The importance of water bodies for insectivorous bats in a Malagasy dry deciduous forest: A case example from Kirindy (CNFEREF)

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Abstract

In seasonal environments, food supply typically fluctuates during the course of the year. Bats, as small endothermic vertebrates, rely on regular and abundant food sources. To assure this in a habitat where these resources are scarce, bats are thought to aggregate in areas where food abundance is highest, such as the last remaining water bodies in dry deciduous forests in the dry season. Further, access to water is perhaps equally or even more essential. We tested these hypotheses in Kirindy Forest (CNFEREF) in central western Madagascar by recording bat activity with a Batlogger in three different habitats: at pools with standing water (in a dry riverbed), in riparian forest along the riverbed, and in forest away from the riverbed. We measured vegetation structure and insect abundance using a simple and effective new method. We found that bat activity of the families Vespertilionidae and Hipposideridae, was highest at the pools and best predicted by distance to water and vegetation structure. For the Molossidae, activity did not vary between habitats. The water pools appeared to have an influence on bat community structure and seem to play an important role on bat survival in fluctuating environments such as the dry deciduous forests of central western Madagascar.

Key words: Bat activity, acoustic monitoring, Kirindy CNFEREF, Madagascar, dry deciduous forest

Résumé détaillé

Dans les environnements saisonniers, les ressources alimentaires fluctuent généralement au cours de l'année. Les chauves-souris, qui sont des petits vertébrés endothermiques, comptent sur des nourritures abondantes et régulières. Pour assurer leur besoin énergétique dans un habitat où ces ressources sont rares, elles sont supposées se regrouper dans des endroits où la nourriture est plus abondante, tels que dans les cours d'eau temporaires ayant encore de l'eau d'une forêt sèche caducifoliée. D'autre part, l'accès à l'eau est peut-être encore plus essentiel. Nous avons testé ces hypothèses dans la forêt sèche caducifoliée de Kirindy (CNFEREF), Madagascar en enregistrant les activités de chauves-souris dans trois différents habitats : tout près de quelques bassins d'eau stagnante ou des lits de rivière asséchés, dans la forêt le long des lits de la rivière et dans la forêt éloignée de cours d'eau.

Les cris de chauves-souris ont été enregistrés avec un « Batlogger » posé sur le sol et tourné respectivement vers l'eau et la zone ouverte. Pendant 10 nuits entre le 13 novembre et le 27 décembre 2011, 1349 chauves-souris sont enregistrées au niveau des 91 points d'échantillonnage, dont chaque point est échantillonné pendant 5 mn. Ces cris sont uniquement attribués au niveau de la famille en raison des incertitudes sur l'identification acoustique des certaines espèces de chauves-souris malgaches. Nous avons mesuré la structure de la végétation et l'abondance des insectes à l'aide d'une nouvelle méthode facile à utiliser et efficace.

Globalement, les activités de chauves-souris sont plus élevées sur les lits de rivière, en particulier au niveau des bassins, et plus bas dans la forêt galerie. Cependant, les différentes familles ont montré différentes tendances. Nous avons constaté que les activités de Vespertilionidae et d'Hipposideridae sont significativement plus élevées dans les bassins et aisées à prédire à partir de la distance au point d'eau et de la structure de la végétation. Pour les Molossidae, leurs activités ne semblent pas varier entre les différents habitats. L'analyse « Biota and/or Environment matching » ou BIOENV a montré que la distance des arbres les plus proches et la distance par rapport à la rivière sont les variables qui ont une

forte corrélation avec la structure de la communauté, même si aucune des corrélations n'est significative au sein de la communauté. Toutefois, les bassins semblent avoir une influence sur la structure de la communauté des chauves-souris.

Nos résultats montrent que les activités de chauves-souris sont plus élevées à proximité des zones où il y de l'eau que dans les endroits loin de celles-ci et que l'eau elle-même semble avoir un impact plus important sur leurs activités que sur l'abondance des insectes. Ainsi, les cours d'eau, fluctuant dans des environnements tels que la forêt sèche caducifoliée de l'Ouest malgache, semblent jouer un rôle important sur la survie des chauves-souris.

