

# Foraging Behavior and Habitat Selection of Noack's Round-Leaf Bat (Hipposideros aff. ruber) and Conservation Implications

Authors: Nkrumah, Evans E., Vallo, Peter, Klose, Stefan M., Ripperger,

Simon P., Badu, Ebenezer K., et al.

Source: Tropical Conservation Science, 9(4)

Published By: SAGE Publishing

URL: https://doi.org/10.1177/1940082916680428

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at <a href="https://www.bioone.org/terms-of-use">www.bioone.org/terms-of-use</a>.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# Foraging Behavior and Habitat Selection of Noack's Round-Leaf Bat (Hipposideros aff. ruber) and Conservation Implications

Tropical Conservation Science
October-December 2016: I-II
© The Author(s) 2016
Reprints and permissions:
sagepub.com/journalsPermissions.nav
DOI: 10.1177/1940082916680428
journals.sagepub.com/home/trc



Evans E. Nkrumah<sup>1</sup>, Peter Vallo<sup>2,3</sup>, Stefan M. Klose<sup>2</sup>, Simon P. Ripperger<sup>2</sup>, Ebenezer K. Badu<sup>1</sup>, Florian Gloza-Rausch<sup>4</sup>, Christian Drosten<sup>5</sup>, Elisabeth K. V. Kalko<sup>2,6,‡</sup>, Marco Tschapka<sup>2,6</sup>, and Samuel K. Oppong<sup>1</sup>

#### **Abstract**

In sub-Saharan Africa, anthropogenic activities such as cocoa (*Theobroma cacao*) farming have replaced the natural forest vegetation, making agricultural environments more readily available to some species of bats. To augment bat conservation in such highly modified agro-environments, we evaluated the foraging decisions of the widely distributed Noack's round-leaf bat (*Hipposideros* aff. *ruber*) in a Ghanaian agro-environment for two factors: (a) foraging durations and (b) habitat selection from radio telemetry data collected from 13 bats. We hypothesized that it opportunistically selects foraging habitats in proportion to its availability. Our compositional analysis revealed, however, a nonrandom use of habitats. A ranking matrix indicated *Hipposideros* aff. *ruber* uses all available habitats but strongly preferred seminatural habitats dominated by fallow lands. Cocoa farms were predominantly used as flight paths for commuting between roosts and other nearby habitats during foraging. We observed a mean foraging duration of 109 min (SD = 62 min) per night for the species. In conclusion, our data suggest that (a) they are flexible in selecting all habitat types in the agro-environment but strongly preferred fallow matrices, (b) the provision of canopy trees within the agro-environment serves as flight paths for commuting from roost to habitats offering higher prey densities, and (3) the maintenance of fallow matrices as conservation units in sub-Saharan agro-environments helps augment conservation efforts of the species.

#### **Keywords**

agro-environment, cocoa farms, fallow lands, seminatural habitats, sub-Saharan Africa

#### Introduction

Changes in the behavior of animals represent their survival chances and reproductive successes. These changes are normally expressed in decisions regarding where to forage, when to forage and terminate, and what to consume when foraging (Pyke, Pulliam, & Charnov, 1977; Schoener, 1971; Stephens & Krebs, 1986). Applications of this foraging theory in behavioral ecology have been mostly applied to observed behavior from controlled experiments collected from few minutes to hours. Foraging behavior however can be observed over relatively long periods at spatiotemporal scales from the movement of the animal within its home range (Owen-Smith, Fryxell, & Merrill, 2010). Through radio telemetry, animals can be remotely monitored with minimal

Received 19 May 2016; Revised 25 June 2016; Accepted 27 June 2016

#### **Corresponding Author:**

Samuel K. Oppong, Department of Wildlife and Range Management, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana. Email: kobbyoppong@yahoo.com

<sup>&</sup>lt;sup>1</sup>Department of Wildlife and Range Management, Kwame Nkrumah University of Science and Technology, Kumasi, Ghana

<sup>&</sup>lt;sup>2</sup>Evolutionary Ecology and Conservation Genomics, University of Ulm, Ulm, Germany

<sup>&</sup>lt;sup>3</sup>Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic, Brno, Czech Republic

<sup>&</sup>lt;sup>4</sup>Noctalis Centre for Bat Protection and Information, Bad Segeberg, Germany

<sup>&</sup>lt;sup>5</sup>Institute of Virology, University of Bonn Medical Centre, Bonn, Germany <sup>6</sup>Smithsonian Tropical Research Institute, Balboa, Panama

<sup>‡</sup>Deceased

disturbance to provide information on their foraging decisions such as habitats selected when foraging.

In conservation biology, the selection of habitats by foraging bats is vital for accomplishing effective management and conservation of the species (Flaguer, Puig-Montserrat, Burgas, & Russo, 2008; Russo et al., 2005; Walsh & Harris, 1996), especially in agro-environments that were once biodiversity hotspots but still maintain a considerable level of native biota. Currently, most tropical forests have been converted to agriculture, thus agro-environments are readily becoming available to some wildlife species (Massara, Paschoal, Hirsch, & Chiarello, 2012; Suazo-Ortuño et al., 2015). This widespread conversion is predicted to increase till the collapse of the final period of rapid agricultural expansion around 2050 (Tilman et al., 2001). This calls for an added urgency in identifying conservation strategies through sound scientific measurements to safeguard populations in such environments.

