Activity patterns and habitat preferences of insectivorous bats in a West African forest–savanna mosaic

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Abstract: We studied activity patterns and habitat use by insectivorous bats in Comoé National Park, Ivory Coast. Bat foraging activity was quantified along five transects representing three different habitat types using acoustic monitoring and captures with mist nets and harp traps. Aerial insect abundance was assessed using a light trap; in addition shrub and tree arthropods were sampled. Bat activity was significantly and positively related to insect availability and ambient temperature, whereas increased visibility of the moon had a negative influence on flight activity. Together, these factors best explained both total bat activity and activity of bats hunting in open space and edge habitats. The interaction between temperature and light intensity was the best predictor of activity by species foraging in obstacle-rich forest habitats, however, the regression model had a low predictive value. Overall, a large proportion (*c.* 50%) of the variation in bat activity appeared to be a consequence of transect- and/or habitat-specific influences. We found a significant non-linear relationship between the activity of QCF (quasi-constant frequency) and FM–QCF (frequency modulated – quasi-constant frequency) bats and the phase of the moon, with lowest levels of activity occurring near full moon. We interpret this lunar-phobic behaviour as a reflection of a higher predation risk during moonlit periods. For FM (steep frequency modulated) and CF (constant frequency) bats, no significant correlation was found, although there was a trend suggesting that these bats at least were not negatively affected by bright moonlight. Foraging activity of bats was positively correlated with the abundance of atympanate moths; however, no such correlation was found for tympanate moths.

Key Words: abiotic factors, activity patterns, Chiroptera, Côte d'Ivoire, guilds, habitat heterogeneity, habitat use, insect abundance, Ivory Coast, moonlight, predation pressure

INTRODUCTION

Nearly all insect-eating bats are nocturnal although several studies have shown that most aerial insects, at least in the northern temperate zone, are predominantly active during the day (Lewis & Taylor 1965, Rydell *et al.* 1996, Speakman 1995). However, there are marked differences both within and between bat species with respect to the timing of their foraging flights, perhaps reflecting spatio-temporal variation in the availability of the preferred prey categories. Thus, aerial insectivores should time their foraging flights according to the maximum nocturnal flight activity of their main prey. Studies in northern Europe have demonstrated that light-dependent predation risk by visually orienting predators

such as raptorial birds could be a major constraint preventing bats from foraging during periods with maximum prey abundance (Rydell *et al.* 1996, Speakman *et al.* 2000). Hence, the actual emergence time of bats from their roosts appears to constitute a trade-off between prey availability and predation risk (Jones & Rydell 1994), sometimes compromised by variations in energetic demand (Duvergé *et al.* 2000) and seasonal fluctuations in insect abundance (Rautenbach *et al.* 1988).

Numerous studies have documented two nocturnal peaks of insect activity, one shortly after dusk and another near dawn (Rautenbach *et al.* 1988, Rydell *et al.* 1996). Several environmental factors such as temperature, humidity, and moonlight have been reported to affect the flight activities of insects (Lewis & Taylor 1965, Taylor 1963, Williams 1961) and can therefore be thought to directly or indirectly influence bat activity as well. However, both animal groups may differ in their response

to any of these environmental factors. Moonlight is an environmental factor that seems to negatively influence the activity of many nocturnal animals including tropical insects and bats (Fleming & Heithaus 1986, Handley & Morrison 1991, Williams & Singh 1951). Lunar-phobic behaviour in bats is usually construed as an adaptive response to selection pressure from visually oriented nocturnal predators. In this context, species that hunt in uncluttered, open habitats or at forest edges should be exposed to a higher risk of predation than those species that forage in obstacle-rich, cluttered environments and therefore the two groups can be expected to respond differentially to factors such as the prevailing light level. This effect could be reduced for fast-flying aerial-hawking species that hunt in open habitats and are therefore less constrained by light-dependent predation risk than slower ones and thus tend to tolerate brighter light levels as indicated by their earlier emergence times (Jones & Rydell 1994). Some bats – especially fast-flying species – may show opportunistic foraging behaviour by exploiting ephemeral patches of locally superabundant prey (Pavey et al. 2001).

Most studies on activity of insectivorous bats have been conducted in the northern temperate zone (Brigham et al. 1997, De Jong 1994, Erickson & West 2002, Kalcounis & Brigham 1994, Rydell et al. 1996) whereas similar studies in the tropics are underrepresented and in the case of Africa have focused on the southern part of the continent (Fenton et al. 1977, Rautenbach et al. 1988, 1996). Moreover, most studies have evaluated just one or a few factors potentially important in determining bat activity (Fenton & Thomas 1980, Fenton et al. 1998, Gannon & Willig 1997) and rarely used a comprehensive multi-factorial approach encompassing a suite of potentially influential factors.

We examined the influence of a range of biotic and environmental factors on the activity of insectivorous bats in a West African forest–savanna mosaic. In particular, we addressed the following questions: (1) Does variation in bat and insect activity follow a consistent and congruent pattern, i.e. do bats time their foraging activity to coincide with peak abundances of their prey? (2) What is the relative contribution of biotic (prey availability) and environmental factors (lunar phase, light intensity, (micro-) climate) to the overall variation in bat activity? (3) Do bats and insects exhibit differential responses to certain environmental factors? (4) Do bat species that forage in cluttered vs. uncluttered habitats show contrasting activity patterns?

