Activity of the insectivorous bat *Pteronotus parnellii* relative to insect resources and vegetation structure

Leonardo Queiroz de Oliveira, Rodrigo Marciente, William E. Magnusson, and Paulo Estefano D. Bobrowiec*

Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia (INPA), Av. André Araújo 2936, CP 2223, Manaus-AM 69080-971, Brazil

* Correspondent: paulobobro@gmail.com

Riparian areas often are assumed to be necessary sites for foraging by insectivorous bats because of high insect availability and ease of movement and echolocation in the forest. However, effects of vegetation clutter and insect availability on bat activity have not been compared between riparian and nonriparian areas. We used autonomous recorders to evaluate the effects of vegetation structure, insect mass, and assemblage composition on the activity of the aerial insectivorous bat *Pteronotus parnellii* along stream channels and nonriparian areas in a tropical rainforest in central Brazilian Amazonia. We quantified vegetation clutter using horizontal photographs, captured nocturnal insects with light traps, and recorded bat activity for 110 nights (1,320 h) in 22 sampling plots. *Pteronotus parnellii* was more active in sites with dense understory vegetation, which were more common away from riparian zones. Bat activity was related to insect availability (mass and composition), independent of the habitat type. Ability to detect insects on vegetation and avoid obstacles should not restrict the activity of *P. parnellii* in cluttered sites. This suggests that mass and species composition of insects had stronger influences on habitat use than did vegetation clutter. *Pteronotus parnellii* probably selects cluttered places as feeding sites due to the availability of higher quality prey.

Áreas ripárias são muitas vezes consideradas locais necessários para o forrageio por morcegos insetívoros por causa da alta disponibilidade de insetos e facilidade de movimento e recepção da ecolocalização na floresta. No entanto, os efeitos da obstrução da vegetação e disponibilidade de insetos sobre a atividade de morcegos não têm sido comparados entre as áreas ripárias e não ripárias. Nós usamos gravadores autônomos de ultrassom para avaliar os efeitos da estrutura da vegetação, massa e composição da assembleia de insetos sobre a atividade do morcego insetívoro aéreo *Pteronotus parnellii* ao longo do canal central de riachos e áreas não ripárias em uma floresta tropical na Amazônia central brasileira. Nós quantificamos a obstrução da vegetação usando fotografias horizontais da floresta, capturamos os insetos noturnos com armadilhas luminosas e gravamos a atividade dos morcegos durante 110 noites (1.320 h) em 22 pontos de amostragem. *Pteronotus parnellii* foi mais ativo em locais com vegetação arbustiva densa, que foram mais comuns longe das zonas ripárias. A atividade dos morcegos foi relacionada com a disponibilidade de insetos (massa e composição), independente do tipo de habitat. A capacidade de detectar insetos sobre a vegetação e evitar obstáculos não deve restringir a atividade de *P. parnellii* em locais obstruídos. Isto sugere que a massa e a composição de espécies de insetos tiveram forte influência sobre o uso do habitat do que a obstrução da vegetação. *Pteronotus parnellii* provavelmente seleciona lugares obstruídos como locais de alimentação devido à disponibilidade de presas de maior qualidade.

Key words: Central Amazon, Chiroptera, foraging habitat, forest structure, insect availability, Mormoopidae, riparian zone, tropical forest, vegetation clutter

The distribution of many bat species has been associated with food abundance and vegetation structure (Sleep and Brigham 2003; Kusch et al. 2004; Rainho et al. 2010). In general, areas that favor movement and have high food availability are visited more frequently (Fukui et al. 2006; Hagen and Sabo 2011). For insectivorous species, food abundance, echolocation, and the ability to detect prey may be the most necessary determinants of habitat use (Aldridge and Rautenbach 1987). Vegetation

and other nonprey objects are sources of echoes that interfere with bat navigation. The risk of collision and the difficulty of achieving aerial maneuvers reduce flight efficiency in cluttered areas (Norberg and Rayner 1987; Schnitzler and Kalko 2001). Furthermore, dense vegetation may interfere with the detection of potential prey (Kusch et al. 2004; Jones and Holderied 2007; Rainho et al. 2010). Structural complexity of vegetation may influence bat foraging as they may avoid navigating in cluttered sites (Sleep and Brigham 2003; Ober and Hayes 2008; Jung et al. 2012).