In sub-Saharan Africa which host the world's leading producers of cocoa (Theobroma cacao), Ghana, Cameroon, Nigeria, and Côte d'Ivoire (Asare, 2006), a mosaic of farmlands and fallow lands have largely replaced the natural forest vegetation. This conversion severely impacts wildlife populations. Some species of bats for example are strongly impacted and clearly need pristine forest habitats (Fenton et al., 1992), whereas others benefit. Megaloglossus woermanni, the smallest fruit bat in Africa was observed to frequently access banana plantations near undisturbed natural forest (Weber, Kalko, & Fahr, 2009). This variation among bat species is due to the high variability in morphology and foraging ecology of bats (Castro-Luna, Sosa, & Castillo-Campos, 2007). Also for species in the same community to achieve stable coexistence, they have to differentiate their strategies in exploiting resources (Russo et al., 2005), leading to exploitation of diverse resources such as foraging habitats. Among insectivorous bats, exploitation of specific habitats is linked to flight capability (Aldridge & Rautenbach, 1987) and echolocation behavior (Schnitzler & Kalko, 2001). For example, bats hunting for insects in cluttered environments require a high maneuverability provided by a specially adapted wing morphology (Norberg & Rayner, 1987), and an echolocation system that avoids masking of prev echoes by the reflections from the background (Schnitzler & Kalko, 2001). These special adaptations of insectivorous bats potentially make them vulnerable within agro-environments. In their hunting strategy, bats often adapt to particular habitats and their hunting success can be significantly affected in the agro-environment due to insect availability and habitat structure. Insectivorous bats using agro-environments may therefore select habitats that are closely adapted to their hunting strategies during foraging.

In this study, we used radio telemetry to quantitatively assess for the first time some of the foraging decisions made by the Noack's round leaf bat Hipposideros ruber from sub-Saharan agro-environment in Africa. We predicted that *Hipposideros ruber* opportunistically uses habitats in proportion to its availability in the agro-environment. We also provide further information on its foraging durations, hunting strategies, and night activity patterns. On the island of São Tomé (Gulf of Guinea), sexes of *Hipposideros ruber* experience temporal niche shift with females dominating activities while males dominating nocturnal activities (Russo, Maglio, Rainho, Meyer, & Palmeirim, 2011), probably caused by depauperate avian predators on the island. We therefore asked whether the sexes of our study species Hipposideros ruber exhibit differences in nightly activities.

#### **Methods**

# Study Area

The study site was located in the Ashanti Region of Ghana in West Africa (Figure 1), 4 km from the town of Kwamang. The study lasted 19 months, between February 2011 and July 2012. The landscape of Kwamang consists mainly of undulating terrain, ranging from hills to lowlands, between 320 m to 540 m asl. The mean annual rainfall is between 1,200 mm to 1,500 mm with an average temperature of 27°C. Decades ago, the surrounding vegetation of Kwamang formed part of the moist semideciduous forest of Ghana (Pappoe, Armah, Quaye, Kwakye, & Buxton, 2010). Currently, it is dominated by a mosaic of agricultural fields ranging from cocoa farms, mixed-cropped farms, fallow lands, and rural settlements (Figure 1). These habitats were therefore characterized based on actual stand type and canopy cover (Table 1). Situated within this agricultural landscape are natural caves that serve as both day and night roost for bats. The Mframabuom cave (07° 00'13" N, 01°18′02″W) which is located 4 km from the Kwamang village was selected for this study. This cave harbors several bat species such as *Hipposideros abae*, *Hipposideros* jonesi, Hipposideros gigas, Hipposideros aff. ruber, and Nycteris cf. gambiensis.

## Study Species

Noack's round leaf bat (*Hipposideros ruber*) is a small bat (forearm length = 51 mm, body mass = 10g). Its range covers most of sub-Saharan Africa (Happold, 2013), and it comprises several sister lineages within its geographic distribution (Monadjem et al., 2013; Vallo et al., 2011; Vallo, Guillén-Servent, Benda, Pires, & Koubek, 2008). In central Ghana, only one of this lineage

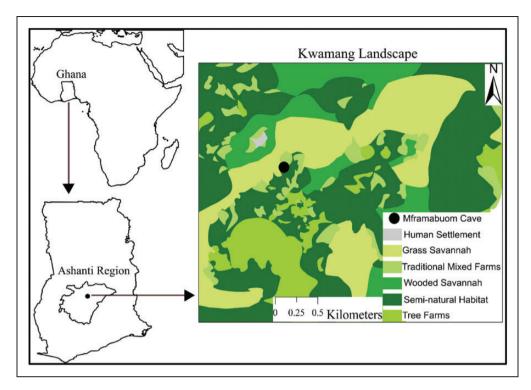


Figure 1. Surrounding habitat of the Mframabuom cave in central Ghana. Refer to Table 1 for habitat definitions.

Table 1. Habitat Characterization Around Mframabuom Cave.

Habitat type	Categories of stand type and definition					
Grass Savannah (GS) <sup>a</sup>	Grass-dominated area with very few isolated trees. Dominant grass is <i>Panicum maximum</i> (Guinea grass). This habitat is fire prone and burned in the dry season (generally in January and February).					
Wooded Savannah (WS) <sup>a,b</sup>	Mixture of grasses and trees. Dominant stand type is short trees. The trees are more dense packed than GS, providing more canopy cover. Grasses here form an understory vegetation. This vegetation is also fire prone in the dry season yet there is no deliberate burning.					
Tree Farms (TF) <sup>b</sup>	This category includes tree monocultures. Cultivated trees include mainly cocoa, oil palm, and cashew farms. There is complete canopy cover with almost no understory vegetation. Dominant type in this study area are cocoa farms.					
Traditional Mixed Farms (TMF) <sup>b</sup>	Includes farmlands with open vegetation, without canopy cover. This category comprises mixed farms cultivating cassava, maize, or plantain.					
Seminatural Habitats (SnH) <sup>b</sup>	Include fallow lands at varying successional stages. Vegetation composed of trees, shrubs, and herbaceous plants. There is canopy cover in some areas, while others are more open due to early succession or illegal logging activities.					
Human Settlement (HS)	Rural dwelling of humans with few ornamental trees.					

