i>Myotis riparius</i>	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 bat passes/night (mean \pm standard deviation). Activity values with the same letter do not differ significantly ($P \leq 0.05$) values accompanied with the letter "a" are the highest values.

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

Up to a limit, 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 insects more easily than fast-flying ones (Ciechanowski et al., 2007; Azam et al., 2015). Bat-species characteristics, such as flight speed, body size, and type of foraging habitat, may compromise the abilities of individuals of such species to respond to predator pressure. Slow-flying bat species avoid sites or 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-flying species (Norberg and Rayner, 1987). That *M. riparius* has morphology typical of species with slow maneuverable flight could explain why individuals of this species show 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 (Stone et al., 2009; Azam et al., 2015).

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 microhabitat could switch from open areas to more protected locations 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).

Pteronotus parnellii can undertake long flights between daytime roosts and feeding areas (Goldman et al., 1977; Marinello and Bernard, 2014). This species produces typical long constant-frequency calls that allow it to forage in highly cluttered habitats, i.e. understory forest (Bernard and Fenton, 2003; Denzinger and Schnitzler, 2013; Oliveira et al., 2015), and 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, but on bright nights we observed two peaks of activity. Insect activity peaks might affect 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 the same night, the activity of most of the species we studied 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 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 components (Rolfe and Kurta, 2012; Salinas-Ramos et al., 2015), and moths are 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 molossid (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 vary greatly within the same lunar phase, and different lunar phases can also overlap in moonlight intensity. During the new moon, 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

by moon phases in our study would show only one species being affected by the moonlight, but a finer measure of percentage of moonlight intensity shows that three species responded to light intensity. Consequently, we encourage further studies to use percentage of moonlight intensity instead of moon phases in order to avoid misinterpretations of bat responses.

Bat species response to moonlight intensity is species-specific and highly dependent on the temporal scale considered. However, the explanatory power of the regressions was very low ($R^2 \leq 0.12$; Table 1), indicating that meteorological conditions such as rainfall, humidity, and temperature also may influence the activity of bats between-nights. The effect of the moonlight intensity is more evident at the longer, between-night, time scale. Within a single night, bat activity was higher in the early 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 foraging in different habitats, as well as predation pressure, may influence specific responses to moonlight. Therefore, we recommend that these factors be considered in future studies, and we suggest the inclusion of different habitats, such as open areas, fragments and forest edge, to assess how species that use such habitats respond to moonlight intensity. Also, as our results come from a rainy season, a period of reduced availability of Diptera, Hymenoptera, Formicidae and Homoptera (Guerrero et al., 2003), and the effects of moonlight intensity may differ during the dry season. Because bat species respond differently to changes in moonlight intensity, we recommend that studies on population and community structure of aerial insectivorous bats should be performed throughout the entire lunar cycle in order to include periods of high activity for all bat species.

Acknowledgements

We are grateful to the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), Centro de Estudos Integrados da Biodiversidade Amazônica (INCT-CENBAM), and the Fundação Amazônia de Defesa da Biosfera (FDB) for financing this study. Infrastructure was provided by the Research Program on Biodiversity (PPBio) and the Long Term Ecological Research Program (PELD). GA was supported by a CAPES scholarship, PEDB by the Foundation for Research of the Amazon scholarship (FAPEAM 062.01 173/2015), and AL-B by the Portuguese Foundation for Science and Technology (FCT PD/BD/52597/2014) and a CNPq scholarship (160049/2013-0). WEM received a productivity grant from CNPq. We thank Maria do Socorro R. Silva and Savio José Figueiras Ferreira of Coordenação de Pesquisas do Clima e Recursos Hídricos (CPCR) of INPA for providing climate data of Reserva Ducke and Leonardo Oliveira for the bat recordings in the field. We thank Adrian Barnett for reviewing the English text. We also thank the two anonymous reviewers and the Subject Editor Danilo Russo that helped us improve our manuscript with valuable comments.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2016.11.005>.