Bats may overcome the physical constraints of vegetation by using trails in the forest (Law and Chidel 2002; Sleep and Brigham 2003). Small forest streams and riparian zones frequently are used by many insectivorous bat species because they create gaps in the forest. Small streams favor the movement of understory bats more than do cluttered nonriparian habitats (Fukui et al. 2006). Small streams often have low vegetation density and form open corridors allowing faster movement of bats by facilitating maneuverability and echolocation (Fukui et al. 2006; Hagen and Sabo 2011). Bats can use a stream channel to commute more easily between sites, avoiding more cluttered areas inside the forest (Ober and Hayes 2008).

Forest streams and riparian zones have a significant influence on the distribution of insects in the forest and represent a foraging habitat for many species of insectivorous bats (Jong and Ahlén 1991; Wickramasinghe et al. 2003; Fukui et al. 2006; Hagen and Sabo 2014). Insect availability along river channels is known to be relatively high compared to nonriparian zones because the water bodies provide habitat for aquatic insects (Fukui et al. 2006; Hagen and Sabo 2014). Higher concentrations of insects and ease of travel and prey capture may result in a higher activity of aerial insectivorous bats above stream channels (Sleep and Brigham 2003; Wickramasinghe et al. 2003; Lloyd et al. 2006; Ober and Hayes 2008; Hagen and Sabo 2011, 2014).

Several studies have investigated the effect of vegetation structure, insect availability, and stream corridors in riparian areas on the spatial distribution of aerial insectivorous bats (Grindal et al. 1999; Wickramasinghe et al. 2003; Fukui et al. 2006; Ober and Hayes 2008; Jung et al. 2012). However, the relative importance of these 3 factors rarely has been evaluated simultaneously (Ober and Hayes 2008; Hagen and Sabo 2011). Most studies have been conducted along a single stream channel, many in areas strongly impacted by humans (Sleep and Brigham 2003; Lloyd et al. 2006; Ober and Hayes 2008; Jung et al. 2012; Hagen and Sabo 2014). This neglects the possible influence of nonriparian sites in continuous forest for the distribution of bats. Furthermore, most studies classify vegetation clutter in qualitative categories (e.g., complex versus simple understory; open versus closed vegetation), instead of using vegetation clutter as a quantitative variable. Herein, we evaluate how the structural characteristics of vegetation and the availability of insect prey influence bat distribution in riparian and nonriparian zones using *Pteronotus parnellii* (Mormoopidae) as a model species.

Pteronotus parnellii is an insectivorous bat that uses high-duty-cycle echolocation that is well suited to detecting fluttering targets in cluttered habitats (Lazure and Fenton 2011; Fenton et al. 2012). The study was undertaken in a 25-km² area of continuous forest in central Brazilian Amazonia, where we monitored bats by use of automated ultrasound detectors located in streamside and nonriparian areas. We hypothesized that vegetation structure and availability of insect prey affect the activity of the species and that activity differs between riparian and nonriparian areas. As clutter levels are high in the understory of the Amazon rainforest, but less in riparian zones, we expected that *P. parnellii* would concentrate its activity in uncluttered corridors of forest streams and areas with higher insect availability.

MATERIALS AND METHODS

Study site.—The study was conducted in the Reserva Ducke (2°58′S, 59°55′W; Fig. 1), located to the north of the city of Manaus at Km 26 of the AM-110 Highway, Amazonas State, Brazil. The reserve is part of the Brazilian Long-term Ecological Research Program of the Brazilian National Research Council (Programa de Pesquisas Ecológicas de Longa Duração - PELD/ CNPq). It covers 10,000 ha of lowland rainforest. Annual rainfall varies between 1,750 and 2,500 mm, with the highest rainfall between November and May and a drier period between June and October (Oliveira et al. 2008). Mean relative humidity was 86%, and mean annual temperature was 26°C (Ribeiro et al. 1999). The relief is undulating with small plateaus, slopes, and valleys that vary between 45 and 140 m in height. Small streams are found in valley bottoms. The forest canopy is generally 30–35 m though emergent trees may exceed 50 m (Ribeiro et al. 1999).

The 25 km² (5 × 5 km) trail system was established according to RAPELD methodology (Magnusson et al. 2005, 2014) that consists of a grid of 6 trails oriented north-south and 6 trails oriented east-west (Fig. 1). The trails give access to 30 uniformly distributed study plots, each separated from the next by 1,000 m. Within the grid, there are also 15 riparian plots located along streams (Fig. 1). The plots were 250 m long. The uniformly distributed plots followed the topographic contour in order to minimize internal heterogeneity in soil properties and drainage, which often correlate with plant assemblage structure (Magnusson et al. 2005). Riparian plots followed the banks of streams.

