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## Activity levels of bats and katydids in relation to the lunar cycle

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**Abstract** Animals are exposed to many conflicting ecological pressures, and the effect of one may often obscure that of another. A likely example of this is the so-called “lunar phobia” or reduced activity of bats during full moon. The main reason for lunar phobia was thought to be that bats adjust their activity to avoid predators. However, bats can be prey, but many are carnivorous and therefore predators themselves. Thus, they are likely to be influenced by prey availability as well as predation risk. We investigated the activity patterns of the perch-hunting *Lophostoma silvicolum* and one of its main types of prey, katydids, to assess the influence of the former during different phases of the lunar cycle on a gleaning insectivorous bat. To avoid sampling bias, we used sound recordings and two different capture methods for the katydids, as well as video monitoring and radio-telemetry for the bats. Both, bats and katydids were significantly more active during the dark periods associated with new moon compared to bright periods around the full moon. We conclude that foraging activity of *L. silvicolum* is probably influenced by prey

availability to a large extent and argue that generally the causes of lunar phobia are species-specific.

**Keywords** Lunar phobia · Moonlight · Activity patterns · Predator · Prey

### Introduction

Many nocturnally active animals alter their behavior and activity with changing light conditions in connection with the lunar cycle. In most cases two major selective forces explain these responses; either change in predation risk or in prey availability. However, the moon phase can affect animals differently depending on whether they are predators, prey, or both. Visually orienting nocturnally active predators may benefit from bright moonlight because their prey is easier to detect. This, in turn, would cause prey to adopt a more cryptic lifestyle through reduction in activity. This assertion is supported by observations of kangaroo rats (e.g. *Dipodomys spectabilis*), which forage less during bright moon phases, presumably to avoid visually hunting owls (Daly et al. 1992; Lockard 1978). Neotropical male tree frogs (*Smilisca sila*) exhibit the opposite response as they tend to call from less concealed sites during bright nights, when they can see their main predator, the bat *Trachops cirrhosus* approaching (Tuttle and Ryan 1982). Sometimes the presumed reaction of an animal to moon phase, may really be the indirect effect of light conditions on its prey. For example, foraging depth of Galapagos fur seals (*Arctocephalus galapagoensis*) is mediated by horizontal migration of fish and squid (Horning and Trillmich 1999).

It is important to distinguish between the effects of predation pressure and prey availability to determine the reasons for lunar phobia. It is mostly neglected that animals are often both predator and prey at the same time. In our study, we focused on a bat and one of its main groups of prey organisms, katydids, to assess the impact of the moon phase on bats in their role as pre-

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dators, while in the past the moon phase was assumed to affect bats acting as prey (e.g. Morrison 1978).

Bats (Chiroptera), which constitute the second-largest mammalian order, are almost exclusively nocturnal, occupy a diversity of habitat types, and exploit a variety of prey (Altringham 1996; Kalko et al. 1996). They present a useful model system to evaluate the reactions of different species to the lunar cycle. Erkert (1974, 1978) and Haeussler and Erkert (1978) were among the first to report reduced activity by bats during the bright nights around full moon. Morrison (1978) reported similar trends in the Neotropical fruit bat *Artibeus jamaicensis*. He hypothesized that this behavior occurred mainly in response to increased predation pressure resulting from better visibility of the bats to their main predators, owls and snakes, and introduced the term “lunar phobia”. Since then, predator avoidance has typically been assumed to be the main cause for lunar phobia in bats. If this were true, most bats should exhibit lunar phobia. Indeed, lunar phobia is also found in other bats, such as the sympatric canopy frugivores *A. lituratus*, (Erkert 1978; Morrison 1978), and *Vampyroides caraccioli* (Morrison 1978), the omnivorous *Phyllostomus hastatus* (Erkert 1974), the sanguivorous *Desmodus rotundus* (Flores-Crespo et al. 1972), the gleaning insectivorous *Lophostoma silvicolum* (Bockholdt 1998) and the gleaning insectivorous/carnivorous *T. cirrhosus* (Haemisch 1998). Studies on island population of bats, which are less exposed to predation and where no relationship between activity and moonlight was found, also support the hypothesis that predation pressure influences behavior patterns (Gannon and Willig 1997; Rodriguez-Duran and Vazquez 2001). By contrast, results for species of the frugivorous genus *Carollia* varied from study to study and no clear relation was found between levels of moonlight and activity (Fleming and Heithaus 1986; Heithaus and Fleming 1978; Thies and Kalko 2004).