Mots clés : activités de chauves-souris, suivi acoustique, Kirindy CNFEREF, Madagascar, forêt sèche caducifoliée

Introduction

In a highly seasonal habitat, resources are unevenly distributed during different portions of the annual cycle. To survive in this fluctuating environment, animals have developed various adaptations. Some species in areas with seasonally limited food supply store fat and enter torpor (Kobbe & Dausmann, 2009; Genoud & Christe, 2011; Yang & Wang, 2011) or migrate to areas where the conditions are more favorable (Berthold, 2001).

In areas where water supply is limited, some species manage to minimize their water needs, enabling them to cover it through food intake only (Grenot, 2001). Insectivorous bats, due to their generally small size and disproportionately large surface area created by the non-insulated wings, have a high basal metabolic rate (Kurta *et al.*, 1990) and therefore are likely to rely on a regular food and water supply. During the dry season, insects are sparse in forest habitats (Lack, 1986) but may be more abundant in close proximity to water sources. This can lead to increased activity of insectivorous bats in riparian areas (Grindal *et al.*, 1999; Francl, 2008; Monadjem & Reside, 2008; Monadjem *et al.*, 2009). In regions with a pronounced dry season, this effect may even be stronger due to the temporary drying up of water bodies. On several continents, it has been shown that the presence and activity of bat species is related to habitat structure (Gehrt & Chelsvig, 2003; Peters *et al.,* 2006; Mueller *et al.*, 2012). Among insectivorous bats, however, the preferred habitat type and structure show considerable specific differences (Meyer *et al.*, 2004; Bader *et al.*, 2015).

In this study, we aim to unravel the factors that determine the activity of insectivorous bats in a highly seasonal dry forest habitat in central western Madagascar. More specifically, we investigated how forest structure, insect abundance and distance to the nearest water source affect the occurrence and activity patterns of bats.

Materials and methods
Study site

The study took place in Kirindy (CNFEREF) Forest (20º 03'S, 44º 39'E, 30-60 m above sea level), a dry deciduous forest 60 km north of Morondava, central western Madagascar. This area is characterized by pronounced seasonality, with a hot wet season generally from December to March/April and little or no rain from May to November (Sorg & Rohner, 1996). The annual average rainfall is 900 mm (Kappeler & Fichtel, 2012). Vegetation comprises well-developed undergrowth and a dense canopy, up to 25 m above ground (Rakotonirina, 1996).

The Kirindy River that bisects this forest is largely waterless during the dry season. In mid-November, when the first sampling was conducted, only three pools were left in the section of the riverbed within our study area, which was assumed to be the only water source in a radius of at least several kilometers. During the second sampling period, by the end of December, only one pool remained. Data were collected along the foot trails of the grid system CS7, installed by the German Primate Centre (DPZ), Göttingen, and along the dry riverbed, covering an area of approximately 2.2 km^2.

Data collection

Acoustic data were collected between 13 and 20 November, as well as on 26 and 27 December 2011. Sampling points were located every 50 m along the riverbed. Away from the river, points were sampled every 50 m for the first 200 m and every 100 m thereafter. Distances in the forest were measured using the grid system, and the points in the riverbed were recorded with a Garmin 60 CSX GPS. During each night of data collection, three habitat types were sampled randomly: 1) riverbed, 2) forest (away from the riverbed) and 3) three pools (within the riverbed). Sampling commenced at 19:00 (November) or 19:30 (December) and ended by 22:30. All recordings were made during the first quarter of the lunar phase

hence, bias caused by moonlight was assumed to be negligible. The temperature during sampling periods ranged from 24.7°C to 31.0°C.

Bat activity was recorded with a Batlogger (www.batlogger.ch), a real time ultrasound recorder, placed on the ground at a 45⁰ angle, pointing towards the river or pool, respectively. Bat activity at each point was sampled for 5 min. At the same time, insect abundance was measured once a minute for 30 s, resulting in 2.5 min of insect sampling time per point. Adapting the methods of Grüebler *et al.* (2008), we used a 65 x 65 cm white paper sheet, with its upper edge held 2 m above ground. An observer stood at a 3 m distance, pointing a Black Diamond Icon head torch with spotlight function to the paper and counting the number of insects passing in front of the sheet.