Study species.—*Pteronotus parnellii* is a medium-sized understory-dwelling Neotropical bat with body length of 7.3– 10.2 cm, wingspan of 30–35 cm, and body mass of 10–20 g (Herd 1983). Its wings are broad, rounded on the tips, and have low wing loading (Emrich et al. 2014). The species uses high-duty-cycle echolocation and produces search-phase signals characterized by a long constant frequency (Rydell et al. 2002; Jones and Teeling 2006). Wing characteristics and high-duty-cycle echolocation suggest that *P. parnellii* is well suited for hunting flying insects in cluttered vegetation (Vater et al. 2003; Jones and Teeling 2006; Emrich et al. 2014). The species occurs
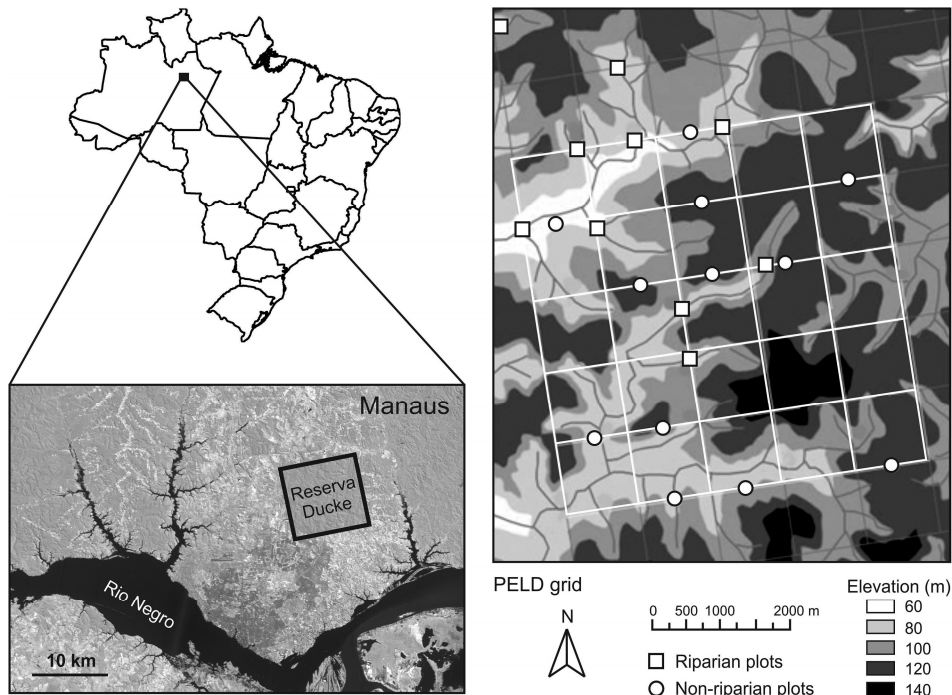
Fig. 1.—Location of Reserva Ducke to the north of Manaus, Amazonas State, Brazil. Topography and stream distribution in the RAPELD grid is shown in detail. Open circles represent nonriparian plots and open squares represent riparian plots adjacent to streams.

from the northern coastal plans of the Gulf of Mexico, along the Caribbean coast, to Trinidad and the Amazon basin, and south to the northern part of Mato Grosso State, central Brazil (Patton and Gardner 2007). The species occurs in a variety of forest types, from lowland rainforest to drier forest, and at elevations from sea level to 3,000 m (Smith 1972; Handley 1976). Recent molecular studies supported by acoustics data have shown that *P. parnellii* is composed of several cryptic species that may not be related to original *P. parnellii* native to Jamaica (Clare et al. 2013; Thoisy et al. 2014). These studies show that the echolocation call frequency may indicate distinct species. All bats recorded in Reserva Ducke emitted calls of 55 kHz, overlapping with those of specimens from French Guiana and Amapá (Brazil).

Bat activity.—We recorded the bat search-phase calls from January to May 2013 during the rainy season. We sampled 22 plots (Fig. 1), 12 in nonriparian and 10 in riparian areas. The nonriparian plots were separated by 1–6 km, and the riparian plots were separated by 0.56–5.2 km. The distance between riparian and nonriparian plots varied from 0.4 to 8.1 km. Each plot was sampled for 5 consecutive nights between 1800 and 0600 h (12 h per night), resulting in 60 h of recordings per plot. We monitored the bats with Song Meter SM2+ autonomous recording units coupled to an SMX-US omnidirectional ultrasonic microphone (Wildlife Acoustics, Maynard, Massachusetts). We recorded bat activity in real time with a sampling frequency of 384 Hz, a full-spectrum resolution of 16 bits with a 1-s pretrigger and a 0.1-s posttrigger with Dig HPF and Dig LPF deactivated and Trigger Level 0 dB. The SM2+ units were placed in the center of each plot. The microphones were positioned at a height of approximately 1.5 m. In the riparian plots, we used one 3-m-long cable to position the microphones over the center of the stream.