Similarly, in the temperate zone, associations between bat activity levels and moonlight remain unclear. Some studies suggest that insectivorous bats change foraging habitats in concert with moon phase (Hecker and Brigham 1999; Reith 1982), while several others found no correlation between light levels and activity patterns (Karlsson et al. 2002; Negraeff and Brigham 1995; Waiping and Fenton 1988).

Mainly anecdotal information is available about the rate and impact of predation on bats (e.g. Fenton et al. 1994; Morrison and Handley 1991; Speakman 1991). As predation on bats is difficult to assess, a focus on prey availability might help to distinguish between different selective pressures. However, the detailed evaluation of prey availability is also difficult and quantitative studies are still lacking.

Insects are the major prey of most bat species and changes in the activity level of insects should also influence foraging behavior and activity level of bats. However, in spite of some early studies suggesting a strong influence of the moon phase on insect activity (e.g. Williams and Singh 1951), those effects are still

poorly understood and remain controversial. Based on the data from suction traps, Williams et al. (1956) found no evidence of a connection between lunar cycle and numbers of insects in Britain. In contrast, Brown and Taylor (1971), applied the same method and reported species-specific fluctuations of up to three-fold in distribution and abundance of insects in East Africa. When nocturnal insects are captured with light traps, there is often distinct periodicity, with low catches at or around full moon and high catches during new moon. This is true for insects in the tropics (Meyer et al. 2004; Pagden 1932) and in the temperate zone (Williams 1936, 1940). Yet, these results may at least partly result from a bias due to method, as the efficiency of light traps at full moon is likely reduced due to the brighter environment (Williams et al. 1956).

The purpose of our study was to evaluate moonlight-dependent behavior in a predator-prey system. The model predator was the Neotropical insectivorous bat *L. silvicolum* (Phyllostomidae, Chiroptera; formerly *Tonatia silvicola*, Lee et al. 2002). This species is the most commonly caught gleaning insectivore in the understorey of the lowland forests along the Panama Canal and especially on Barro Colorado Island (Kalko et al. 1996). *L. silvicolum* is mainly a perch hunter (Kalko et al. 1999; Servatius 1997). This means it listens for sounds generated by prey, which are then caught in short sally flights and consumed after returning to a perch. Katydid (Tettigoniidae, Orthoptera) constitute the major prey of this bat, as well as of many other vertebrate and invertebrate predators in tropical rainforests (Belwood 1988; Nickle 1992). Most male katydids produce mating (advertisement) calls in the higher audible, and lower ultrasonic frequency range. These calls also serve as acoustic cues for gleaning insectivorous bats to localize and capture them (Belwood and Morris 1987; Servatius 1997). Bright nights around full moon are thought to offer favorable conditions for visually orienting predators other than bats (for example insects, Daly et al. 1992; or rodents, Lockard 1978). In response, insects may remain inactive and acoustically silent, to reduce conspicuousness. Our preliminary observations suggested a strong reduction of nocturnal activity of katydids with increasing brightness of the nights before and after full moon. Thus, we predicted that lunar phobia of *L. silvicolum* was at least partially caused by reduced prey availability, and this implies that the latter may be at least as important as predation risk for this species.