<sup>&</sup>lt;sup>a</sup>Trees height approximation: (<10 m high).

(lineage D of Vallo et al., 2008) has been reported which is evolutionarily distant to *Hipposideros ruber* s. str. from East Africa. *Hipposideros* aff. *ruber* is thus used in this article to refer to this lineage. *Hipposideros* aff. *ruber* roost in groups ranging from few individuals in trees to several thousands in caves and mines but are

flexible in selecting tree roosts (Happold, 2013). In Ghana, the species is mostly in caves (Nkrumah et al., 2016).

Its echolocation contains both constant frequency (CF) and frequency modulated (FM) components with peak frequency approximately 127 kHz (Monadjem

<sup>&</sup>lt;sup>b</sup>Timber species are present but isolated (Cola gigantea, Triplochiton scleroxylon, and Ceiba pentandra).

et al., 2013). These components of their calls enable them to forage in very dense and cluttered vegetation (Aldridge & Rautenbach, 1987; Monadjem, Taylor, Cotterill, & Shoeman, 2010). Its hunting strategies are not known but suspected to be similar to those of *Hipposideros ruber s.str.*, which is equally successful in using both gleaning and aerial hunting strategies in capturing prey (Bell & Fenton, 1984). In both approaches, it occasionally captures prey with the mouth but more frequently scoops with the wing membrane and transfers it to the mouth in flight or gleans from surface, occasionally touching down (Happold, 2013).

# Bat Capture, Tagging, and Radio Telemetry

Thirteen bats were captured with a 6-m nylon mist net in front of the Mframabuom cave between 4:30 a.m. and 6:00 a.m. in the early morning. Bat sampling and capture at the Mframabuom cave was approved by the Ghana Wildlife Division and by the community council of the Kwamang village. Only adult bats were selected in this study. This was done by looking at the degree of closure of the phalangeal epiphyses after Anthony (1988). Selected bats were fitted with radio transmitters (BD-2 Transmitter; Holohil Systems Ltd., Ontario, Canada) with latex adhesive at the lower back of the bat (Osto-Bond, OC, Canada). The weight of transmitters used was 0.65 g, thus corresponding to the 10% body to transmitter ratio recommended by Sikes, Gannon, and Animal Care and Use Committee, of the American Society of Mammalogist (2011). Radio tracking began the evening after capture. During tracking, one bat was tracked per night by two trackers equipped with radio receivers (VR 500; Yaesu Musen Co. Ltd., Japan, modified by Andreas Wagener Telemetrieanlagen, Cologne, Germany), GPS, and a compass. Transmitters broadcasted on radio frequencies around 151 MHz. The two trackers communicated by walkie-talkie (Albrecht CTE 180) and recorded the direction of the strongest signal every 2 min when the bat was in flight and every 5 min when resting. This assessment of bat activity was made possible by the variation in pulse rate of the positionsensitive transmitters. The pulse rate doubled when the bat was flying after a resting phase. This fluctuation in pulse allowed the bats' activity to be monitored while collecting bearing data for determining the location of the bat.

#### Data Analysis

Bearing data from the 13 bats collected by both observers were triangulated using the software LOAS (Ecological Software Solutions LLC, 1998–2012) to determine the location of the bats. For assuring high-quality data, we included only pairs of bearings with crossing angles larger

than 15° and less than 165° (Weber et al., 2009). The home range of all tracked bats (study area) and foraging area of each individual bat were estimated using local convex hulls (LoCoH; Getz et al., 2007; Getz & Wilmers, 2004) carried out in LoCoH web application (http://locoh.cnr.berkeley.edu; University of Berkeley) as applied in Nkrumah et al. (2016). For the purpose of defining the available habitat to bats around the Mframabuom cave, data from all tracked bats were pooled together to generate the home range (100% isopleths) of all bats, which represented our study area. The foraging area of each bat, that is, the area probably used for gathering and processing of food (Weber et al., 2009), was considered as the area limited by the 95% isopleths.

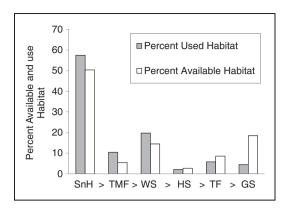
For habitat analysis, polygons of the foraging areas were superimposed on the study area habitat map using ArcGIS version 10. To assess habitat selection of Hipposideros aff. ruber, we compared habitat composition within the foraging areas of each bat to habitat availability within the entire study area (Appendix A). This comparison was conducted by a compositional analysis (Aebischer, Robertson, & Kenward, 1993) using the software Compos Analysis version 6.3+ (Compositional Analysis Plus Microsoft Excel tool 6.3, Smith Ecology Ltd., Abergavenny, UK). Randomization tests (1,000 iterations) were performed to solve the problem of nonnormality of the data in multivariate analysis, and 0.01% (less than the smallest non-zero value in available or used habitat) was used to replace missing values in use and available habitats (Aebischer et al., 1993). We calculated Wilk's λ as a weighted mean. We then used a ranking matrix to determine the relative importance of each of the habitat to this bat.