References

- Adams, A.M., McGuire, L.P., Hooton, L.A., Fenton, M.B., 2015. How high is high? Using percentile thresholds to identify peak bat activity. *Can. J. Zool.* 93, 307–313. <http://dx.doi.org/10.1139/cjz-2014-0230>.
- Azam, C., Kerbiriou, C., Vernet, A., Julien, J.-F., Bas, Y., Plichard, L., Maratrat, J., Le Viol, I., 2015. Is part-night lighting an effective measure to limit the impacts of

- artificial lighting on bats? *Glob. Change Biol.* 21, 4333–4341. <http://dx.doi.org/10.1111/gcb.13036>.
- Barataud, M., Giosa, S., Leblanc, F., Rufay, V., Disca, T., Tillon, L., Delaval, M., Haquart, A., Dewynter, M., 2013. *Identification et écologie acoustique des chiroptères de Guyane française*. Le Rhinolophe 19, 103–145.
- Barclay, R.M.R., 1991. Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. *J. Anim. Ecol.* 60, 165–178.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2016. Linear mixed-effects models using “Eigen” and S4. R Packag. version 1.1-12.
- Bernard, E., Fenton, M.B., 2003. Bat mobility and roosts in a fragmented landscape in central Amazonia, Brazil. *Biotropica* 35, 262–277.
- Bernard, E., 2001. Vertical stratification of bat communities in primary forests of Central Amazon, Brazil. *J. Trop. Ecol.* 17, 115–126.
- Bidlingmayer, W.L., 1964. The effect of moonlight on the flight activity of mosquitoes. *Ecology* 45, 87–94.
- Bradbury, J.W., Vehrencamp, S.L., 1976. Social organization and foraging in Emballonurid bats: I. Field studies. *Behav. Ecol. Sociobiol.* 1, 337–381.
- Breviglieri, C.P.B., 2011. Influência do dossel na atividade de morcegos (Chiroptera: Phyllostomidae) em três fragmentos no estado de São Paulo. *Chiropt. Neotrop.* 17, 817–825.
- Briónes-Salas, M., Peralta-Pérez, M., García-Luis, M., 2013. Acoustic characterization of new species of bats for the State of Oaxaca, Mexico. *Therya* 4, 15–32. <http://dx.doi.org/10.12933/therya-13-106>.
- Campos, R.A., 2013. *Almanaque Astronômico Brasileiro*. CEAMIG, São Paulo, Brazil.
- Carvalho, W.D., De Freitas, L.N., Freitas, G.P., Luz, J.L., De, L., Costa, M., Esbérard, C.E.L., 2011. Efeito da chuva na captura de morcegos em uma ilha da costa sul do Rio de Janeiro, Brasil. *Chiropt. Neotrop.* 17, 808–816.
- Cichocki, J., Łupicki, D., Bojarski, J., Ważna, A., 2015. The impact of the moon phases on winter activity of the Noctule Bat *Nyctalus noctula*. *Polish J. Ecol.* 63, 616–622. <http://dx.doi.org/10.3161/15052249PJE2015.63.4.014>.
- Ciechanowski, M., Zajac, T., Biłas, A., Dunajski, R., 2007. Spatiotemporal variation in activity of bat species differing in hunting tactics: effects of weather, moonlight, food abundance, and structural clutter. *Can. J. Zool.* 85, 1249–1263. <http://dx.doi.org/10.1139/Z07-090>.
- Denzinger, A., Schnitzler, H.-U., 2013. Bat guilds, a concept to classify the highly diverse foraging and echolocation behaviours of Microchiropteran Bats. *Front. Physiol.* 4, 1–15. <http://dx.doi.org/10.3389/fphys.2013.00164>.
- Digby, A., Towsey, M., Bell, B.D., Teal, P.D., 2014. Temporal and environmental influences on the vocal behaviour of a nocturnal bird. *J. Avian Biol.* 45, 591–599. <http://dx.doi.org/10.1111/jav.00411>.