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## Methods

### Study site and study period

The study was conducted on Barro Colorado Island (BCI), a field station of the Smithsonian Tropical Research Institute in Panama. The 1,500-ha island is located in Gatun Lake bordering the Panama Canal in

central Panama (09°10'N, 79°51'W). BCI is mostly covered with secondary and primary semi-deciduous lowland tropical forest that varies in age from 80 years to 600 years (Leigh 1999). Rainfall averages 2,600 mm per year, about 90% of which falls during the rainy season from May to December (Windsor 1990). Data collection took place over a period of 18 months between 1997 and 2003 encompassing four dry and four rainy seasons. Data on the lunar cycle were taken from the website of the US Naval Observatory (USNO).

#### Katydid activity

We used three methods to measure katydid activity. First, katydids were collected at a total of eight mercury-vapor lights outside four laboratory buildings on BCI next to the forest in November/December 1999 and April 2001, covering nearly two complete lunar cycles. We systematically counted katydids twice each night, at 21:00 h and 24:00 h and collected them for determination of species and gender.

Second, we caught flying katydids in mist nets. Although mist nets were employed to catch bats, they also represented an obstacle for large flying insects. As part of another project on the BCI bat community by CD Weise from September 2001 to July 2002, twenty mist nets (12×2.6 m) were checked hourly from sunset to sunrise, and all katydids caught in the nets were collected, counted and identified. Mist nets were set on two consecutive nights three times each month, and the phase of the moon was noted. The lunar cycle was divided into four periods according to the percentage of the lunar disk illuminated: 0–25% (new moon), 26–50%, 51–75% and 76–100% (full moon). We netted bats during 12 nights when the percentage was 0–25%, four nights with 26–50%, eight with 51–75% and four nights with 76–100%.

Third, we quantified singing insects, the major source of noise at night, using acoustic monitoring. Singing is correlated with general activity, such as feeding, walking or flying, and should be a direct indicator of predator avoidance behavior (Lang et al. 2005). Noise-levels were recorded from late October to early December 2001, as well as in February, May and June 2002. All recordings were made at the same site in the hunting area of our bats, with the microphone directed at the understorey and lower canopy. Recordings of each 24-h period were later averaged over 2-min intervals with a custom written computer program. We calculated an average sound pressure level for the 5-h time period between 22:00 h and 03:00 h, to compare nights between moon phases. Average values are given in dB SPL (sound pressure level) ± SE. The recording system consisted of a sound level meter (CEL 414 with attached CEL-296 digital filter-settings: A&LIN-weighting; slow time constant; Casella, UK) with a calibrated condenser microphone (LD2540, Type 4133, range 4 Hz–40 kHz; Larson Davis, USA). The setup was protected from rain by an

umbrella and heated 2°C above ambient temperature with an infrared bulb to prevent humidity from fogging the microphone membrane. The DC-output of the sound level meter was monitored at intervals of 5 s for 24 h a day with a Maclab/Powerlab 4E data acquisition system (AD Instruments Pty Ltd, Australia) connected to a portable computer (PCG-F707, Sony Europe). We recorded rainfall events and excluded data from the affected time periods in the data analysis (weather data available from the STRI website <http://www.stri.org>).

#### Bat flight activity

We radio-tracked adult, nonreproductive *L. silvicolum*; captured in mist nets; between March 1997 and June 1997 to assess bat activity. Bats were weighed to the nearest 0.5 g using a 100 g Pesola spring scale. We glued transmitters with position sensors (BD-2GP, Holohil Systems, Canada) to the back of six adult male bats with surgical adhesive (Skin-Bond, Smith and Nephew, USA). The 1.5 g transmitters weighed 4.2–5.1% of the bats' mass, and were near the 5% threshold, above which transmitter mass may influence on flight performance (Aldridge and Brigham 1988). Position sensors cause transmitters to increase signal pulse frequency when a bat is horizontal (=flying) instead of vertical (=hanging) and thus allow quantification of activity.