Foraging behavior of *Hipposideros* aff. *ruber* was analyzed for the duration of foraging flights. This was calculated as the total time spent in flight during all foraging flights per night. This analysis included only nights with more than 70% contact time with the bat. Maximum contact time possible was 11 h for each night beginning from 7:00 p.m. to 6:00 a.m. of the next morning. Mann–Whitney test performed in Minitab version 16 (Minitab Inc. State College, PA, USA; www.minitab.com) was used to access the differences between the night activities of both sexes and between the activity of the first and second half of the night. All statistical tests were accepted at a critical alpha level of p < .05.

#### **Results**

#### Habitat Selection

Analysis of 1192 valid radio locations from the 13 individuals indicates a variety in their selection of habitats during foraging (Appendix A). The comparison of the



**Figure 2.** Comparison of used and available habitat within the home range of *Hipposideros* aff. *ruber* (n=13). Habitat on the left were selected over those on the right, but no significant differences were observed between adjacent habitats (i.e., where there is '>'). Abbreviations listed in Table 1.

proportional habitat use within the foraging area to the available habitats within the entire study area indicates a nonrandom habitat use by the foraging bats (Wilk's  $\lambda = 0.17$ , Chi-square test = 23.42, p = .0003 or p < .001by randomization, df = 5). This analysis allowed the ordering of habitats according to their relative importance to the bats and to access significant differences in spatial use between them. The bats used the available habitats in the following order, from most to least used: seminatural habitats > traditional mixed farms > wooded savannah > human settlement > tree farms > grass savannah, with no significant differences observed between adjacent habitats (Figure 2). Seminatural habitats were significantly preferred (+++) over all other habitats with the exception of the traditional mixed farms (+) (Table 2). The ranking matrix also indicates that tracked bats preferred traditional mixed farms (+++) over tree farms (Table 2), while grass savannah was the least important habitat for foraging bats although more was available than the three other habitats (Figure 2).

#### Foraging Activity

Foraging activity showed a trimodal activity pattern. Flight activity peaked immediately after emergence in the evening, around midnight, and again in the morning (Figure 3). Emerging time of the bats was mostly around 6:25 p.m., characterized by first flying multiple times in and out of the cave before finally leaving to forage. After emerging, it actively searched the foraging area before resting, with intermittent feeding bouts as the night progressed. Males tended to be more active throughout the night than their female counterparts (Figure 3). We did not observe any difference in the activity patterns of males and females (W=173, p=.19; males = 8, females = 5). The foraging activities of bats appeared to

be higher in the first half of the night than in the second, but there was no significant difference (W = 179, p = .09). We found the foraging duration of this bat to be 109 min (SD = 62 min) per night.

During radio tracking, we noticed that *Hipposideros* aff. *ruber* embarked on very brief flight episodes while resting in the foraging area. The duration of these flights was about 4 s and they happened about 7 times per night, depending on the individual bat. This activity was, however, difficult to quantify, as these flight events were extremely short. Also, we were able to collect photographic images of *Hipposideros* aff. *ruber* feeding around street lights in the Kwamang town (Appendix B). We have to clarify, however, that these images are not from bats involved in radio tracking.

#### **Discussion**

#### Habitat Selection

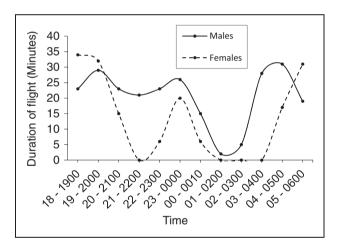
The decision of animals in selecting certain habitat types within their home range is of prime importance for conservation and wildlife management. Our initial hypothesis that Hipposideros aff. ruber uses habitats in proportion to its availability was rejected based on the compositional analysis. The bat preferred to forage in seminatural habitats, followed by the traditional mixed farm areas. Savannah grasslands were least utilized by foraging bats, followed by tree farms. Preference for a single habitat type during foraging is uncommon among insectivorous bats, and the results are consistent with other studies reporting the use of multiple habitat types (Zeale, Davidson-Watts, & Jones, 2012; Zukal & Řehak, 2006). Foraging in all habitat types around the roost cave indicates considerable flexibility in habitat use. In bats, ecological and behavioral patterns such as foraging strategies and spatial use are expected to be similar in phylogenetically related species that share similarities in morphology and diets (Weber et al., 2009). Little is published about the foraging decisions and behavior of Hipposideros aff. ruber, but data from phylogenetically similar species might provide some useful comparisons.

Bats in the genus *Hipposideros* have been categorized as highly cluttered space aerial insectivorous species based on the nature and structure of their echolocation calls, that is, the use of long-duration, medium- to high-frequency CF and CF-FM signals (Schnitzler & Kalko, 2001). The seminatural habitats surrounding the roost cave are made of fallow lands with trees, shrubs, and herbaceous plants forming a well-developed undergrowth thicket. This cluttered environment might perhaps explain why *Hipposideros* aff. *ruber* preferred this habitat over the others. Additionally, prey availability and distribution also affect where a bat concentrates its foraging activities (Warren, Waters, Altringham, & Bullock, 2000;

<b>Table 2.</b> Ranking Matrix for the Radio Tracked Individuals of Hipposideros aff. ruber ( $n = 13$ ) based on comparison of percent habitat use
within individual foraging area (95% isopleths) to the available habitat within the study area (home range of all tracked bats at 100%
isopleths).