STUDY SITE

The study was conducted in Comoé National Park (CNP) in north-eastern Ivory Coast, the largest National Park in West Africa covering an area of 11 500 km². CNP is located between 8°30′–9°36′N and 3°07′–4°25′W. With a north–south extension of c. 120 km the park encompasses a great proportion of the steep West African climatic gradient with dry Sudan savanna in the north-east to moist Guinea savanna in the south (Poilecot et al. 1991). Our study site was in the south-western part of the park within the Guinea savanna. Embedded in the matrix of shrubby savanna are isolated patches of forest islands ranging in size from > 1 ha to several km². Gallery forests occur along the main rivers. These three major habitat types result in an overall mosaic-like landscape structure. For a more detailed description of the vegetation see Poilecot et al. (1991) and Hovestadt et al. (1999).

The climate is characterized by a rainy season typically lasting from April to October, with a pronounced peak in August and September (mean annual precipitation 900–1100 mm). December to February are the driest months, usually with no rainfall at all. The annual mean temperature is 26.5–27 °C. Field work was carried out in October and November 2000 at the end of the rainy season/beginning of the dry season. During this period mean daily temperature was 25.5 ± 0.9 °C ($\pm$ SD, mean maximum and minimum temperature, respectively, 34.8 ± 1.7 °C and 20.5 ± 0.7 °C). While in October 2000 it rained on a more or less regular basis (rainfall totalling c. 110 mm), no rainfall was recorded in November.

METHODS

Data collection

Transects. We monitored activity of bats and insects along five transects established in the three major habitat types in the study area, i.e. two transects each in savanna and forest islands, and one in gallery forest along the Comoé river. All transects were rectangles 2 ha in size (200 × 100 m) and located between 0.5 and 7.5 km from the research station (8°45′N, 3°49′W) operated by the University of Würzburg. For each transect, data on bat and insect activity were collected on two consecutive nights for a total of 10 sampling nights using a combination of methods for both animal groups.

Bats. We used acoustic monitoring (recording of bat echolocation calls) and captures with mist nets and harp traps to quantify bat activity. In each transect a total of 12 mist nets (12 × 3 m, four shelves) were placed at 50-m intervals in an alternating fashion perpendicular to one another. This allowed for a direct comparison between transects. In addition, a canopy system was installed

between two of the tallest trees available at each site (at heights of 15–25 m) consisting of a system of four stacked nets with a combined net area of 12×12 m. Furthermore, a harp trap was placed in a naturally occurring corridor likely used by commuting and foraging bats. Trapping began before dusk between 18h00 and 18h30 and continued until 06h00. Nets and the harp trap were regularly checked for captured bats, usually in 30-min intervals. We recorded the time each bat was encountered in the net or trap and the bats were then removed and bagged for species identification. Acoustic sampling was performed using a custom-made bat detector ('Delay Line', University of Tübingen, Germany) positioned at a fixed point about 50 m from the respective transect. Echolocation calls were picked up with an ultrasonic microphone (flat frequency response (± 3 dB) between 30–120 kHz; down to 15 and up to 170 kHz sensitivity dropped by 0.2 dB per kHz) mounted on a pole *c*. 1 m above the ground and tilted approximately $45°$ up from horizontal. Recording commenced at dusk and continued until dawn during which we monitored bat activity in 30-min intervals. We recorded the echolocation calls of passing bats for 10 min per 30-min sampling interval. Specifically, we scanned the surrounding area by slowly but continuously sweeping up and down through a frequency range from 15 to 120 kHz in heterodyne mode. The detector was manually triggered whenever a bat call was audible through the speaker or a bat was directly observed flying past the microphone. The time-expanded ($15\times$) signals were then recorded onto CrO_2 audio tapes using a tape recorder (Sony WM-D6C).

Insects. The abundance of aerial insects was assessed using a mercury vapour (125 W) light trap set up approximately 100 m from the transect. Every 30 min the light trap was operated for 5 min (always after the acoustic samples of bat calls had been taken); all insects that were present within a predefined rectangle of 1 m² on the cloth were afterwards removed and immediately transferred into vials with 70% ethanol for subsequent analysis. In addition, we sampled foliage insects and spiders by holding a collecting cloth beneath the branches and stems of shrubs and trees and beating them with a pole. To standardize this method, the part of the vegetation chosen for sampling was beaten five times after which arthropods were immediately removed from the collecting cloth and transferred to ethanol-filled vials. This procedure was repeated for a total sampling number of five branches per 30-min sampling interval. Each time we sampled a different plant individual and species to minimize the likelihood of sampling an arthropod fauna specifically associated with a particular plant species. For each 30-min sample arthropods were counted and identified to order. In the case of

the Lepidoptera, we subdivided the samples, following Pavey & Burwell (1998), into individuals belonging to families that are characterized by the possession of abdominal or thoracic tympanal organs (Pyralidae, Geometridae, Notodontidae, Arctiidae, Noctuidae) and those that belong to families containing mainly atympanate species (e.g. Lasiocampidae, Saturniidae, many Sphingidae). The former group is capable of detecting the echolocation sounds of most bats and as a corollary these moths have developed certain avoidance mechanisms which can substantially reduce the moth's chance of being caught (Miller & Surlykke 2001).

Environmental factors. Measurements of light intensity (Skye Instruments High Output Light Sensor SKL 2640) and barometric pressure were taken from the weather station located at the research station. Temperature and relative humidity (using a combined digital thermometer/hygrometer), precipitation (including fog), cloud cover, wind and visibility of the moon were recorded locally at the respective transect. The latter were categorical variables which could have a varying number of discrete values with higher numbers corresponding to higher intensities: (1) visibility of the moon (based on cloud cover): 0 = invisible, 1 = visible; (2) fog: 0–2; (3) cloud cover: 0–3; (4) wind: 0–3. All variables were measured and recorded at 15-min intervals.