- Elangovan, V., Marimuthu, G., 2001. Effect of moonlight on the foraging behaviour of a megachiropteran bat *Cynopterus sphinx*. *J. Zool. L.* 347–350.
- Emrich, M.A., Clare, E.L., Symondson, W.O.C., Koenig, S.E., Fenton, M.B., 2014. Resource partitioning by insectivorous bats in Jamaica. *Mol. Ecol.* 23, 3648–3656. <http://dx.doi.org/10.1111/mec.12504>.
- Erkert, H.G., 1982. Ecological aspects of bat activity rhythms. In: Kunz, T.H. (Ed.), *Ecology of Bats*. Springer, Boston, pp. 201–236. <http://dx.doi.org/10.1007/978-1-4613-3421-7>.
- Erkert, H.G., 2000. Bats—flying nocturnal mammals. In: Halle, S., Stenseth, N.S. (Eds.), *Activity Patterns in Small Mammals: An Ecological Approach*. Springer, New York, pp. 212–240.
- Esbérard, C.E.L., 2007. Influência do ciclo lunar na captura de morcegos Phyllostomidae. *Iheringia Ser. Zool.* 97, 81–85.
- Fenton, B.M., Boyle, N.G.H., Harrison, T.M., 1977. Activity patterns, habitat use, and prey selection by some African insectivorous bats. *Biotropica* 9, 73–85.
- Gardner, A.L., 2007. *Mammals of South America. Marsupials, Xenarthrans, Shrews and Bats, volume 1*. University of Chicago Press, Chicago, p. 669.
- Goldman, L.J., Henson, O.W., Henson, O.W.J., 1977. Prey recognition bat and selection: by the Constant Frequency Bat *Pteronotus parnellii*. *Behav. Ecol. Sociobiol.* 2, 411–419.
- Gonsalves, L., Law, B., Webb, C., Monamy, V., 2013. Foraging ranges of insectivorous bats shift relative to changes in mosquito abundance. *PLoS One* 8, e64081. <http://dx.doi.org/10.1371/journal.pone.0064081>.
- Guerrero, J.C.H., Fonseca, C.R.V.da., Hammond, P.M., Stork, N.E., 2003. Seasonal variation of canopy arthropods in Central Amazon. In: Basset, Y., Novotny, V., Miller, S.E., Kitching, R.L. (Eds.), *Seasonal Variation of Canopy Arthropods in Central Amazon*. Cambridge, United Kingdom, pp. 170–175.
- Gutierrez, E.D.A., Pessoa, V.F., Aguiar, L.M.S., Pessoa, D.M., 2014. Effect of light intensity on food detection in captive great fruit-eating bats, *Artibeus lituratus* (Chiroptera: Phyllostomidae). *Behav. Processes* 109, 64–69. <http://dx.doi.org/10.1016/j.beproc.2014.08.003>.
- Haeussler, U., Erkert, H., 1978. Different direct effects of light intensity on the entrained activity rhythm in Neotropical Bats (Chiroptera: Phyllostomidae). *Behav. Processes* 3, 223–239.
- Herd, R.M., 1983. *Pteronotus parnellii*. *Mamm. Species* 209, 1–5.
- Hibbard, F.N., 1925. A short method of determining the time of moonrise and moonset. *Mon. Weather Rev.* 43, 447–448.
- Hickey, M.B.C., Acharya, L., Pennington, S., 1996. Resource partitioning by two species of Vespertilionid bats (*Lasiurus cinereus* and *Lasiurus borealis*) feeding around street lights. *J. Mammal.* 77, 325–334.
- Holland, R.A., Meyer, C.F.J., Kalko, E.K.V., Kays, R., Wikelski, M., 2011. Emergence time and foraging activity in Pallas' Mastiff Bat, *Molossus molossus* (Chiroptera: Molossidae) in relation to sunset/sunrise and phase of the Moon. *Acta Chiropterologica* 13, 399–404. <http://dx.doi.org/10.3161/15081101X624875>.
- Hyndman, R.J., Fan, Y., 1996. Sample quantiles in statistical packages. *Am. Stat.* 50, 361–365.