Starting the night after the transmitter had been attached, we tracked a single individual at a time using a five-element YAGI-antenna (Wildlife Materials, USA) connected to YAESU FT26-receivers (Wagner, Germany). Two observers remained in radio contact and took simultaneous bearings every 6 min (for method see Weinbeer and Kalko 2004). We first followed bats throughout one to three full nights (18:00–06:30 h) with the exception of one bat, which was only tracked during half nights. Afterwards, when home range size did not increase anymore, we alternated regularly between the first (ca. 18:00–24:00 h) and second half (ca. 24:00–06:30 h) of nights. Civil twilight, when the sun is six degrees below the horizon, began about 20 min before sunrise, and ended about 20 min after sunset. Time of sunset and sunrise varied by only 2 min during our study period (United States Naval Observatory), allowing us to consider all nights to be of equal length.

We checked every minute whether the tagged bat was flying or stationary to assess activity using signal frequency. For flights lasting less than 1 min, we counted the number of pulses of the transmitter signal. We calculated total flight activity of *L. silvicolum*, by dividing nights into 30-min intervals. For every interval, we calculated number and duration of flights. We roughly categorized activity in the following way: bats were classified as inactive when the number of flights was two or less per interval, medium activity described intervals with three to ten flights, and high activity intervals consisted of more than ten flights within a 30-min period.

## Bat roosting behavior

*Lophostoma silvicolom* excavates active termite nests and uses them as roosts (Dechmann et al. 2004; Kalko et al. 1999). The bats used the same roosts as day- and nighttime shelter and returned to them between foraging bouts, enabling us to quantify nocturnal resting activity by infrared video monitoring at the roost. Video recordings were made in two termite nest roosts during five lunar periods between June 2002 and June 2003. A CCD Camera (IR-CCD VK-121, Eneo; lens AO8Z1-5NDDCI, 8/8–120 mm, Eneo, Germany) with a custom-built infrared illumination system was placed at least 2-m below the entrance to the roost. We filmed cavities from 18:00 h to 06:00 h and recorded the video signal on a Sony Video walkman (GV-D1000 Portable DVCR Digital Video, Sony Europe). All captured *L. silvicolom* on BCI were marked with subcutaneous passive transponders since 2001 (PIT tags, ID 100, Trovan, UK). We used a self-made antenna, installed around the cavity entrance, to identify exits and entries by marked bats based on their individual transponder code. The setup included an antenna amplifier, reader, and data logger (EUR 3200, EUR 4100-24, EUR 5060, Euro I.D. Identifikationsysteme, Germany). Exit and entry times and the identity of all bats on the videos were also recorded.

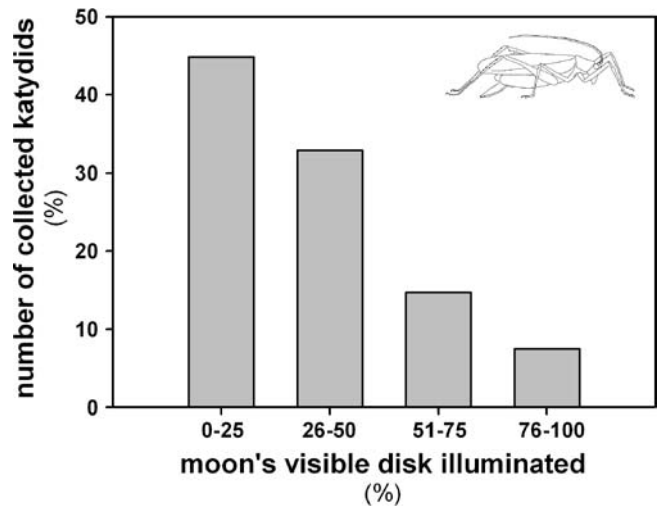
## Statistical analyses

We predicted that bats and katydids would react only to the amount of light in the forest, rather than the moon-phase as such and consequently we pooled data from the waxing and the waning period. We used “percentage of visible disc illuminated” as an index to light levels (Brigham and Barclay 1992; Mills 1986). All bat activity data were log-transformed before analysis. Each dataset (number of katydids collected at lights, number of katydids caught in nets, minutes after sunset of bat’s emergence, average bat activity and flight time per night and time spent in roost) was analyzed using Spearman’s correlations with the percentage of visible disc of the moon illuminated during the corresponding night. All data were tested with two-tailed Spearman correlations, two-tailed *t* tests or a One-Way RM ANOVA (SPSS 11, SPSS Inc., Chicago, USA) assuming an alpha level of 0.05.