Data analysis

Echolocation calls were digitized using the sound analysis program BatSound (version 1.3.1., Pettersson Elektronik, Uppsala, Sweden). From the sonograms generated, for each search call sequence we measured the initial and terminal frequencies of the component echolocation calls and used those along with the overall shape of the signals to assign the calls to one of four categories: FM (steep frequency-modulated), CF (constant frequency), QCF (quasi-constant frequency, by some authors also referred to as narrowband FM calls) and FM-QCF (also called broadband FM) following Schnitzler & Kalko (1998, 2001). For our analyses, we defined bat activity measured by acoustic monitoring as the number of call sequences (two or more calls = one bat pass) recorded per sampling interval. When there were call sequences from more than one individual present in a recording, we included these in our analyses only if the number of individual bat call sequences was clearly discernible.

Statistical tests were performed using STATISTICA (version 5.5., StatSoft Inc., Tulsa, OK, USA). Data were tested for normality and homogeneity of variance (standard transformations were applied where necessary). Whenever these assumptions were not met,

non-parametric tests were used. We performed one-way ANOVA (or the corresponding non-parametric Kruskal–Wallis ANOVA, KW-ANOVA) to assess temporal variation in environmental factors and activity. Bat and insect activity, respectively, were entered as dependent variables into stepwise multiple regression analyses (forward inclusion with retrospective deletion, P to enter or remove $= 0.05$) in order to explore the factors influencing the activities of the two animal groups. The following range of independent variables or a subset thereof were included in all multiple regression analyses performed: insect abundance (for bats only), temperature, relative humidity, precipitation, barometric pressure, light intensity, and light intensity × temperature interaction; wind, relative cloud cover, fog, visibility of the moon and lunar phase were included as dummy variables. For analyses we pooled data across transect nights and used 30-min intervals as sample units.

For several groups of insectivorous bats comparative studies have established a clear link between echolocation call design and foraging habitat (Fenton 1990, Neuweiler 1989, Schnitzler & Kalko 1998, 2001). Depending on the level of environmental clutter encountered, bats that produce steep FM or CF calls usually forage within or close to vegetation, i.e. in highly cluttered space. Species that use FM-QCF calls belong to a foraging guild that usually hunts in edge habitats (background-cluttered space), whereas those characterized by QCF calls typically forage in open situations (uncluttered space, Schnitzler & Kalko 1998, 2001). Based on this classification we carried out separate analyses for bats belonging to guilds that hunt in open and/or edge habitats (QCF and FM-QCF species) and those foraging preferentially in obstacle-rich forest habitats (FM and CF bats). We used an analysis of covariance (ANCOVA) to assess to what extent variation in bat and insect activities can be attributed to differences in structural heterogeneity of the different habitat types and transects. Linear regression analysis was used to determine the relationship between bat activity and availability of tympanate vs. atympanate lepidopterans.

RESULTS

Environmental factors

During the study period, nightly temperatures ranged from 20.6 to 27.7 °C (23.0 ± 0.1 °C, mean $\pm$ SE). Apart from three short (< 1 h) events, no rainfall occurred during the sampling nights although cloud cover was often high. Fog frequently developed in the early morning hours. Barometric pressure ranged from 983 to 992 mbar, generally increasing towards midnight and decreasing thereafter.

Insect activity

Our 10 nights of sampling of arthropods resulted in 3194 captures at the light trap, foliage insects captured totalled 4261. Hemipterans and lepidopterans dominated the aerial samples (55%) followed by coleopterans and dipterans (13% each). In contrast, ants and spiders were most abundant in foliage samples (54%, coleopterans 13%). The temporal variation in abundance of aerial insects was significant (Figure 1, one-way ANOVA, F = 2.19, df = 21, P = 0.003) and revealed two phases of maximum activity, one shortly after dusk and one before dawn, mainly due to fluctuations of homopterans, dipterans and lepidopterans. The latter group had two abundance peaks, at 19h30 and 03h00 (Figure 2), a pattern we consistently observed for every transect.
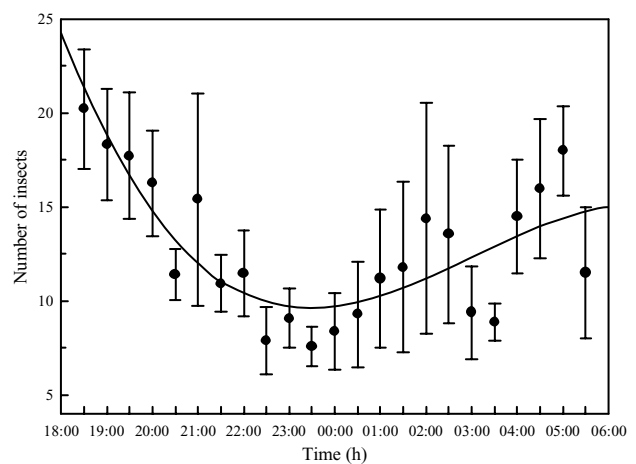

Figure 1. Temporal variability in aerial insect activity (mean $\pm$ SE, non-linear curve fit: $r^2 = 0.68$, P < 0.001).
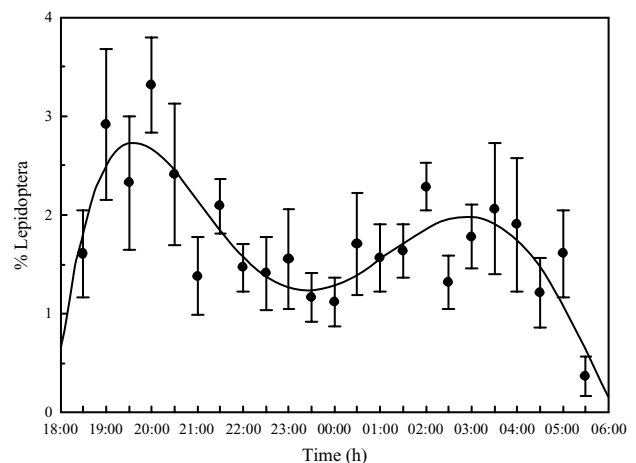

Figure 2. Temporal variation in the activity of lepidopterans as a percentage of total insect catch (mean $\pm$ SE). The non-linear relationship illustrated by the fitted curve accounted for 68.1% of the variance in moth activity.