Vegetation surrounding the sampling points was characterized by measuring the distance to the nearest tree (>10 cm diameter at breast height) in the four adjacent forest sectors, with the sectors defined by two orthogonal trails each, or by the river and its perpendicular line. To define the undergrowth, we measured its density by using a paper sheet with 15 squares, 20 x 20 cm each (100 x 60 cm total surface). The sheet was held with its upper edge 2 m above ground, at a 5 m distance to the recording point, in the middle of two trails, and the number of squares obscured by plants was counted. In both cases, an index was created, calculated from the mean value of the four measurements per sampling point.

Data analysis

Bat calls were analyzed with BatSound 3.30 (www.batsound.com) and BatScope 2.0 (www.batscope.ch), respectively, by comparison of call type and peak frequency. Calls of a bat species were counted once per recording (maximum record length: 10 s) and, following Monadjem *et al.* (2010a), were defined as a bat pass. Calls could not be identified to species level due to overlap in call parameters of some taxa, such as within the Vespertilionidae (Goodman *et al.*, 2015). However, nearly all the calls could be assigned to one of four families (known species from the site are given in parentheses based on Goodman [2011]; Rakotondramanana & Goodman [2011]; Goodman *et al.* [2015]): 1) Hipposideridae (*Hipposideros commersoni*, *Triaenops menamena*); 2) Molossidae (*Chaerephon leucogaster, Mops leucostigma, M. midas*); 3) Vespertilionidae (*Scotophilus marovaza, Hypsugo bemainty, Pipistrellus raceyi, P. hesperidus, Myotis goudoti*); and 4) Miniopteridae (*Miniopterus gleni*), based on parameters outlined by Monadjem

et al. (2010b) and Goodman (2011). The genus *Triaenops* has recently been assigned to a separate family, the Rhinonycteridae (Foley *et al.*, 2015), but for this study we retain the genus in the Hipposideridae due to the similarity of their call structure (Monadjem *et al.*, 2010b). We could not confidently distinguish all the species in the Vespertilionidae and Miniopteridae based on call parameters, and therefore these two families were combined for all analyses.

Normality was determined with a Kolmogorov-Smirnov test. To infer the possible attraction effect of the head torch light on insects, we compared the number of insects counted in consecutive 30 seconds intervals in different habitat types, using a Kruskal-Wallis rank test. The latter was also used to assess insect abundance, bat activity and vegetation structure (average tree distance and undergrowth density) by habitat type.

We used generalized linear models based on data-fitted Poisson distributions to develop models linking bat activity to different variables including distance from water pools and the riverbed, insect abundance, distance to nearest tree and undergrowth cover. We used the Akaike Information Criterion (AIC) to select the most appropriate model. The model with the lowest AIC was considered the best model; models that differed by less than two from the best model were deemed indistinguishable from it. All statistical analyses were conducted in the program R version 2.15.2 (R Core Team, 2014).

Non-Metric Multi-Dimensional Scaling (NMDS) was conducted using Bray-Curtis similarities and square root transformation, to infer the spatial distance between points across habitat types, according to the different bat sonotypes recorded at each site. Analysis of Similarities (one-way ANOSIM) was used to determine differences between the distinct habitat types. Biota and/or Environment matching (BIOENV) was used to relate the environmental parameters (insect abundance, vegetation data and distance to river) with the bat community structure. All multivariate analyses were conducted in Primer 5.2 (http://www.primer-e.com).

Results

A total of 91 points were sampled at 68 different locations. A total of 1349 bat passes were recorded, 847 belonging to the family Vespertilionidae, 299 to the Hipposideridae, 194 to the Molossidae, and nine that could not be identified (Table 1). During approximately 230 minutes, 1114 insects were counted.

Table 1. The different sonotypes of bats recorded at Kirindy (CNFEREF) Forest, Madagascar, during this study. Below each family (presented in bold) is listed the possible species which were recorded. Also included is either the maximum frequency (for those calls with a constant frequency component) or the peak frequency (for those without a constant frequency component). It should be noted that these species identifications are tentative and for this reason, all analyses were conducted at a family level.

	Constant frequency component?	Maximum frequency (kHz)	Peak frequency (kHz)
Hipposideridae*	Present		
Hipposideros commersoni		64–66	
Triaenops menamena		81–96	
Molossidae	Absent		
Mops midas			12–14
Chaerephon leucogaster			22–25
Mops leucostigma			26–31
Vespertilionidae/Miniopteridae	Absent		
Scotophilus sp./*Miniopterus* sp.			42–49
Pipistrellus spp./*Hypsugo* sp.			50–60

*Includes *Triaenops* that is now placed in a separate family Rhinonycteridae.