## Results

### Katydid activity

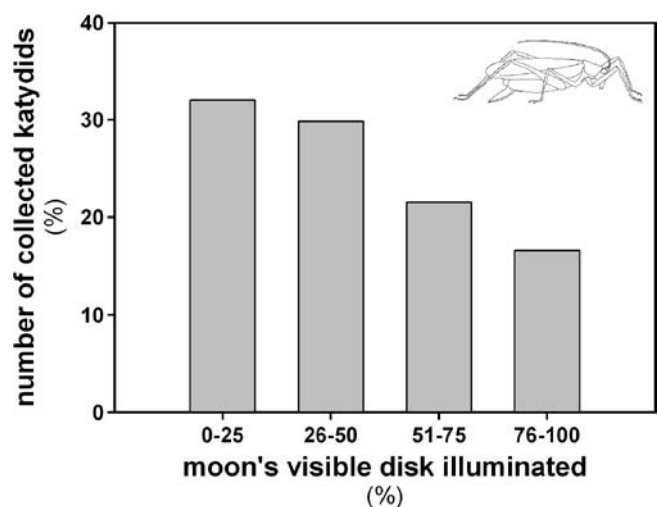
Katydids were collected at lights during 43 nights. There was a highly significant relationship ( $r_s = -0.812$ ,  $P < 0.001$ ) between the percentage disk illuminated and the number of katydids collected (Fig. 1). Around new moon, we collected up to 38 katydids per night, while



**Fig. 1** Capture rates of katydids at laboratory lights. Results corrected for number of nights of each moon phase (number of nights: 0–25%,  $n = 20$ ; 26–50%,  $n = 7$ ; 51–75%,  $n = 6$ ; 76–100%,  $n = 10$ )

the nightly number of katydids dropped to as few as two during full moon.

Our data on katydids captured in nets revealed the same pattern as the collection at laboratory lights (number of nights = 57,  $r_s = -0.489$ ,  $P < 0.001$ ; maximum of katydids/night = 11, total = 176; Fig. 2). We caught 62% of all katydids during dark nights around new moon and before half moon. By contrast, the number of captures decreased to 22% in the brighter period after half moon and only 17% were caught around full moon. Values were corrected for number of nights in each moon phase. The percentage of the moon’s visible disk illuminated and the number of ka-



**Fig. 2** Capture rates of katydids in mist-nets during different moon phases. Results corrected for number of nights of each moon phase (number of nights: 0–25%,  $n = 21$ ; 26–50%,  $n = 18$ ; 51–75%,  $n = 14$ ; 76–100%,  $n = 4$ )

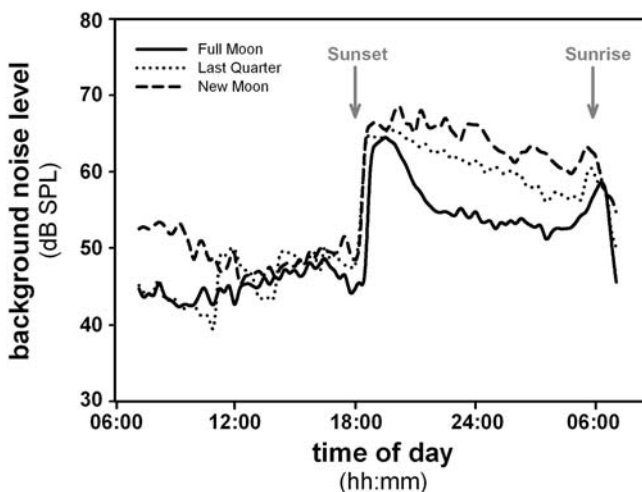
tydids captured in mist nets were significantly correlated ( $r_s = -0.489$ ,  $P < 0.001$ ).