- Jiang, Y., 2016. Lunar Phase Impact on *Coquillettia perturbans* and *Culex erraticus* Host Seeking in Northern Florida. *Tec Bull. Flo. Mosq. Cont. Assoc. Cilek*, pp. 108–111.
- Jones, G., Rydell, J., 1994. Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philos. Trans. R. Soc. Biol. Sci. B* 346, 445–455.
- Jung, K., Kalko, E.K.V., 2010. Where forest meets urbanization: foraging plasticity of aerial insectivorous bats in an anthropogenically altered environment. *J. Mammal.* 91, 144–153, doi: 10.1644/08-MAMM-A-313R.1.Key.
- Jung, K., Kalko, E.K.V., von Helversen, O., 2007. Echolocation calls in Central American Emballonurid Bats: signal design and call frequency alternation. *J. Zool.* 272, 125–137, <http://dx.doi.org/10.1111/j.1469-7998.2006.00250.x>.
- Jung, K., Molinari, J., Kalko, E.K.V., 2014. Driving factors for the evolution of species-specific echolocation call design in new world free-tailed bats (Molossidae). *PLoS One* 9, e85279, <http://dx.doi.org/10.1371/journal.pone.0085279>.
- Karlsson, B.-L., Eklöf, J., Rydell, J., 2006. No lunar phobia in swarming insectivorous bats (Family Vespertilionidae). *J. Zool.* 256, 473–477, <http://dx.doi.org/10.1017/S0952836902000511>.
- Kramer, K.M., Birney, E.C., Journal, S., May, N., 2001. Effect of light intensity on activity patterns of Patagonian leaf-eared mice, *Phyllotis xanthopygus*. *J. Mammal.* 82, 535–544.
- Kuenzi, A.J., Morrison, M.L., 2003. Temporal patterns of bat activity in Southern Arizona. *J. Wildl. Manage.* 67, 52–64.
- Kuijper, D.P.J., Schut, J., Dulleman, D., Van, Toorman, H., Goossens, N., Ouweland, J., Limpens, H.J.G.A., 2008. Experimental evidence of light disturbance along the commuting routes of pond bats (*Myotis dasycneme*). *Lutra* 51, 37–49.
- López-Baucells, A., Rocha, R., Bobrowiec, P.E.D., Bernard, E., Palmeirim, J., Meyer, C., 2016. Field Guide to Amazonian Bats. Editora INPA, Manaus, 168 p.
- Lang, A.B., Kalko, E.K.V., Römer, H., Bockholdt, C., Dechmann, D.K.N., 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia* 146, 659–666, <http://dx.doi.org/10.1007/s00442-005-0131-3>.
- Lima, S.L., O'Keefe, J.M., 2013. Do predators influence the behaviour of bats? *Biol. Rev. Camb. Philos. Soc.* 88, 626–644, <http://dx.doi.org/10.1111/brv.12021>.
- Magnusson, W.E., Lima, A.P., Luizão, R., Luizão, F., Costa, F.R.C., Castilho, C.V., de, Kinupp, V.F., 2005. Rapeld: a modification of the Gentry method for biodiversity surveys in long-term ecological research. *Biota Neotrop.* 5, 1–6.
- Magnusson, W.E., Lawson, B., Baccaro, F., Volkmer, Carolina Castilho, D., Castley, J.G., Costa, F., Drucker, D.P., Franklin, E., Lima, A.P., Luizão, R., Mendonça, F., Pezzini, F., Schiatti, J., Toledo, J.J., Tourinho, A., Luciano, M.V., Hero, J.-M., 2014. Applied ecology and human dimensions in biological conservation. In: Luciano, M.V., Lyra-Jorge, M.C., Piña, C.I. (Eds.), *Applied Ecology and Human Dimensions in Biological Conservation*. Springer, New York.
- Mancina, C.A., 2008. Effect of moonlight on nocturnal activity of two Cuban nectarivores: the Greater Antillean long-tongued bat (*Monophyllus redmani*) and Poeys's flower bat (*Phyllonycteris poeyi*). *Bat Res. News* 49, 71–80.
- Marinello, M.M., Bernard, E., 2014. Wing morphology of Neotropical bats: a quantitative and qualitative analysis with implications for habitat use. *Can. J. Zool.* 147, 141–147.