When all calls were combined, bat activity was highest in the riverbed, particularly in close proximity to the pools, and lowest in the forest away from the riverbed (Table 2). However, different bat families did not show the same trends. The Vespertilionidae and Hipposideridae had significantly different activity across the habitats with values highest at the pools and lowest in the forest (H = 48.40 and 46.72, respectively, $P < 0.01$ for both). In contrast, the Molossidae did not differ significantly in activity between habitats ($P > 0.05$).

Insect activity differed significantly between the habitats and was highest at the pools and lowest in the forest (H = 10.80, $P < 0.05$, Figure 1). However, there was no significant difference ($P > 0.05$) in the number of insects counted in consecutive time intervals in any habitat type or between nights.

The distance to the nearest tree, as well as undergrowth density, differed significantly with habitat (H = 61.95 and 67.90, respectively, $P < 0.05$ for both). Distance to nearest tree was greater in the riverbed than in the forest away from the riverbed (Figure 2a);

in contrast, undergrowth density was greatest in the forest (Figure 2b).

The best model of bat activity was the one that included all the variables (Table 3). However, individual families responded in different ways. The best model for Vespertilionidae activity was the same as for all bats combined, and included all variables (Table 3). For the Hipposideridae, the two competing models were within two AIC points; one included the distance to the pools and to the riverbed and the other all variables except insect abundance. For Molossidae, there were three competing models: 1) all variables, 2) all variables except distance to the riverbed 3) all variables except undergrowth density
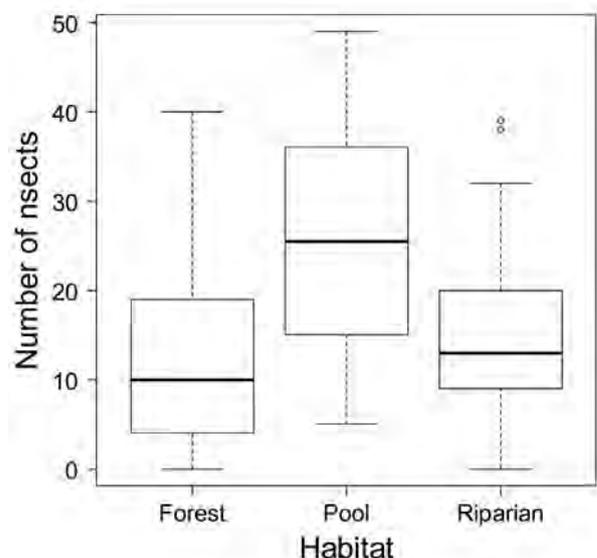
Table 2. The number of bat passes per family in different habitats at Kirindy (CNFEREF) Forest, Madagascar. The number of times the habitat was sampled (n) is given in parentheses.

	Forest (n = 41)	Riparian (n = 38)	Pool (n = 12)
Hipposideridae	4	134	161
Molossidae	58	103	33
Vespertilionidae	53	429	365
Total	**115**	**666**	**569**

Figure 1. Insect abundance in the different habitats of the Kirindy (CNFEREF) Forest, Madagascar.

(Table 3). There was a negative relationship between bat activity and distance to pool, distance to riverbed, increasing tree cover (i.e. decreasing distance between trees), increasing density of undergrowth, and decreasing insect abundance (data not shown) (Figure 3).

NMDS analyses produced a well separated group of points, representing the water pools, but were not able to separate the forest points from the river points (Figure 4). However, the stress value (0.1) showed