Table 1. Bat activity measured as number of bat passes per guild based on call types and the total number of call sequences recorded in each of the five transects. Given are absolute values as well as percentages (in parentheses). The number of recorded echolocation call sequences differed significantly between QCF calls and the other call types (KW–ANOVA, H = 185, df = 3, P < 0.001, Dunn's post hoc test, P < 0.001, all other pairwise comparisons non-significant).

Guild	Forest island no. 1	Forest island no. 2	Gallery forest	Kongo savanna	Lola savanna	Total
QCF (Molossidae and Emballonuridae)	69	13	6	178	15	281
	(89.6)	(54.2)	(66.7)	(93.7)	(51.7)	(85.5)
FM-QCF (Vespertilionidae)	4	5	3	11	10	33
	(5.2)	(20.8)	(33.3)	(5.8)	(34.5)	(10.0)
FM (Nycteridae and Vespertilionidae)	1	1	0	1	2	5
	(1.3)	(4.2)	(0.0)	(0.5)	(6.9)	(1.5)
CF (Rhinolophidae and Hipposideridae)	3	5	0	0	2	10
	(3.9)	(20.8)	(0.0)	(0.0)	(6.9)	(3.0)
Total	77	24	9	190	29	329
	(23.4)	(7.3)	(2.7)	(57.8)	(8.8)	

Tympanate moths were significantly more abundant than atympanate ones (Mann–Whitney U-test, Z = 4.43, P < 0.001). Temporally clearly definable abundance maxima were restricted to the Lepidoptera and were not exhibited to the same extent by other insect orders whose abundance peaks were often temporally shifted by environmental factors, e.g. fog or moonlight. Contrary to our light trap samples, there was no discernible temporal pattern for foliage arthropods (one-way ANOVA, F = 1.05, df = 22, P = 0.405).

Light intensity, the interaction between light intensity and temperature, and fog were the best predictor variables for insect activity at the light trap. The best-fit multiple regression equation was: log (insect catch) = 1.66 − 8.05 light intensity + 0.29 (temperature and light intensity interaction) + 0.10 fog (r^2 = 0.19, F = 8.69, df = 3, P < 0.001). To assess the influence of structural heterogeneity and microhabitat differences between the different habitat types and transects, respectively, on insect activity, an analysis of covariance was performed. Both habitat type and transect explained *c.* 40% of the variance in aerial insect activity when all environmental factors were accounted for (ANCOVA, habitat type: F = 36.8, df = 2, P < 0.001, r^2 = 0.40; transect: F = 19.7, df = 4, P < 0.001, r^2 = 0.42). The influence of structural heterogeneity on the activity of shrub and tree arthropods was less pronounced (habitat type: F = 12.4, df = 3, P < 0.001, r^2 = 0.22; transect: F = 7.65, df = 4, P < 0.001, r^2 = 0.27).

Bat activity

We recorded a total of 329 echolocation call sequences (bat passes) during the 10 sampling nights, the majority (60%) in the Kongo savanna transect (Table 1). Members of the QCF guild, presumably for the most part molossids, comprised more than 90% of all recordings from this transect. The difference in number of bat passes between transects was highly significant (KW-ANOVA, H = 89.4, df = 4, P < 0.001). Molossidae were most common (*c.* 85%), followed by Vespertilionidae which comprised about 10% of all recordings. Rhinolophidae, Hipposideridae, Nycteridae and Emballonuridae together accounted for less than 5%.

During the 10 nights of mist-netting and harp-trapping we captured 65 bats (Table 2). Most (nearly 40%) were caught in the forest island no. 1, but the difference between the transects was not significant (KW-ANOVA, H = 4.64, df = 4, P = 0.326). Overall, members of the Rhinolophidae and Hipposideridae were captured most frequently (43%), but were absent from both savanna transects. Almost 50% of all captured individuals belonged to species characterized by QCF or FM-QCF calls, i.e. species commonly assumed to forage in open space or edge and gap habitats. No Molossidae were caught in the two forest islands; however, seven specimens were captured in the gallery forest (Table 2). Nycteridae were captured least often. At the family level, Nycteridae and Vespertilionidae did not exhibit any preferences with respect to habitat type. The slightly higher number of captures of vespertilionids in both savanna transects might indicate a preference for open habitats, however, our small sample size did not allow for statistical evaluation.

The temporal variation in bat activity was significant for captures but not acoustic monitoring data (KW-ANOVA, captures: H = 37.1, df = 22, P = 0.023; acoustic monitoring: H = 17.5, df = 21, P = 0.681). However, when analysed by non-linear regression, the best-fit equation explained 58% of the variation in number

Table 2. Bat activity measured as numbers of bats captured per guild/call type as well as total number of captures in each transect. Given are absolute values as well as percentages (in parentheses). There was a significant difference in abundance between the guilds (KW–ANOVA, H = 8.80, df = 3, P = 0.032).

