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Original investigation

Aerial insectivorous bat activity in relation to moonlight intensity

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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.

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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-

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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 speciesí 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 km^2 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 pretrigger 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

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