that this ordination is a good representation of the community structure. The three habitat types were significantly different from each other, but the separation is not clear (ANOSIM, R = 0.092, *P* = 0.016). Looking at the pairwise tests, forest seemed to differ from river and pool (ANOSIM, R = 0.073, *P* = 0.028 and R = 0.131, *P* = 0.046, respectively), but river and pool did not significantly differ from each other (R = 0.018, *P* > 0.05). BIOENV analyses showed that none of the environmental parameters
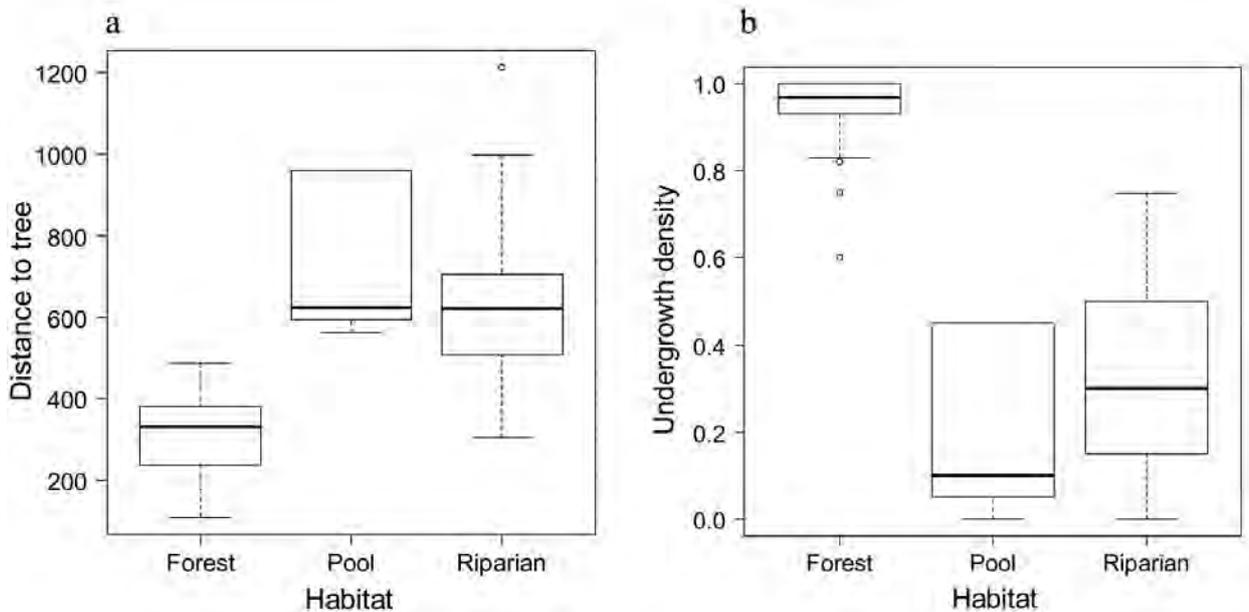

Figure 2. Vegetation characteristics in the different habitats for: a) distance to nearest tree (cm); and b) undergrowth density in the Kirindy (CNFEREF) Forest, Madagascar.

Table 3. Generalized linear models with Poisson distribution for overall bat activity, activity of the families Hipposideridae, Molossidae and Vespertilionidae, with respect to habitat variables in Kirindy (CNFEREF) Forest, Madagascar. Pool = distance to pool; riverbed = distance to riverbed; undergrowth = density of undergrowth; tree = distance to nearest tree; insect = insect abundance. The best model (i.e. with the lowest AIC value) is highlighted in bold and underlined.