Guild	Forest island no. 1	Forest island no. 2	Gallery forest	Kongo savanna	Lola savanna	Total
QCF (Molossidae and Emballonuridae)	2	0	7	7	0	16
	(9.1)	(0.0)	(53.8)	(46.7)	(0.0)	(24.6)
FM-QCF (Vespertilionidae)	2	1	2	8	4	17
	(9.1)	(11.1)	(15.4)	(53.3)	(66.6)	(26.2)
FM (Nycteridae and Vespertilionidae)	0	1	1	0	2	4
	(0.0)	(11.1)	(7.7)	(0.0)	(33.3)	(6.1)
CF (Rhinolophidae and Hipposideridae)	18	7	3	0	0	28
	(81.8)	(77.7)	(23.1)	(0.0)	(0.0)	(43.1)
Total	22	9	13	15	6	65
	(33.8)	(13.8)	(20.0)	(23.1)	(9.2)	

of recorded echolocation call sequences (P = 0.001, Figure 3a) whereas the curve-fit for captures was not significant ($r^2 = 0.24$, P = 0.155, Figure 3b). The marked increase in captures around 05h30 (Figure 3b) can be attributed to bats returning to their roosts, and therefore hardly constitutes any genuine change in activity. The temporal variation was not significant when the 05h30

Figure 3. Nightly variation in bat activity (mean ± SE) inferred from (a) acoustic monitoring and (b) captures (mist nets and harp traps).

sample was excluded from the analysis. It should be noted that the number of bats captured was small based on 30-min samples.

In a stepwise multiple regression analysis we found that insect availability, ambient temperature, cloud cover and visibility of the moon explained 32% of the variation in activity (sqrt (echolocation data + 0.5) = −1.43 + 0.01 insect catch (light trap) + 0.01 insect catch (foliage sampling) + 0.13 temperature − 0.36 cloud cover − 0.45 visibility of the moon, $r^2 = 0.32$, F = 10.3, df = 5, P < 0.001). Multiple regression analysis could not be performed for the capture data as a result of small sample size. We carried out a separate analysis for bats foraging in uncluttered/background cluttered habitats and those hunting in highly cluttered space, i.e. in the forest interior. In the former case, we obtained a model similar to the one for overall bat activity, with the same predictor variables being included in the model (sqrt (echolocation data QCF & FM-QCF + 0.5) = −1.30 + 0.01 insect catch (light trap) + 0.02 insect catch (foliage sampling) + 0.12 temperature − 0.37 cloud cover − 0.60 visibility of the moon, $r^2 = 0.36$, F = 12.6, df = 5, P < 0.001). The regression equation for the species foraging in clutter-rich environments was significant, however, the predictive value of the model was low (sqrt (echolocation data FM & CF + 0.5) = 0.48 + 0.05 (temperature and light intensity interaction), $r^2 = 0.11$, F = 14.5, df = 1, P < 0.001).

There was a strong and significant non-linear relationship between the activity of QCF and FM-QCF bats and the phase of the moon ($r^2 = 0.67$, P = 0.043). Activity in these guilds was lowest around full moon and increased towards new moon, as illustrated in Figure 4a, thus suggesting a negative influence of moonlight on bat activity. Conversely, no significant relationship was found for the CF and FM guilds (Figure 4b), again possibly as a result of the small sample size obtained for these bats.
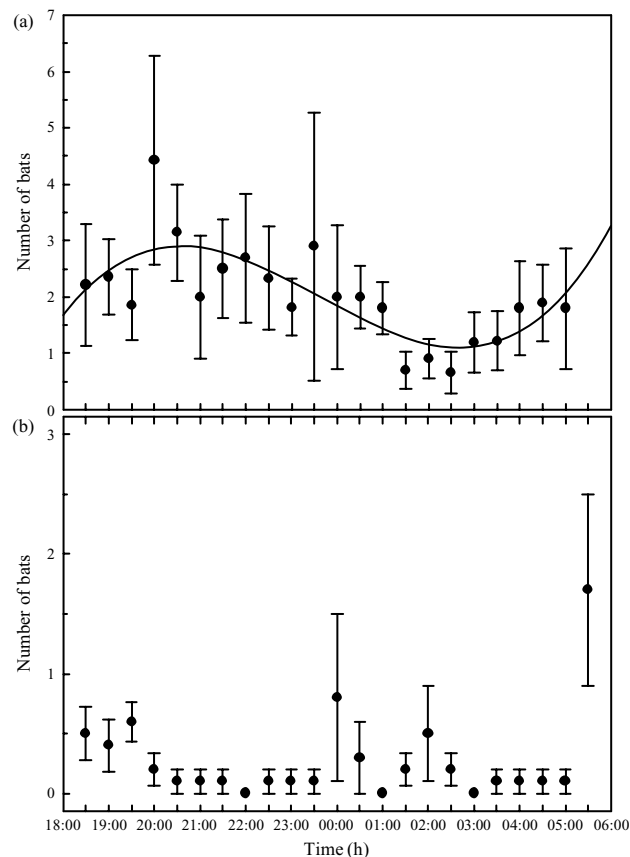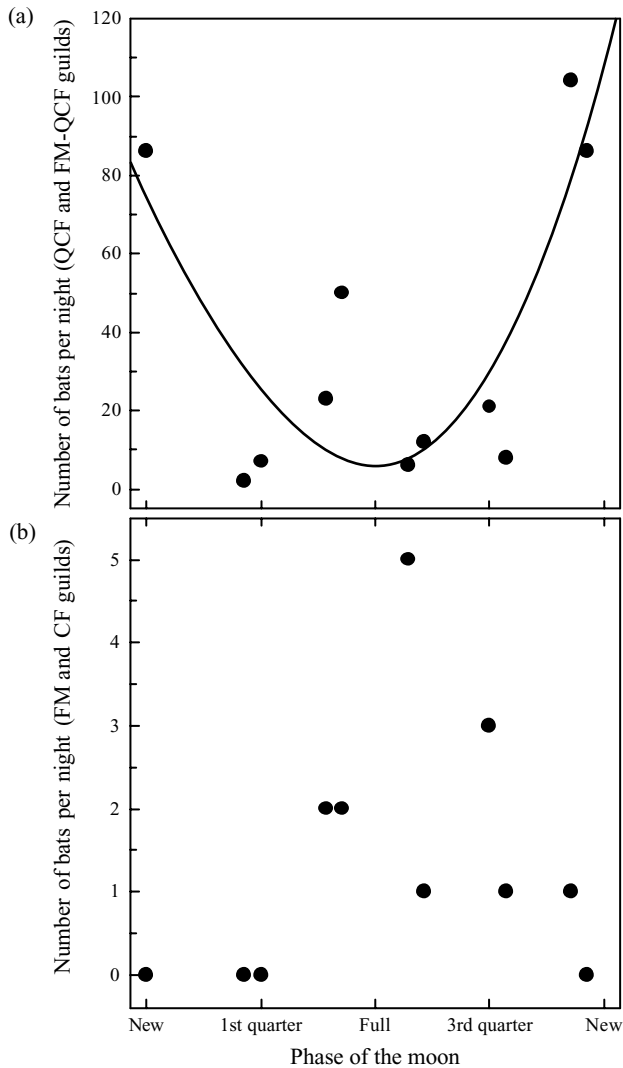
Figure 4. Relationship between number of recorded echolocation call sequences per night and moon phase for the guilds of (a) uncluttered and background-cluttered space (QCF and FM–QCF, best-fit non-linear regression: $r^2 = 0.67$, $P = 0.043$) and (b) highly cluttered space (FM and CF bats, non-linear relationship non-significant).