The SM2+ units were programed to create audio files in a WAC format at intervals of 30 min, producing as many as 24 files for each 12-h sampling period. Each WAC file was converted to WAV format and divided into segments of 5-s duration using the program Kaleidoscope (Wildlife Acoustics, Maynard, Massachusetts). The acoustic signals were visualized with the Avisoft-SASLab Pro program, version 4.34 (Specht 2005). Spectrogram resolution characteristics were set to a hamming evaluation window with a fast Fourier transformation of 512 points and a frame size of 100%. One bat acoustic signal was defined as a 5-s segment that contained 2 or more *P. parnellii* search-phase calls. Data were expressed as the number of search-phase calls per night per recording plot (total number of search-phase calls/5 nights). No feeding buzz was recorded in the segments that were analyzed.

Understory-vegetation clutter.—We measured vegetation clutter using horizontal photographs of vegetation, adapted from the method of Marsden et al. (2002). A white cloth was mounted in a 3×3 m aluminum frame to create a panel that contrasted with the vegetation (Supporting Information S1). The white panel was positioned perpendicular to the angle of vision of a digital camera located 8 m from the panel. In nonriparian plots, the vegetation was photographed every 10 m along a 100 m stretch of the central line of the plot located around the point where vocalizations were recorded ($n = 10$ vegetation photographs per plot). In riparian plots, photographs were made of vegetation over the stream with the white panel positioned perpendicular to the central channel at distances of 10 m along a 180 m transect of the stream course ($n = 10$ vegetation

photographs per plot). In each plot, we positioned the SM2+ unit at the midpoint of the transect used to quantify the vegetation clutter.

Understory-vegetation clutter was quantified by transforming the photographs into black-and-white images so that black areas represented vegetation and white areas represented open space. The black areas for each of the 10 images from each plot were summed to quantify the percentage of area covered by vegetation, equivalent to one large photograph per plot. We used the program ImageJ 1.38x (Rasband 2007) to quantify the vegetation clutter.

Insect prey.—Flying nocturnal insects were collected in light traps, consisting of a 20-cm diameter plastic cone attached to a 100-ml insect collecting pot with 70% alcohol. A 25-cm diameter plate was suspended above the cone to protect against rain. To attract insects, a flashlight with 10 LED lights was positioned beneath the plate and pointed toward the cone. Two light traps were installed per plot at a distance of 70 m from the SM2+ unit. Light traps remained lit for a 48-h period during the time that bat calls were recorded. The light traps were unlikely to have affected the foraging behavior of bats, and consequently the recordings, as it was not possible to see the light of the traps from where the SM2+ unit was placed. All plots received the same treatment.

Trapped insects were identified to order, and only those orders known to be eaten by *P. parnellii* were included in the analyses because prey preferences and foraging strategies vary among bat species (Fenton 1990). Identification of insect orders used in the analysis followed Rolfe and Kurta (2012) and included Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, and Orthoptera. Insects were dried with filter paper to remove excess alcohol and weighed individually on a precision balance (limit of reading 0.0001 g; Ohaus Discovery, Pine Brook, New Jersey) to estimate the total mass of insects captured in each plot. We estimated the average insect mass per plot by dividing the mass by the number of insects. Higher values indicate plots with larger insects.

Data analysis.—We compared vegetation clutter and insect mass between riparian and nonriparian plots using a *t*-test. To evaluate the effect of vegetation clutter on the composition of insect orders known to be eaten by *P. parnellii*, we used a generalized linear model (GLM). Insect composition was summarized using nonmetric multidimensional scaling (NMDS) with the Bray–Curtis index as the dissimilarity measure (Legendre and Legendre 1998). We used the mass of each insect order in the *P. parnellii* diet as a measure of relative abundance to create 1 NMDS ordination axis. Insect-order composition among riparian and nonriparian plots was compared using a *t*-test.