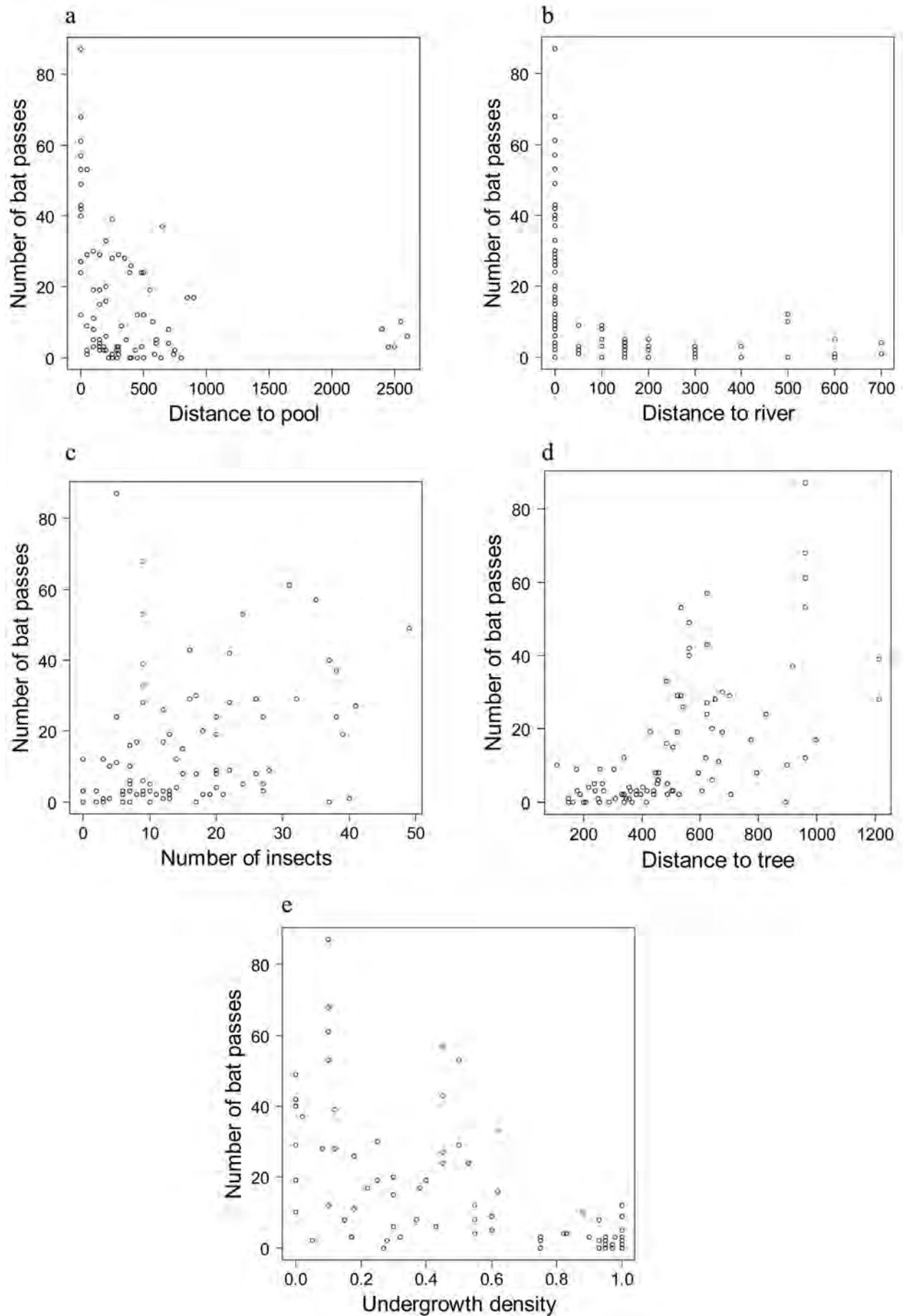|	AIC values			
	All bats	**Hipposideridae**	**Molossidae**	**Vespertilionidae**
All variables	**951.64**	422.3	**514.1**	**750.9**
Pool + riverbed + tree + undergrowth	981.0	**420.3**	519.8	767.9
Pool + insect + tree + undergrowth	984.9	463.1	**512.8**	784.9
Pool + riverbed + insect + tree	1010.3	422.2	**514.0**	786.3
Pool + riverbed + insect + undergrowth	1016.5	420.5	539.2	812.2
Riverbed + insect + tree + undergrowth	1072.9	632.0	526.7	851.7
Tree + undergrowth	1176.8	706.2	526.7	930.3
Undergrowth	1225.6	704.5	548.6	978.6
Pool + riverbed	1250.9	**418.4**	549.7	958.1
Tree	1398.9	820.3	526.0	1103.3
Riverbed	1424.8	666.9	559.2	1106.1
Pool	1818.7	517.4	553.3	1429.6
Insect	1865.0	852.3	560.0	1503.6

Figure 3. Scatter plot showing the number of bat passes in relation to the following variables in the Kirindy (CNFEREF) Forest, Madagascar: a) distance to pools (m); b) distance to river (m); c) relative insect abundance; d) distance to nearest tree; and e) undergrowth density.

Figure 4. Non-metric dimensional scaling of the 91 points in three habitats sampled in relation to the number of bat species in Kirindy (CNFEREF) Forest, Madagascar.

was significantly correlated with the bat community structure ($P > 0.05$). Nevertheless, nearest tree distance and distance to the river were the variables that were best correlated with the community structure ($r_s = 0.094$).