Since lepidopterans constitute a major food source for bats we assessed this relationship separately. Bats appeared to be most active when availability of atympanate moths was high ($r^2 = 0.42$, $P = 0.042$, Figure 5a). No such correlation was found for tympanate moths ($r^2 = 0.004$, $P = 0.862$, Figure 5b).

Using habitat type and transect as explanatory variables and with all other environmental variables and insect activity entered as covariates, 46% and 52%, respectively, of the variation in bat activity could be accounted for by individual differences, e.g. regarding structural heterogeneity among the five transects or different habitats (ANCOVA with dependent variable sqrt (echolocation data + 0.5), habitat type: $r^2 = 0.46$, $F = 23.8$, df = 2, P < 0.001, transect: $r^2 = 0.52$, $F = 26.9$,
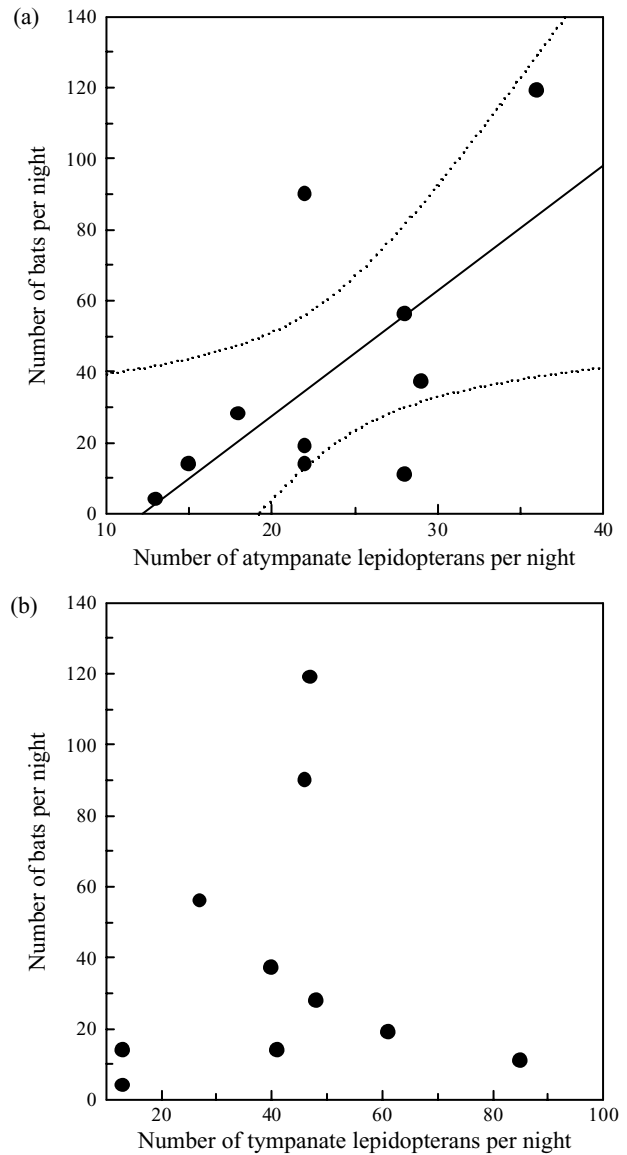

Figure 5. Relationship between bat activity (total number of bats recorded/captured per day) and abundance of (a) atympanate and (b) tympanate Lepidoptera captured at the light trap. The fitted regression in (a) explained 42.3% of the variation in bat activity ($y = -42.87 + 3.52x$, $P = 0.042$, dotted lines give 95% confidence intervals). In contrast, activity of bats and tympanate moths was not significantly correlated ($r^2 = 0.004$, $P = 0.862$).

df = 4, P < 0.001). Similar results were obtained for the guild of bats flying in open space or hunting in edge habitats (ANCOVA with dependent variable sqrt (echolocation data QCF & FM-QCF + 0.5), habitat type: $r^2 = 0.46$, $F = 20.4$, df = 2, P < 0.001, transect: $r^2 = 0.53$, $F = 21.7$, df = 4, P < 0.001). For those species foraging in obstacle-rich, cluttered habitats (FM and CF-bats) neither of the two variables was included in the ANCOVA model, probably again an effect of the small sample size.