Bat activity (number of search-phase calls per night) between riparian and nonriparian plots was compared using a *t*-test. To examine the effect of vegetation clutter and insect mass on the activity of *P. parnellii*, we used a multiple GLM test. A Pearson correlation test indicated little collinearity between the explanatory variables vegetation clutter and insect mass ($r = 0.41$). Hierarchical partitioning was employed

to estimate the independent contribution of each explanatory variable in a multiple GLM test (Mac Nally 2002). The effects of insect-order composition and insect size on bat activity were examined with GLM tests. The variance explained by the GLM analysis was calculated as [1 − (residual deviance of the full model/deviance of the null model)]. When vegetation clutter and insect mass were used as response variables, we used a Poisson distribution controlled for overdispersion in the GLM analysis (Zuur et al. 2009). A Gaussian error distribution was used in analyses of insect-order composition (NMDS axis) as the ordination axis was not count data. All analyses were conducted in the R program, version 2.12.1 (R Development Core Team 2014). The NMDS ordination was undertaken in the R package "vegan" (Oksanen et al. 2013) and hierarchical partitioning in the "hier.part" package (Mac Nally and Walsh 2004).

RESULTS

Light traps captured 1,006 insects from 12 orders (Table 1). Total insect mass was 4.2 g (Table 1). Mass of the 6 orders known to be eaten by *P. parnellii* comprised 86.3% of the total mass of insects, and the most abundant orders (Table 1) were Coleoptera (64.5%; 2.7 g), Hemiptera (13.4%; 0.6 g), and Diptera (4.1%; 0.2 g). The mass of insects eaten by *P. parnellii* in the nonriparian plots was slightly higher than in the riparian plots ($t = -2.14$, *d.f.* = 20, $P = 0.048$). Insect-order composition differed between riparian and nonriparian plots ($t = 2.24$, *d.f.* = 20, $P = 0.043$).

Vegetation clutter varied from 43% to 63.8% ($\bar{X} \pm SD = 54.9 \pm 6.0$) in nonriparian plots and between 13.6% and 42.8% (27.5 ± 12.6) over the stream channels of riparian plots. The nonriparian plots had about twice as much cluttering vegetation as the riparian plots ($t = -6.29$, *d.f.* = 20, $P < 0.001$). The distribution of insect orders (Fig. 2) indicated structuring of insect assemblages as a function of vegetation clutter and habitat type. The NMDS ordination axis of the insect orders explained 61% of the total variation among plots (NMDS stress = 0.12). The insect-order composition (Fig. 3), summarized by the single NMDS axis, was related to vegetation clutter (GLM, $r^2 = 0.22$; $t = -2.21$; $P = 0.039$) and differed between riparian and nonriparian plots ($t = -2.24$; *d.f.* = 20; $P = 0.043$).

We monitored the activity of *P. parnellii* for 110 nights and successfully recorded ultrasound on 99 nights (90% of recording nights). In 1,320 h of recordings, we registered 3,648 search-phase calls of *P. parnellii* (165.8 ± 228.1), of which 3,343 calls were in nonriparian plots (278.6 ± 260.8) and 305 were in riparian plots (30.5 ± 30.8). *Pteronotus parnellii* was recorded in all 22 plots, and activity varied between 3 and 347 calls per plot. Bat activity in nonriparian plots was 9.3 times greater than in riparian plots ($t = -3.27$, *d.f.* = 20, $P = 0.007$). Activity of *P. parnellii* (Fig. 4) was positively related to insect mass (GLM, $t = 4.17$, *d.f.* = 21, $P < 0.001$) and vegetation clutter (GLM, $t = 2.28$, *d.f.* = 21, $P = 0.034$). These variables combined accounted for 65% of the variance explained. Independently, insect mass and vegetation clutter explained 67% and 33% of

Table 1.—Number of individual insects, mass (g), and percentage of the mass of the insect orders collected in Reserva Ducke, Central Amazonia, Brazil. Asterisks indicate orders known to be eaten by *Pteronotus parnellii* following Rolfe and Kurta (2012).