Finally, our measurements of background noise level in the rainforest understorey revealed distinct differences between moon phases (see Fig. 3 for subset of data). During daylight, average background noise level varied between 30 dB and 50 dB SPL ( $\bar{x} = 40.9 \pm 5.6$  dB SPL,  $n = 62$ ). All recordings indicated a 20-dB peak at sunset. This strong increase in sound levels at the beginning of each night is at least partially caused by crickets and frogs (unpublished data; S. Rand, personal communication). During nights near full moon, noise level decreased immediately after the initial peak at 60 dB ( $\bar{x} = 60.6 \pm 2.6$  dB SPL,  $n = 62$ ), and remained low (about 10 dB above daytime level;  $\bar{x} = 50.7 \pm 4.8$  dB SPL,  $n = 62$ ) until dawn. In contrast, around new moon and during the first/last quarter of the lunar cycle, noise levels declined more slowly throughout the night. There was a decrease by about 10 dB after a second smaller peak at sunrise, for which awakening birds and monkeys are responsible (unpublished data). The best time to observe differences in orthopteran activity between moon phases is from 21:00 h until 05:00 h (Riede 1997). During this time period, singing katydids are the main source of noise, and in our study noise levels differed cyclically by about 10 dB depending on the moon phase. No published data are available for moon light levels in the understorey between the different moon phases. However, preliminary experiments with highly sensitive light sensors showed only a negligible effect of cloud cover compared to the high differences in light levels due to the moon phase (up to 10,000 times; unpublished data; see also Erkert 1974; Munz and McFarland 1977) between full and new moon nights. The percentage of the moon's visible disk illuminated was significantly correlated with average sound pressure

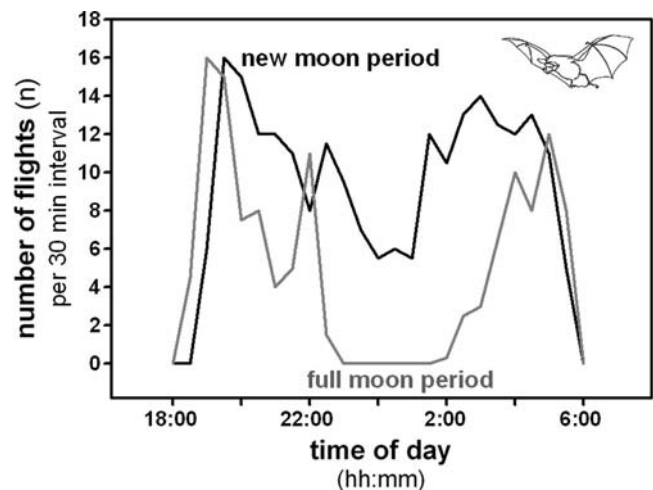
level for each night (5 h average over the time period from 22:00 h to 03:00 h; November 2001:  $n = 13$  nights,  $r_s = 0.848$ ,  $P < 0.001$ ; March 2002:  $n = 16$  nights,  $r_s = 0.971$ ,  $P < 0.001$ ). Only male individuals sing and were recorded in this dataset, while we captured equal numbers of males and females with the other two methods (data not shown).