DISCUSSION

Insect activity

The two different sampling methods for measuring insect abundance yielded different results with regard to the observed activity pattern. Aerial insects exhibited one maximum of flight activity in the hours just after dusk and a second, though smaller peak before dawn, similar to patterns frequently reported by other authors (Rautenbach *et al.* 1988, Rydell *et al.* 1996). Overall, the activity pattern of moths (Figure 2) matched the one shown by aerial insects, however, peaks of total aerial insect catch occurred at dusk and dawn (Figure 1), whereas for moths maxima were attained somewhat later and earlier, respectively. Speakman *et al.* (2000) have documented a similar temporal activity pattern for insects in northern Europe, but Rydell *et al.* (1996) reported a maximum around midnight. Apart from abundance fluctuations within any one night, there were also qualitative differences regarding taxonomic composition. In this context, the chosen sampling time of 5 min during which the light trap was run may have influenced the abundance and composition of the attracted insects. It can be assumed that insects respond differentially to a light source, depending on sampling time and distance, resulting in a more reliable estimate of activity as the light trap is operated for increasingly longer time spans. Bright moonlight can also lead to a decrease in trapped insects by competing with the artificial light source. Nevertheless, as Williams & Singh (1951) noted, nightly insect activity inferred from sampling with a suction trap indeed follows a lunar cycle, being highest around new moon (see also below).

In contrast to light-trapped aerial insects there was no discernible activity pattern for foliage arthropods. Catch varied unpredictably around a certain mean value with no definable maximum of activity. Ants and spiders were dominant in all samples. Although non-flying ants (i.e. workers) are probably rarely if at all taken by gleaning bats, many species are known to include arachnids in their diet (Bowie *et al.* 1999), and some even specialize on spiders (Schulz 2000). In general it is questionable whether prey availability for gleaning bats can be adequately estimated with the employed method. Given that gleaners often rely on passive cues for prey detection, e.g. prey-generated sounds, data based on presence/absence of potential prey alone might not necessarily reflect what is really available to them.

Temperature, light intensity and fog seemed to exert only a moderate influence on aerial insect activity, while the structure of the vegetation and individual transect explained a large proportion (40%) of the observed differences in abundance and species composition. Insect activity was generally higher for the savanna habitat than for either island or gallery forest, presumably a consequence of the higher production of plant biomass available to phytophagous insects during the rainy season as opposed to forest habitats. A positive effect of higher temperature on insect flight has repeatedly been reported in previous studies (Lewis & Taylor 1965, Taylor 1963). In a study in northern Scandinavia, Speakman *et al.* (2000) also found temperature, light intensity and the interaction between light intensity and temperature to be the best predictors of insect activity. Although qualitatively matching our results, in contrast to their study we found light intensity to suppress insect activity, which might be due to an enhanced predation risk for insects by visually hunting nocturnal insectivores such as nightjars (Caprimulgidae) that are very abundant at our study site.

Bat activity

As for insects, the three methods employed for estimating bat activity gave very different results. In our study, acoustic monitoring turned out to be the most appropriate method for measuring flight activity, better than either mist-netting or harp-trapping, mainly because of the overall small number of bat captures. Notwithstanding the low capture rate, these latter sampling techniques serve to complement assessments of activity based on acoustic sampling alone, resulting in an overall more accurate estimate of bat activity. However, one might only rarely be able to sample the different guilds equally well. Any study trying to assess the activity of bats in different habitats by means of acoustic monitoring is faced with the problem of substantial variation in detectability among species arising from differences in intensity of their echolocation calls (Hayes 2000) – a problem one has to be aware of when making inferences and interpreting results. For instance, species producing low-intensity echolocation calls ('whispering bats', at our study site, e.g. *Nycteris* and *Kerivoula* spp.) are hardly detectable or only at very close range (Waters & Jones 1995), whereas other species, such as molossids that use low-frequency, far-reaching calls often dominate acoustic samples.

In our study, acoustic monitoring revealed no statistically significant pattern for within-night variation in bat activity, although there was a certain trend suggesting two periods of high foraging activity (at approximately 20h30 and 05h00, Figure 3a). Since the data for this analysis, however, were pooled across transect nights, any clearer patterns evident on a per-transect basis, might as a consequence have been obscured, causing the overall non-significant temporal variation. Higher levels of overall insect availability as well as temperature positively influenced foraging activity of bats. Our findings regarding insect abundance are