| Insect orders	Riparian plots (n = 10)			Nonriparian plots (n = 12)			Total (n = 22)		
	n	Mass (g)	%	n	Mass (g)	%	n	Mass (g)	%
Hymenoptera*	101	0.2	11.9	155	0.4	14	256	0.6	13.4
Coleoptera*	48	0.6	44.4	110	2.1	73.2	158	2.7	64.5
Diptera*	79	0	0.8	74	0.2	5.5	153	0.2	4.1
Hemiptera*	8	0	0.8	23	0.1	2.2	31	0.1	1.7
Lepidoptera*	44	0.1	4	10	0.1	1.7	54	0.1	2.4
Isoptera	48	0.1	4	5	0	0.3	53	0.1	1.4
Blattodea	5	0	0.2	2	0	0.3	7	0	0.3
Ephemeroptera	184	0.2	16.7	1	0	0	185	0.2	5
Orthoptera*	36	0	0.8	0	0	0	36	0	0.2
Mantodea	2	0	0	0	0.1	2.7	2	0.1	1.9
Plecoptera	8	0	2.4	0	0	0	8	0	0.7
Trichoptera	63	0.2	14.3	0	0	0	63	0.2	4.3
Total	626	1.3	100	380	2.9	100	1,006	4.2	100
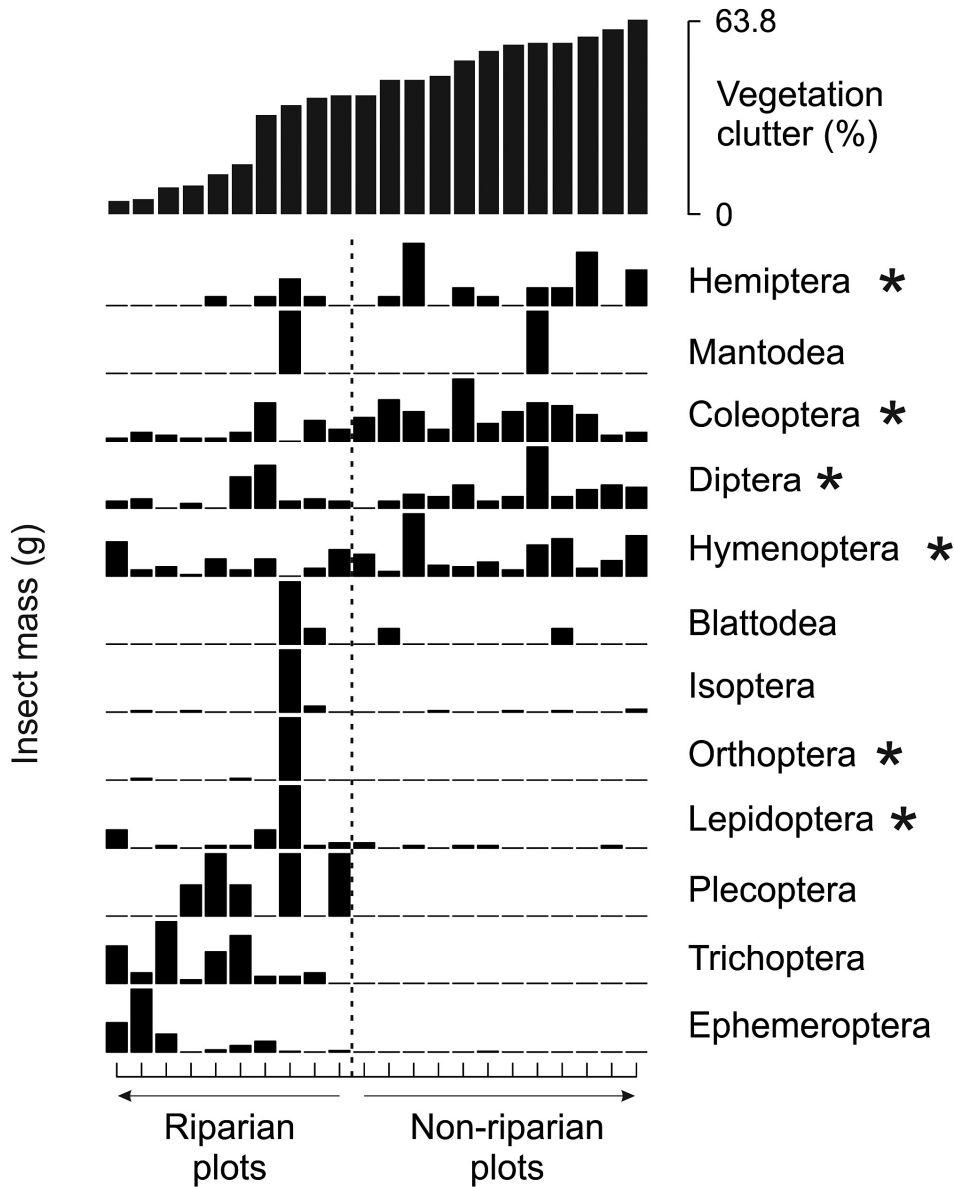
Fig. 2.—Distribution of insect orders along the gradient of vegetation clutter in study plots at Reserva Ducke, Central Amazonia, Brazil. Asterisks indicate the orders of insects eaten by *Pteronotus parnellii*. Solid bars represent the mass of each insect order in sampling plots. The total for each order is 100%, so it is not possible to make graphical comparisons of total mass between orders, but these are given in Table 1.
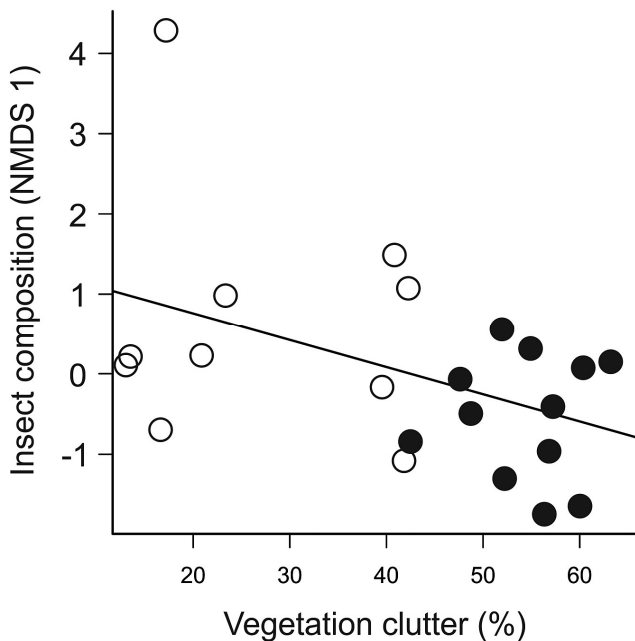
Fig. 3.—Relationship between the insect-order composition, summarized by a single NMDS axis, and vegetation clutter. Black circles represent nonriparian plots and open circles represent riparian plots. NMDS = nonmetric multidimensional scaling.