Discussion

Our results from the Kirindy CNFEREF Forest in central western Madagascar support observations from other regions of the world that bat activity is higher close to water than away from it (Grindal *et al.*, 1999; Francl, 2008). This aspect was most pronounced in the Hipposideridae, where on average 134 times more passes were recorded per sampling unit at pools than in the forest, and 35 times more than in the riverbed away from the pools of water. These results were similar but less pronounced in the Vespertilionidae, with approximately 23 times more bat passes at the pools than in the forest and three times more bat passes at the pools than elsewhere in the riverbed. In the Molossidae, we found no difference in activity between pools and riverbed, but about twice as much activity in those two habitats compared to the forest. Furthermore, our results indicate that all the recorded variables – distance to pool, distance to riverbed, tree cover, density of undergrowth and insect abundance – influence distribution and activity of the sampled bat assemblage, even though some slight differences were found among variables and bat families.

It is likely that the availability of water has a much stronger effect on distribution and activity of bats in the sampled forest than the abundance of insects, at least for vespertilionid and hipposiderid bats (also see

Rakotondramanana *et al.*, 2015). The best evidence for this comes from the Hipposideridae, where the two models (first model: distance to the riverbed and the pools; and second model: all variables except insect abundance) were almost identical. In the Vespertilionidae, despite the model including all variables being the best, we still counted three times more bat passes at the pools than in the riverbed. Even though there was a significant correlation between insect abundance and bat activity, the causal relationship is not clear. These results are also supported by observations in late December of one of the authors (EB). Even though insect abundance was more evenly distributed among different sampling points and habitats, bat activity at the last remaining pool was much higher than during the first sampling period. One night, right after dusk, in an air volume of about 60 m³, up to 15 different individual bats were observed to be flying around. This high density, causing high levels of noise, seemed to confuse and disorientate the bats, with some of them flying into tree trunks and one colliding with the observer.

These patterns are not necessarily the same for molossid bats. This family did not seem to rely on pools as much as the other two families, as we found no indications of increased molossid activity close to water. However, interpretation of these findings pertaining to molossid activity in this study should be treated with caution, since our data set on this taxon was smaller than for the other two bat families.

Our findings raise a question: What allows molossid bats to forage away from the pools? This may simply be a function of the echolocation call and wing morphology of this family, allowing them

to fly fast in open habitats (Aldridge & Rautenbach, 1987; Monadjem *et al.*, 2010b), such as above the forest canopy. In contrast, the Hipposideridae and Vespertilionidae/Miniopteridae are adapted for foraging in cluttered and edge habitats, respectively (Schoeman & Jacobs, 2008). An alternative explanation is that their diet has an influence on their foraging habitat. Previous studies found that Malagasy molossids eat reasonable amounts of beetles, mainly during summer (Andrianaivoarivelo *et al.*, 2006; Andriafidison *et al.*, 2007). Beetles have a high water content of two-thirds to three-quarters of their body weight (Gray, 1944). In moths, which are important prey for other Malagasy species like *Triaenops* sp. and *Paratriaenops* sp. (Rakotoarivelo *et al.*, 2007), water content is less than 60% (Studier & Sevick, 1992). Further research is required to elucidate the role of diet in the foraging ecology of African bats.

At a community level, however, there were no significant correlations between the environmental variables and bat activity. Since bats are known to be highly mobile (Monadjem *et al.*, 2009; Lehmkuhl Noer *et al.*, 2012), the study area of less than 3 km^2 could have been too small to get an adequate resolution of the community structure. Nevertheless, the pools seem to have an important influence on the bat community (Figure 4), even though there were no significant differences between pool and river community.

There might have been several aspects causing a bias in our results. Bats foraging in cluttered habitats call with a lower intensity (Monadjem *et al.*, 2010b) therefore are less likely to be recorded and could be underestimated in this study. Also, the water pools we sampled and were reported to be the only ones in a radius of several kilometers, but this aspect was not verified.

Our insect census only focused on aerial insects of the lower forest strata. Ground dwelling arthropods or those on leaves, on the water surface or above the canopy were not sampled, even though they could play an important role in bat diet and distribution. The insect census method using flipchart paper so far had only been used to count diurnal insects; further testing of its utility for nocturnal insects is suggested. Even though there was no evidence that the head-torch light acted as an insect attractant over time, an impact of the illuminated paper could not be excluded.

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