	Seminatural habitats	Tree farms	Wooded savannah	Grass savannah	Traditional mixed farms	Human settlement	Rank
Seminatural habitats		+++	+ (+++)	+++	+	+++	5
Tree farms			_	+	<b>–</b> ()	_	I
Wooded savannah	<b>–</b> ()	+		+	_	+	3
Grass savannah		_	_			_	0
Traditional mixed farms	_	+ (+++)	+	+++		+	4
Human settlement		+	_	+	_		2

The habitat in every row is compared with the corresponding habitat in the column. The symbol '+' indicate habitat in row category were more used by the bat than expected, compared with the habitat in the corresponding column whiles '-' indicate a lesser use. In either case where '+' or '-' symbol appears, significant differences were not observed between the two compared habitats (p > .05), whereas the triple symbols '+++' or '---' indicate 'preference' and 'least preferred respectively, at a significance level of p < .05. These significance values are chosen from the randomization results but instances where significant differences were found using a standard t test, they are shown in parenthesis. The rank for each habitat was calculated from the number of '+' or '+++' in the rows. The rank number in the last column indicates the relative importance of the habitat to the bat from 0 (least important) to 5 (most important).



**Figure 3.** Night activity pattern of male and female bats of *Hipposideros* aff. *ruber*.

Zukal & Řehak, 2006). Insectivorous bats are known to respond opportunistically to areas with high prey densities (Rydell, 1992), so their use of a particular habitat type is strongly linked to prey availability (Kusch, Weber, Idelberger, & Koob, 2004). The seminatural habitats present a higher structural complexity than the other habitats, which might enhance insect diversity and abundance (Lassau & Hochuli, 2005). *Hipposideros ruber* is highly specialized in hunting lepidopterans (Bell & Fenton, 1983) and thus can be expected to select habitats rich in lepidopterans over other habitats. Prey availability in the various habitats around the Mframabuom cave was not investigated, but dietary analysis from over

1,000 individuals of *Hipposideros* aff. *ruber* from the Mframabuom cave suggests it as a lepidopteran specialist (E. K. Badu, unpublished data). Their preference for using the seminatural habitats may therefore indicate locally higher densities of lepidopterans within this habitat type. However, a confirmation of this is needed in future studies also including a quantitative assessment of lepidopterans from habitats within the home range of this bat.

Although Hipposideros aff. ruber at first glance preferred seminatural habitats over other habitats, there was no significant difference in the use of this habitat over traditional mixed farms (Table 2), indicating that both habitats might support insect prey of importance for the bats. This finding to some extent suggests that a foraging bat might place the highest priority on the availability of prey, instead of directly deciding which habitat type to select for foraging. Decisions considering just prey availability might result in foraging in very open areas, such as the traditional mixed farms, and around street lights (Appendix B) irrespective of a potentially increased exposure to predation. Provided the availability of sufficient prey, open habitats could be selected over more cluttered areas, despite less protection from predators than in more sheltered habitat types such as savannah woodland or tree farms. However, at similar prey availability, habitats providing more cover from predators like the seminatural habitats should be selected over more open areas (e.g., traditional mixed farms) as indicated in Table 2.

This however contrasts other reports stating that the first decision of a foraging bat is on the type of habitat,

with prey availability being the second (Johnson, Lacki, & Baker, 2007; Whitaker Jr., 1994). This contrary finding, however, needs clarifications through future studies that also consider local prey availability within the different habitat types. Actually, telemetry data reflect not only the habitat choice of a bat individual but also to some extent prey availability. A bat will not choose to stay too long in a habitat that provides no prey. On the other hand, prey availability for a particular bat species might also depend on the plant species composition of a given habitat, how insects are distributed in the habitat structure, and how these structures match the species-specific echolocation behavior. In consequence, foraging decisions concerning habitat and prey availability are probably rather closely linked to each other.

The least used habitats during foraging were the savannah grasslands. This might be a consequence of the season when bats were tracked, as at this time most places were burnt and probably could support little to no prey items. Contrary to expectation, tree farms, mainly cocoa farms were the second least preferred habitat by foraging bats after the grass savannahs. Human settlements were even more frequently used for foraging than the tree farms. Insectivorous bats respond readily to high insect abundance around street lights within human settlement (Rydell, 1992). For example, Tadarida teniotis and Tadarida brasiliensis have been observed to forage opportunistically in illuminated cities and rural settlements (Avila-Flores & Fenton, 2005; Carmel & Safriel, 1998). Near our study area (Kwamang town), Hipposideros aff. ruber was recorded on many occasions catching prey around streetlight (Appendix B). The results indicate that the cocoa farms were of less importance to foraging bats. The severe use of agrochemicals on these farms might have decreased insect availability and consequently also hunting success for Hipposideros aff. ruber (Desneux, Decourtye, & Delpuech, 2007). Also, the lack of understorey vegetation in these farms might additionally have reduced insect diversity and abundance (Lassau & Hochuli, 2005). Bats therefore use these farms predominantly as flight paths for commuting between roost cave and foraging areas, as the canopy closure provided good coverage from predators such as owls that were ubiquitous in the study area. From a conservation point of view, this certainly underlines the importance of providing canopy trees in agro-environments to provide cover from predators (Jones & Rydell, 1994; Russo, Cistrone, & Jones, 2007).