- Meeus, J., 1991. *Astronomical Algorithms*. Willmann-Bell, Richmond, Virginia.
- Mello, M.A.R., Kalko, E.K.V., Silva, W.R., 2013. Effects of moonlight on the capturability of frugivorous phyllostomid bats (Chiroptera: Phyllostomidae) at different time scales. *Zoologia* 30, 397–402.
- Meyer, C.F.J., Schwarz, C.J., Fahr, J., 2004. Activity patterns and habitat preferences of insectivorous bats in a West African forest-savanna mosaic. *J. Trop. Ecol.* 20, 397–407, <http://dx.doi.org/10.1017/S0266467404001373>.
- Milne, D.J., Fisher, A., Rainey, I., Pavey, C.R., 2005. Temporal patterns of bats in the top end of the northern territory. *Aust. J. Mammal.* 86, 909–920.
- Morrison, D.W., 1978. Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. *Ecology* 59, 716–723.
- Navarro-Castilla, Á., Barja, I., 2014. Does predation risk, through moon phase and predator cues, modulate food intake, antipredatory and physiological responses in wood mice (*Apodemus sylvaticus*)? *Behav. Ecol. Sociobiol.* 68, 1505–1512, <http://dx.doi.org/10.1007/s00265-014-1759-y>.
- Norberg, A.U.M., Rayner, J.M.V., 1987. Ecological morphology and flight in bats (Mammalia; Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. *Philos. Trans. R. Soc. B: Biol. Sci.* 316, 335–427.
- O'Donnell, C., 2000. Influence of season, habitat, temperature, and invertebrate availability on nocturnal activity of the New Zealand long-tailed bat (*Chalinolobus tuberculatus*). *N. Z. J. Zool.* 27, 207–221, <http://dx.doi.org/10.1080/03014223.2000.9518228>.
- Oliveira, M.L., Baccaro, F.B., Braga-neto, R., Magnusson, W.E., 2008. Reserva Ducke: A Biodiversidade Amazônica através de uma grade. Attema Design Editorial, Manaus.
- Oliveira, L.Q., Marciente, R., Magnusson, W.E., Bobrowiec, P.E.D., 2015. Activity of the insectivorous bat *Pteronotus parnellii* relative to insect resources and vegetation structure. *J. Mammalogy* 96, 1036–1044, <http://dx.doi.org/10.1093/jmammal/gyv108>.
- Penteriani, V., Kuparinen, A., del Mar Delgado, M., Palomares, F., López-Bao, J.V., Fedriani, J.M., Calzada, J., Moreno, S., Villafuerte, R., Campioni, L., Lourenço, R., 2013. Responses of a top and a meso predator and their prey to moon phases. *Oecologia* 173, 753–766, <http://dx.doi.org/10.1007/s00442-013-2651-6>.
- Prugh, L.R., Golden, C.D., 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. *J. Anim. Ecol.* 83, 504–514, <http://dx.doi.org/10.1111/1365-2656.12148>.
- Racey, P.A., Swift, S.M., 1987. Reproductive adaptations of heterothermic bats at the northern borders of their distribution. *South Afr. J. Sci.* 83, 635–638.
- R Core Team: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, 2015, Vienna, Austria.
- Refinetti, R., Menaker, M., 1992. The circadian rhythm of body temperature. *Physiol. Behav.* 51, 613–637.
- Ribeiro, J.E.L.S., Hopkins, M.J.G., Vincentini, A., Sothers, C.A., Costa, M.A.S., Brito, J.M., Souza, M.A.D., Martins, L.H.P., Lohmann, L.G., Assunção, P.A.C.L., Pereira, E.C., Silva, C.F., Mesquita, M.R., Procióp, L.C., 1999. *Flora da Reserva Ducke*. Manaus, Amazonas. Editora INPA, Manaus.
- Riek, A., Körtner, G., Geiser, F., 2010. Thermobiology, energetics and activity patterns of the Eastern tube-nosed bat (*Nyctimene robinsoni*) in the Australian tropics: effect of temperature and lunar cycle. *J. Exp. Biol.* 213, 2557–2564, <http://dx.doi.org/10.1242/jeb.043182>.