the response-variable variance, respectively. The activity of *P. parnellii* was positively associated with mean insect size (GLM, $r^2 = 0.30$; $t = 3.13$; $P < 0.005$) and insect-order composition (GLM, $r^2 = 0.62$; $t = 5.35$; $P < 0.001$).

DISCUSSION

Vegetation clutter was greater in nonriparian than in riparian areas as has been recorded in other regions (Fukui et al. 2006; Hagen and Sabo 2011). Bats tend to be more active along river channels in many areas because the channels facilitate bat movement in forests (Ober and Hayes 2008). However, contrary to our expectations, the activity of *P. parnellii* was greater in plots with high levels of vegetation clutter in nonriparian areas. *Pteronotus parnellii* activity also was higher in plots with a higher mass of insects, regardless of whether the plot was in riparian or nonriparian areas. Insect mass was greater in more cluttered plots, and this could explain the greater levels of activity by *P. parnellii* in areas with more closed vegetation. Although we did not record any feeding buzz, the positive association between bat activity and insect availability is evidence that the relationship between bat activity and foraging is strong and direct. Plots with highest *P. parnellii* activity likely are to be the plots with highest foraging activity, indicating higher foraging effort in plots with higher general activity. These results suggest that insect mass was a greater influence on habitat use by *P. parnellii* than vegetation clutter.