#### Bat flight activity

We tracked six adult male *L. silvicolum* for a total of 14,100 min over 39 nights. Time of contact ranged between 66% and 90% ( $78.3 \pm 10.3\%$  on average) of total tracking time. *L. silvicolum* performed both, long (> 1 min) and short (< 1 min) flights, but flights shorter than one min clearly prevailed ( $98.5 \pm 0.9\%$ ) adding supporting evidence to the placement of this species as a passive listening perch hunter as suggested by Kalko et al. (1999). The number of short flights may have been slightly overestimated, as whenever bats briefly left reception range, this was recorded as the end of the respective flight event even though the bat may have kept flying. However, as overall contact time with all of the tagged animals was high, this is negligible. Longer flights had a maximum duration of 4 min. Total cumulative flight time for each individual during one night ranged between 20 min and 40 min ( $28.0 \pm 8.7$  min). There were no significant differences in flight activity (cumulative flight time) of bats between the two halves of the night ( $t = 1.3$ ,  $df = 16$ ,  $P = 0.21$ ). Bats remained active during the entire night around new, but not around full moon ( $F = 10.319$ ,  $df = 1$ ,  $P = 0.04$ ,  $n = 48$ ; Fig. 4), and the mean time spent flying was significantly correlated with percentage of the moon's visible disc ( $r_s = -0.407$ ,  $n = 30$ ,  $P = 0.035$ ).



**Fig. 3** Background noise level over different moon phases. Measurements of background noise level in the rainforest on BCI averaged over 24 h for a subsample of four nights during each full moon, last quarter, and new moon, in November 2001 and March 2002



**Fig. 4** Number of flights per 30-min interval of one *L. silvicolum* during six full moon and one *L. silvicolum* during six new moon nights

Number of flights per 30-min interval varied from none to 18 ( $\bar{x} = 6.4 \pm 1.8$ .) Near new moon, the bats exhibited high activity for 64% and medium activity for 36% of the night. In contrast, during full moon *L. silvicolom* was highly active only for 22% of the night while medium activity occurred during 44% of the night, and 34% of the night were spent inactive. We recorded an activity peak at the beginning of the night under all light conditions. The timing of this peak shifted with emergence time. During the 28 nights, when we recorded time of emergence, radio-tagged bats left their roosts 16–65 min after sunset ( $42.9 \pm 14.3$  min). Around full moon, bats emerged from their roost about 30 min earlier than around new moon ( $r_s = -0.775$ ,  $P < 0.001$ ; Fig. 4). After 22:00 h, tagged bats typically returned to their day roosts for periods ranging from a few minutes to several hours. Another peak of activity was observed just before sunrise. There was no flight activity at all between 23:00 h and 02:00 h during the full moon period. During all moon phases, all bats returned to their day roost before sunrise. Compared to emergence, time of return was more variable, the bats returned to the termite roosts between 431 min and 702 min after sunset (mean =  $646 \pm 72$  min,  $n = 17$ ). This translates to periods of a few minutes up to 4.5 h before sunrise.

#### Bat roosting behavior

Our video recordings revealed that bats ( $n = 18$  individuals) spent significantly more time in their roosts around full moon than around new moon ( $t = -8.24$ ,  $df = 16$ ,  $P < 0.001$ ). During bright nights around full moon, individual *L. silvicolom* spent up to 72% of the nights (mean =  $453 \pm 67$  min,  $n = 8$ ) in the roost. In contrast, only 28% of the nights were spent roosting in dark nights around new moon (mean =  $203 \pm 62$  min,  $n = 10$ ). Absence of bats from the roost coincided with the bimodal flight activity pattern observed in the telemetry study. All members of a roosting group typically returned to the roost for an extended period around midnight regardless of the moon phase. Our video observations, which in contrast to the telemetry, included members of both sexes, confirmed that females also reduced flight activity during full moon.

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#### Discussion

We combined several measurement methods of katydid activity and foraging activity of a bat, to assess changes in behavior of predators and prey in the context of the lunar cycle (Belwood 1988). We found a significant correlation between the prevailing moon phase and katydid flying and singing activity, time of emergence of bats, as well as the time bats spent foraging and roosting each night. While both bats and katydids were active throughout the nights around new moon, activity

decreased significantly during the brightest nights of the month.