- Rolfe, A.K., Kurta, A., 2012. Diet of mormoopid bats on the Caribbean Island of Puerto Rico. *Acta Chiropr.* 14, 369–377, <http://dx.doi.org/10.3161/150811012X661684>.
- Rydell, J., Avenue, T., Jones, U.K.A.G., 1995. Echolocating bats and hearing moths: who are the winners? *Oikos* 73, 419–424.
- Rydell, J., Entwistle, A., Racey, P.A., 1996. Timing of foraging flights of three species of bats in relation to insect activity and predation risk. *Oikos* 76, 243–252.
- Rydell, J., 1991. Seasonal use illuminated of areas by foraging northern bats *Eptesicus nilssonii*. *Holarct. Ecol.* 14, 203–207.
- Rydell, J., 1992. Occurrence of bats in northernmost Sweden (65°N) and their feeding ecology. *J. Zool. L.* 517–529.
- Saldaña-Vázquez, R.A., Munguía-Rosas, M.A., 2013. Lunar phobia in bats and its ecological correlates: a meta-analysis. *Mamm. Biol.* 78, 216–219, <http://dx.doi.org/10.1016/j.mambio.2012.08.004>.
- Salinas-Ramos, V.B., Herrera Montalvo, L.G., León-Regagnon, V., Arrizabalaga-Escudero, A., Clare, E.L., 2015. Dietary overlap and seasonality in three species of mormoopid bats from a tropical dry forest. *Mol. Ecol.* 24, 5296–5307, <http://dx.doi.org/10.1111/mec.13386>.
- Santos-Moreno, A., Velásquez, E.R., Martínez, A.S., 2010. Efecto de la intensidad de la luz lunar y de la velocidad del viento en la actividad de murciélagos filostómidos de Mena Nizanda, Oaxaca, México. *Rev. Mex. Biodivers.* 81, 839–845.
- Smit, B., Boyles, J.G., Brigham, R.M., McKechnie, A.E., 2011. Torpor in dark times: patterns of heterothermy are associated with the lunar cycle in a nocturnal bird. *J. Biol. Rhythms* 26, 241–248, <http://dx.doi.org/10.1177/0748730411402632>.
- Smith, K.W., Reed, J.M., Trevis, B.E., 2011. Nocturnal and diurnal activity patterns and roosting sites of green sandpipers *Tringa ochropus* wintering in southern England. *Ring. Migr.* 19, 315–322, <http://dx.doi.org/10.1080/03078698.1999.9674200>.
- Speakman, J.R., Rydell, J., Webb, P.L., Hayes, J.P., Hays, G.C., Hulbert, I.A.R., Mcdevitt, R.M., 2000. Activity patterns of insectivorous bats and birds in northern Scandinavia (69° N), during continuous midsummer daylight. *Oikos* 88, 75–86.
- Speakman, J.R., 1995. Chiropteran nocturnality. *Oikos* 88, 187–200.
- Stone, E.L., Jones, G., Harris, S., 2009. Street lighting disturbs commuting bats. *Curr. Biol.* 19, 1123–1127, <http://dx.doi.org/10.1016/j.cub.2009.05.058>.
- Tarlow, E.M., Hau, M., Anderson, D.J., Wikelski, M., 2003. Diel changes in plasma melatonin and corticosterone concentrations in tropical Nazca boobies (*Sula granti*) in relation to moon phase and age. *Gen. Comp. Endocrinol.* 133, 297–304, [http://dx.doi.org/10.1016/S0016-6480\(03\)00192-8](http://dx.doi.org/10.1016/S0016-6480(03)00192-8).
- Weinbeer, M., Meyer, C.F.J., 2006. Activity pattern of the trawling phyllostomid bat, *Macrophyllum macrophyllum*, in Panamá. *Biotropica* 38, 69–76.
- Wolfe, L., Summerlint, C.T.A.N., Station, B., Box, P.O., Placid, L., 1989. The influence of lunar light on nocturnal activity of the old-field mouse. *Anim. Behav.* 37, 410–414.
- Yancey, B.F.D., Goetze, J.R., Jones, C., Schreber, S., 1998. *Saccopteryx leptura*. *Mamm. Species* 582, 1–3.
- York, J.E., Young, A.J., Radford, A.N., 2014. Singing in the moonlight: dawn song performance of a diurnal bird varies with lunar phase. *Biol. Lett.* 10, 10–13, <http://dx.doi.org/10.5061/dryad.q2s0s>.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York, USA.