# Foraging Behavior

Hipposideros aff. ruber emerged from the cave during the late twilight phase. Emergence before full darkness might increase the predation risk from raptorial birds (Jones & Rydell, 1994), such as crows and black kites. It was expected that the emergence of *Hipposideros* aff. *ruber* from the cave coincides with the flight activity of lepidopterans which predominantly form a larger part of its diet. The flight activity of most lepidopterans, especially moths, in both the Neotropic and Afrotropic peaks around 6:30 p.m. and 9:45 p.m. (Axmacher et al., 2004; Brehm, Pitkin, Hilt, & Fiedler, 2005). However, peak activity of some geometrid moths, one of the largest families of moths with over 21,000 species (Scoble, 1999), occurs later at night (Brehm et al., 2005).

Foraging activity of *Hipposideros* aff. ruber followed a distinct trimodal pattern for both sexes (Figure 3) with major peaks in early night and morning. A trimodal activity pattern has also been observed in other insectivorous bats, for example, in the European noctule bat, Nyctalus noctula (Kronwitter, 1988). Prior to midnight, activity increases and declines again immediately after the late twilight perhaps to coincide with the first activity peak of moths. In addition, it could be that the early emergence, immediately after twilight, serves to take also an advantage of the peak abundance of other insects, although these may form a lesser percentage of its diet. Also, it is very likely that Hipposideros aff. ruber increased its foraging activities around midnight to coincide with some moth species such as those in the family Geometridae that have a very late activity peak (Brehm et al., 2005).

Foraging activity patterns did not differ between both sexes of Hipposideros aff. ruber. Female activities, however, stopped completely around 10:00 p.m. and between 2:00 a.m. and 4:00 a.m., whereas the males kept up at least some minimal activity during this time. It was noticed while resting within the foraging area, bats made repeatedly short flies of few seconds. We suspect that these short flight events represent brief feeding flight towards an insect detected through echolocation by a perch hunting bat. Although this is highly speculative, perch hunting has been recorded in other Hipposiderid bats such as Hipposideros commersoni (Terry, 1977) and Hipposideros diadema (Brown & Berry, 1983), so our observations might be a confirmation of this hunting strategy also for Hipposideros aff. ruber.

## Implications for Conservation

As a result of the loss of pristine forests, bat populations increasingly depend on modified habitats from agro-environments (Stebbings, 1995). This study shows that *Hipposideros* aff. *ruber* was flexible in the choice of habitats selected during foraging in the Kwamang agro-environment. Their preference for seminatural habitats

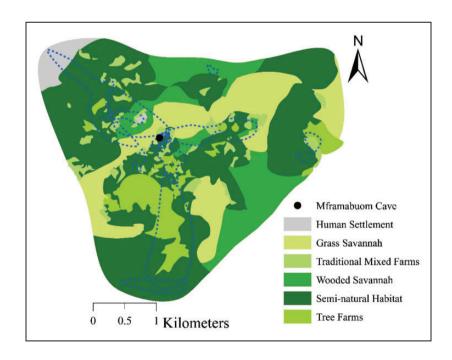
that are dominated by agricultural fallow lands suggests that these areas are important to the survival of the species. Conservation strategies should therefore aim at maintaining these fallow lands within the sub-Saharan agro-environments as conservation units to primarily serve as foraging destinations for these insectivorous bats. This is because, within the fallow lands, natural succession begins to take over, thereby improving vegetation quality and faunal diversity and composition of especially insects.

Also, the tree farms that were mostly dominated by the cocoa farms were of less importance to foraging bats. It is not uncommon to find cocoa farmers using agrochemicals in this region to improve crop yield. Severe use of agrochemicals might have rendered these farms unfavorable for insects and consequently for the foraging bats

(Desneux et al., 2007). The bats mainly used these farms as flight paths to commute from the roost cave to foraging areas to perhaps avoid predators that are ubiquitous in the area. Within sub-Saharan agro-environments, especially in areas where significant canopy cover is lacking, we propose the provision of canopy trees to serve as potential commuting routes to allow bats commute to close-by habitats that support higher prey densities. Herein also lies the urgency of educating Kwamang farmers through strategic conservation education programs to incentivize them to take specific actions that are favorable to the long-term maintenance of these fallows. Importantly, for them to see the bats using their farms as nonharmful inhabitants but as rather important providers of ecosystem services such as control of pest insect populations.

# Appendix A

Habitats selected around the Mframabuom cave by foraging bats within the study area (home range of all tracked bats). Dotted lines indicate foraging areas of bats. Refer to Table 1 for habitat definitions.



# Appendix B

Street light from Kwamang teaming with insects (a), and *Hipposideros* aff. ruber in flight around this street light (b).



#### **Acknowledgments**

We would like to thank the following field workers especially for their outstanding contribution to nocturnal data collection: David Ofori Agyei, Kathrin Kubicek (University of Ulm), and Ebenezer Gyimah. We are grateful to the following volunteers who also contributed their time and effort to the project: Julia Morrison and Lucinda Kirkpatrick. We are also grateful to Heather J. Baldwin for assisting in the transportation of needed field supplies from Germany to Ghana.

# **Declaration of Conflicting Interests**

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

#### **Funding**

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: The study was supported with funds from the German Research Foundation (DFG) awarded to E. K. V. K. (KA 1241/18-1).

#### References

Aebischer, N. J., Robertson, P. A., & Kenward, R. E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology*, 74, 1313–1325.