corroborated by studies conducted in southern Africa (Rautenbach *et al.* 1988, 1996) and the temperate zone (Hayes 1997, Speakman *et al.* 2000). We suppose, however, that under tropical conditions increased ambient temperatures do not affect bats directly because of their homoeothermic physiology, but rather indirectly via their stimulating effect on insect activity (but see for instance Rachwald *et al.* (2001) for temperate zone species). By contrast, light intensity was shown to suppress bat activity, especially affecting species of the QCF and FM-QCF guilds. Cloud cover often reduced light intensity; nevertheless, our regression model suggests a negative effect on bat activity. In our case, sharp differences in the prevailing light level were mainly caused by moonlight (visibility and phase), in contrast to other studies conducted in northern latitudes where large variations in light intensity mainly occurred at the beginning and the end of the activity period of bats due to prolonged periods of dusk and dawn (Rydell *et al.* 1996, Speakman *et al.* 2000). Lunar phobia appears to be widespread among tropical bats, where it has mainly been documented for neotropical frugivores (Fleming & Heithaus 1986, Handley & Morrison 1991) although a negative effect of bright moonlight on bat activity has also been suggested by Fenton *et al.* (1977) for insectivorous species in southern Africa. In contrast, to this date there are no clear-cut examples of insect-eating bats in temperate areas exhibiting lunar-phobic behaviour (Hayes 1997, Karlsson *et al.* 2002, Negraeff & Brigham 1995). Karlsson *et al.* (2002) argued that insectivorous bats at high latitudes may not have been exposed to the same levels of nocturnal predation pressure, leading to the evolution of lunar phobia, as have many tropical bats, thus explaining the lack of clear-cut examples of this behaviour in temperate-zone bats. There is some evidence, however, that bright light levels might suppress foraging activity within a particular area when bats suffer from a substantial predation risk by nocturnal or diurnal raptors. For instance, Gannon & Willig (1997) found evidence that in Puerto Rico, where visually orienting predators are virtually absent, *Stenoderma rufum* remained active even during bright moonlight, whereas results of other studies point to a decrease in activity during periods of high illumination due to the presence of aerial predators (Fenton *et al.* 1977, Jones & Rydell 1994, Rydell *et al.* 1996). At our study site several species of owls and the bat hawk (*Machaerhamphus alcinus* Westerman) occur that are known to prey on bats (Aulagnier 1989, Black *et al.* 1979, Fenton *et al.* 1994, Lang & Chapin 1917), therefore our results can also be interpreted as reflecting an anti-predator response (see also Figure 4a).

For bats foraging in uncluttered and background-cluttered space, determinants of activity were the same as for overall bat activity, which can be attributed to the fact that bats belonging to these guilds constituted the vast majority of all ultrasound recordings. Conversely, low sample size prevents solid conclusions about activity patterns of bats hunting in cluttered habitats. As mentioned above, this bias in the recorded echolocation call types might reflect, at least to some degree, differences in detectability among species and therefore be a general methodological problem. For species hunting in cluttered habitats, the regression model explained only about 10% of the variance in our data, with the interaction between temperature and light intensity being the sole factor included. That is, the effect of temperature on bat activity was less pronounced with increasing light levels. Interestingly, in this guild there was a discernible though non-significant trend towards increased flight activity during the brighter light conditions associated with full moon (Figure 4b). This does not imply, however, that these bats are more active during full moon but only that activity levels may not be substantially lower than usual. If this was indeed a genuine pattern, these results might hint at these bats being less susceptible to predation, most likely since they tend to forage within vegetation where their manoeuvrability might constitute an advantage over most nocturnal predators (Kalko 1998). However, more data are needed to assess this relationship.

As for insects, we found bat activity (overall and for QCF and FM–QCF species) to be largely dependent on habitat- or transect-specific influences. Indeed, the differences in structural heterogeneity between the sampled transects and the microclimatic differences among the three habitat types (J. Fahr, unpubl. data) appear to have had a more profound influence overall on the bats ($r^2 = 0.46$–0.53) than any environmental factor or prey availability ($r^2 = 0.32$–0.36). The two forest islands differed from each other as well as from the gallery forest in their humidity level, vegetational composition, tree density, understorey vegetation and availability of day roosts. In the Kongo savanna transect shrub and tree density were generally higher than in the Lola savanna. Our data confirm the preference of bats producing QCF and FM–QCF calls for open, sparsely cluttered habitats. Consequently, molossids, emballonurids and most vespertilionids were recorded in the two savanna transects and the forest island no. 1. The fact that molossids were present in high numbers in our acoustic samples of the latter transect is probably due to the relatively open canopy structure, which led to an increased detectability of QCF calls. On the other hand, FM and CF bats seemed to restrict their foraging activity mostly to the forests, being highest in the forest island no. 1. It has to be noted that activity levels at a given time might not only vary considerably between transects for any particular guild but also that factors such as prey availability or increased predation risk during bright moonlight may result in transient habitat shifts of certain species or guilds (Fenton *et al.* 1977, but see Negraeff & Brigham 1995). As a corollary, for these

transient differences to be elucidated one would have to sample all transects simultaneously, which, however, in our case was not possible for logistical reasons.

We found a significant correlation between bat activity and abundance of atympanate moths, while no such correlation was found for bats and tympanate lepidopterans. Thus, one might conclude that bats selectively choose to hunt during peak availability of atympanate moths in order to maximize their net energy intake per unit foraging time. Since these moths are unable to detect approaching bats, this could result in an overall higher rate of successful prey captures. These results should, however, be interpreted cautiously, given the fact that tympanate moths are overall far more abundant; the resulting higher encounter rate would compensate for the higher number of unsuccessful attacks due to evasive responses by moths (Miller & Surlykke 2001).

In summary, apart from the distinctive differences in bat abundance and guild composition among the five different study sites, bat activity appeared to be governed largely by the spatially and temporally heterogeneous availability of insects, however, taking into consideration those factors closely associated with an increased predation risk and a lower net energy gain per unit foraging time. A generally higher predation risk might arise as a consequence of greater light intensity caused primarily by moonlight. It tended to affect bats foraging in highly cluttered space less than those of more open habitats. Fog was observed to depress bat activity even though insect activity remained at high levels, implying that bats might experience a decrease in net energy gain due to a lower foraging success.

The present study was the first to explore factors affecting bat activity in tropical Africa using a multivariate approach. Comparative studies, preferably involving a larger data set, are certainly needed to further advance our knowledge of the factors that influence bat activity at the community level in tropical environments.

ACKNOWLEDGEMENTS

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