Bright nights during full moon should favor visually orienting predators, compared to predators relying on other senses, when hunting the same prey. Between full and new moon, light intensity may vary by 3–4 orders of magnitude (Erkert 1974; Munz and McFarland 1977), and full moon ambient light levels in the understorey of BCI are high enough for dark adapted humans to orient themselves. It is likely that these light conditions favor a variety of visually orienting insectivorous predators (e.g. rodents or owls) and force many of their prey species, including katydids, to adopt a cryptic lifestyle. This may further restrict overall activity of those animals, which, like katydids, are thought to be nocturnal to avoid high diurnal predation pressure for example by birds and monkeys (Nickle and Heymann 1996). Gleaning insectivorous bats, such as *L. silvicolom*, which rely mainly on passive acoustic cues to find prey (Schnitzler and Kalko 2001) are likely indirectly affected by the lunar cycle due to its effect on prey behavior and activity.

Katydid were more active during dark periods of the lunar cycle as evidenced by captures at lights and in mist nets as well as by recordings of noise levels. Changes in katydid abundance at lights coincided with strong long-term fluctuations in background noise level. Orthopterans are the most speciose group of sound producing insects in tropical lowland forests and are assumed to be responsible for the majority of nocturnal background noise (Riede 1997). Thus background noise is well suited for a method-independent assessment of katydid activity. Direct support for this comes from a study on the Neotropical *Docidocercus gigliotosi*. This species is more active and communicates mainly by singing during new moon nights. Near full moon, it moves less, avoids moonlit spots, and signals predominantly by tremulation (Lang et al. 2005). Consequently, bats such as *L. silvicolom* searching for katydids by passive listening (Belwood 1988; Kalko et al. 1999) would be much less efficient around full moon. This hypothesis is corroborated by our telemetry results, which showed a significant decrease of bat activity with increasing light intensity.

The two peaks in bat activity at the beginning and end of the night during full moon occur at the same time as the peaks in background noise level and thus probably prey availability (Fig. 4). Full moon nights are darkest just after sunset and before sunrise when the moon is close to the horizon and light hits the forest at a narrow angle. One would expect these to be the parts of nights near full moon, when insect calling and flight activity is highest. Many predators, which prey on bats, also hunt early in the evening, often catching their prey when emerging from the roost (e.g. Fenton et al. 1994). This prompts the question of why a bat would become active earlier around full moon, well within the civil twilight period, if lunar phobia is

a reaction to predation pressure. *L. silvicolum* use individual foraging areas, which are reached by commuting for several minutes. Early emergence may allow bats to be in their foraging areas at the beginning of the night, coinciding with the short increase in activity and thus presumably availability of insects. An assessment of the effect of cloud cover on bat and katydid activity would also be interesting in this context. Studies addressing this topic were so far mainly conducted on aerial insectivorous bats in the temperate zone and found no change in activity with increasing cloud cover (e.g. Negraeff and Brigham 1995; Russo and Jones 2003).

What is the relevance of our findings to other species or feeding guilds of bats? We argue that frugivorous species face a different situation from the understory gleaner *L. silvicolum*. A rich supply of food like a fruiting fig tree in the open canopy attracts high numbers of bats ("big bang" strategy), making them a predictable food source for predators, but only for a short period of time. In contrast, understory plants such as *Piper*, attract few bats, but over a longer time period ("steady state" strategy; see also Korine et al. 2000; Thies and Kalko 2004), making it less favorable for a predator to wait near them. Similarly, many nocturnal insects such as katydids are probably evenly spread throughout the forest, and the bats, which prey on them, should also be evenly dispersed, rendering them unpredictable for their own predators. In addition, it is difficult for aerial predators to hunt flying bats in the dense undergrowth. In summary, bat species flying and foraging in the canopy of tropical forests are presumably more likely to be exposed to predation than bats using the understory.

Our results indicate that while predation pressure cannot be fully excluded as a selective force, activity of *L. silvicolum* is strongly correlated with the behavior of prey in connection with the lunar cycle. The influence of lunar cycle on various aspects in the behavior of animals is probably more species-specific than previously suggested. Most importantly, moon related activity could be caused by several, potentially contradictory, ecological pressures.

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