Aldridge, H. D. J. N., & Rautenbach, I. L. (1987). Morphology, echolocation and resource partitioning in insectivorous bats. *Journal of Animal Ecology*, 56, 763–778.

- Anthony, E. L. P. (1988). Age determination in bats. In: T. H. Kunz (ed.) *Ecological and behavioral methods for the study of bats* (pp. 47–58). Washington, DC: Smithsonian Institution Press.
- Asare, R. (2006). A review on cocoa agroforestry as a means for biodiversity conservation. Paper presented at the World Cocoa Foundation Partnership Conference, Brussels, Belgium.
- Avila-Flores, R., & Fenton, M. B. (2005). Use of spatial features by foraging insectivorous bats in a large urban landscape. *Journal* of Mammalogy, 86, 1193–1204.
- Axmacher, J. C., Holtmann, G., Scheuermann, L., Brehm, G., Müller-Hohenstein, K., & Fiedler, K. (2004). Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. *Diversity and Distributions*, 10, 293–302.
- Bell, G. P., & Fenton, M. B. (1983). Echolocation and foraging behavior of *Hipposideros ruber* (Chiroptera). *Journal of the Acoustical Society of America*, 74(S1): S32.
- Bell, G. P., & Fenton, M. B. (1984). The use of Doppler-shifted echoes as a flutter detection and clutter rejection system: The echolocation and feeding behavior of *Hipposideros ruber* (Chiroptera: Hipposideridae). *Behavioral Ecology and Sociobiology*, 15, 109–114.
- Brehm, G., Pitkin, L. M., Hilt, N., & Fiedler, K. (2005). Montane Andean rain forests are a global diversity hotspot of geometrid moths. *Journal of Biogeography*, *32*, 1621–1627.
- Brown, P. E., & Berry, R. D. (1983). Echolocation behavior in a "flycatcher" bat. *Hipposideros diadema. The Journal of the Acoustical Society of America*, 74(S1): S32.
- Carmel, Y., & Safriel, U. (1998). Habitat use by bats in a Mediterranean ecosystem in Israel – Conservation implications. *Biological Conservation*, 84, 245–250.
- Castro-Luna, A. A., Sosa, V. J., & Castillo-Campos, G. (2007). Bat diversity and abundance associated with the degree of secondary succession in a tropical forest mosaic in south-eastern Mexico. *Animal Conservation*, 10, 219–228.
- Desneux, N., Decourtye, A., & Delpuech, J.-M. (2007). The sublethal effects of pesticides on beneficial arthropods. *Annual Review of Entomology*, 52, 81–106.
- Fenton, M. B., Acharya, L., Audet, D., Hickey, M. B. C.,
  Merriman, C., Obrist, M. K.,...Syme, D. M. (1992).
  Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica*, 24, 440–446.
- Flaquer, C., Puig-Montserrat, X., Burgas, A., & Russo, D. (2008). Habitat selection by Geoffroy's bats (*Myotis emarginatus*) in a rural Mediterranean landscape: Implications for conservation. *Acta Chiropterologica*, 10, 61–67.
- Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryana, S. J., & Wilmers, C. C. (2007). LoCoH: Nonparameteric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE*, 2, e207.
- Getz, W. M., & Wilmers, C. C. (2004). A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography*, 27, 489–505.
- Happold, M. (2013). Hipposideros ruber Noak's leaf-nosed bat. In: M. Happold, & D. Happold (Eds.). Mammals of Africa Volume IV, Hedgehogs, Shrews and bats London, England: Bloomsbury, p. 800.
- Johnson, J. S., Lacki, M. J., & Baker, M. D. (2007). Foraging ecology of long-legged myotis (*Myotis volans*) in North-Central Idaho. *Journal of Mammalogy*, 88, 1261–1270.

- Jones, G., & Rydell, J. (1994). Foraging strategy and predation risk as factors influencing emergence time in echolocating bats. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 346, 445–455.
- Kronwitter, F. (1988). Population structure, habitat use and activity patterns of the noctule bat, *Nyctalus noctula* Schreb., 1774 (Chiroptera: Vespertillionidae) revealed by radio-tracking. *Myotis*, 26, 23–85.
- Kusch, J., Weber, C., Idelberger, S., & Koob, T. (2004). Foraging habitat preferences of bats in relation to food supply and spatial vegetation structures in a western European low mountain range forest. *Folia Zoologica*, 53, 113–128.
- Lassau, S. A., & Hochuli, D. F. (2005). Wasp community responses to habitat complexity in Sydney sandstone forests. *Austral Ecology*, 30, 179–187.
- Massara, R. L., Paschoal, A., Hirsch, A., & Chiarello, A. G. (2012).Diet and habitat use by maned wolf outside protected areas in eastern Brazil. *Tropical Conservation Science*, 5, 284–300.
- Monadjem, A., Richards, L., Taylor, P. J., Denys, C., Dower, A., & Stoffberg, S. (2013). Diversity of Hipposideridae in the Mount Nimba massif, West Africa, and the taxonomic status of *Hipposideros lamottei*. *Acta Chiropterologica*, *15*, 341–352.
- Monadjem, A., Taylor, P. J., Cotterill, F. P. D., & Shoeman, M. C. (2010). Bats of Southern Africa: A biogeographic and taxonomic synthesis. Johannesburg, South Africa: University of the Witwatersrand.
- Nkrumah, E. E., Peter, V., Klose, S., Ripperger, S., Badu, K. E., Drosten, C.,... Oppong, S. (2016). Home range of Noack's round-leaf bat (*Hipposideros* aff. *ruber*) in an agricultural land-scape of central Ghana. *Acta Chiropterologica*, 18, 239–247.
- Norberg, U. M., & Rayner, J. M. V. (1987). Ecological morphology and flight in bats (Mammalia; Chiroptera): Wing adaptations, flight performance, foraging strategy and echolocation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 316, 335–427.
- Owen-Smith, N., Fryxell, J., & Merrill, E. (2010). Foraging theory upscaled: The behavioural ecology of herbivore movement. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365, 2267–2278.
- Pappoe, A. N. M., Armah, F. A., Quaye, E. C., Kwakye, P. K., & Buxton, G. N. T. (2010). Composition and stand structure of a tropical moist semi-deciduous forest in Ghana. *International Research Journal of Plant Science*, 1, 95–106.
- Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: A selective review of theory and tests. *Quarterly Review of Biology*, *52*, 137–154.
- Russo, D., Almenar, D., Aihartza, J., Goiti, U., Salsamendi, E., & Garin, I. (2005). Habitat selection in sympatric *Rhinolophus mehelyi* and *R. euryale* (Mammalia: Chiroptera). *Journal of Zoology*, 266, 327–332.
- Russo, D., Cistrone, L., & Jones, G. (2007). Emergence time in forest bats: The influence of canopy closure. *Acta Oecologica*, 31, 119–126.
- Russo, D., Maglio, G., Rainho, A., Meyer, C. F. J., & Palmeirim, J. M. (2011). Out of the dark: Diurnal activity in the bat *Hipposideros ruber* on São Tomé island (West Africa). *Mammalian Biology*, 76, 701–708.
- Rydell, J. (1992). Exploitation of insects around streetlamps by bats in Sweden. *Functional Ecology*, *6*, 744–750.

Schnitzler, H.-U., & Kalko, E. K. V. (2001). Echolocation by insect-eating bats. *BioScience*, *51*, 557.

- Schoener, T. W. (1971). Theory of feeding strategies. *Annual Review of Ecology and Systematics*, 2, 369–404.
- Scoble, M. J. (1999). Geometrid moths of the world: A catalogue (Lepidoptera, Geometridae). The Natural History Museum. London, England: CSIRO.
- Sikes, R. S., & Gannon, W. L.; Animal Care and Use Committee of the American Society of Mammalogist. Guidelines of the American Society of mammalogist for the use of wild mammals in research (2011) *Journal of Mammalogy*, 92, 235–253.
- Stebbings, R. E. (1995). Why should bats be protected? A challenge for conservation. *Biological Journal of the Linnean Society*, 56, 103–118.
- Stephens, D. W., & Krebs, J. R. (1986). Foraging theory. Princeton. NJ: Princeton University Press.
- Suazo-Ortuño, I., Alvarado-Díaz, J., Mendoza, E., López-Toledo,
  L., Lara-Uribe, N., Márquez-Camargo, C., ... Rangel-Orozco, J.
  D. (2015). High resilience of herpetofaunal communities in a human-modified tropical dry forest landscape in western
  Mexico. Tropical Conservation Science, 8, 396–423.
- Terry, A. V. (1977). Foraging behaviour of the giant leaf-nosed bat (Hipposideros commersoni). African Journal of Ecology, 15, 237–249.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., . . . Swackhamer, D. (2001). Forecasting agriculturally driven global environmental change. *Science*, 292, 281–284.
- Vallo, P., Benda, P., Martinkova, N., Kanuch, P., Kalko, E. K. V., Cerveny, J.,...Koubek, P. (2011). Morphologically uniform bats *Hipposideros* aff. *ruber* (Hipposideridae) exhibit high

- mitochondrial genetic diversity in southeastern Senegal. *Acta Chiropterologica*, 13, 79–88.
- Vallo, P., Guillén-Servent, A., Benda, P., Pires, D., & Koubek, P. (2008). Variation of mitochondrial DNA in the *Hipposideros caffer* complex (Chiroptera: Hipposideridae) and its taxonomic implications. *Acta Chiropterologica*, 10, 193–206.
- Walsh, A. L., & Harris, S. (1996). Foraging habitat preferences of vespertilionid bats in Britain. *Journal of Applied Ecology*, 33, 508–518.
- Warren, R. D., Waters, D. A., Altringham, J. D., & Bullock, D. J. (2000). The distribution of Daubenton's bats (*Myotis daubentonii*) and pipistrelle bats (*Pipistrellus pipistrellus*) (Vespertilionidae) in relation to small-scale variation in riverine habitat. *Biological Conservation*, 92, 85–91.
- Weber, N., Kalko, E. K. V., & Fahr, J. (2009). A first assessment of home range and foraging behaviour of the African long-tongued bat *Megaloglossus woermanni* (Chiroptera: Pteropodidae) in a heterogeneous landscape within the Lama Forest Reserve, Benin. *Acta Chiropterologica*, 11, 317–329.
- Whitaker, J. O. Jr (1994). Food availability and opportunistic versus selective feeding in insectivorous bats. Bat Research News, 35, 75–77.
- Zeale, M. R. K., Davidson-Watts, I., & Jones, G. (2012). Home range use and habitat selection by barbastelle bats (*Barbastella barbastellus*): Implications for conservation. *Journal of Mammalogy*, 93, 1110–1118.
- Zukal, J., & Řehak, Z. (2006). Flight activity and habitat preference of bats in a karstic area, as revealed by bat detectors. *Folia Zoology*, 55, 273–281.