Higher *P. parnellii* activity in areas with denser vegetation is not in line with the results of most studies of activity patterns of aerial insectivorous bats, which reported greater activity above streams (Grindal et al. 1999; Fukui et al. 2006; Akasaka et al.
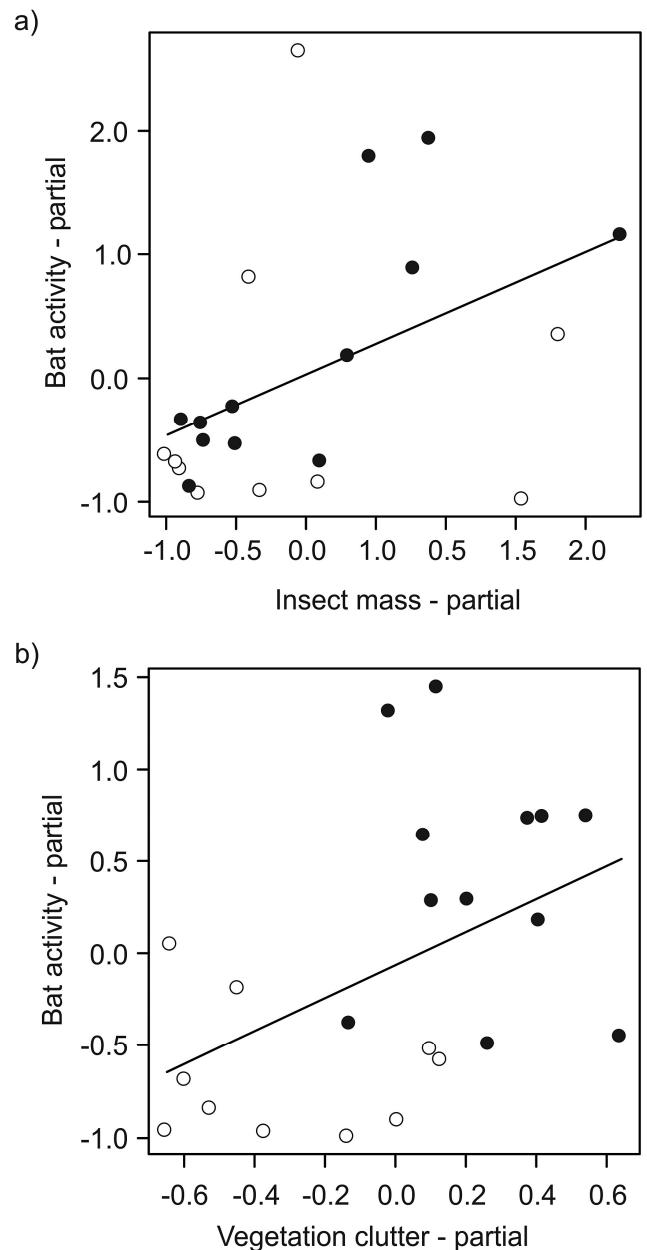

Fig. 4.—Partial regression results of *Pteronotus parnellii* activity (search-phase calls per night) with a) mass of insects known to be part of the *P. parnellii* diet and b) vegetation clutter. Black circles represent nonriparian plots and open circles represent riparian plots.

2009). The ability to use different habitats by bats is related to flight and echolocation characteristics. *Pteronotus parnellii* produce long-duration constant frequency (CF) signals terminating with a broadband sweep, which enhance prey localization (Schnitzler et al. 2003). Long CF signals often are used by bats searching for moving targets (prey or vegetation obstacles) in cluttered habitats and are associated with Doppler-shift compensation (Jones 2005). The wing morphology of *P. parnellii* is that of a generalist, with a flexible and adaptable flight, so that it may exploit different habitats (Marinello and Bernard 2014), including highly cluttered sites. Ability to detect vegetation objects should not limit *P. parnellii* flight in forest understory,

so it can use both riparian and nonriparian areas. This suggests that the amount of vegetation clutter encountered in this study did not restrict the activity of *P. parnellii*. This species probably selects cluttered places as feeding sites because it is attracted by higher quality prey.

The difference in use of riparian and nonriparian areas should be more closely correlated with amount and type of insects. Mass of insects of orders eaten by *P. parnellii* was higher in nonriparian plots and species composition varied between riparian and nonriparian areas. The combined mass of Hemiptera, Diptera, Coleoptera, and Hymenoptera was higher in nonriparian areas. These terrestrial insect orders are frequent components of the *P. parnellii* diet (Emrich et al. 2014). In contrast, aerial aquatic insects (Ephemeroptera, Plecoptera, and Trichoptera), which are rarely eaten by the species, made up one-third of the insect mass in the riparian plots but were not captured in nonriparian plots. The activity of *P. parnellii* was strongly affected by insect composition along a clutter gradient, with activity concentrated in locations with more insects that form part of its diet. Areas away from streams may be necessary because they provided food resources that are scarce near streams.

Despite the greater availability of food in nonriparian plots, *P. parnellii* also used riparian areas, although with less intensity. Riparian areas often are considered to be important foraging areas for insectivorous bats because of the availability of aerial aquatic insects (Hagen and Sabo 2014). However, *P. parnellii* rarely eats aquatic insects (Emrich et al. 2014). Hagen and Sabo (2011) showed that insect resources were more abundant in parts of streams where vegetation density was greater, suggesting that sites with highly cluttered vegetation close to a stream channel may provide more terrestrial insects. In our study area, the streams were narrow (< 3.3 m of width) and may have attracted terrestrial insects from nearby riparian areas. Terrestrial insects common in the diet of *P. parnellii* were captured in all riparian plots, although their mass averaged lower there than in nonriparian plots.

Use of cluttered sites demands greater energy expenditure to maneuver and avoid obstacles in the understory (Norberg and Rayner 1987; Schnitzler and Kalko 2001). Flying in more cluttered sites could be advantageous when they contain more high-quality food. The extra energy expenditure due to the use of more cluttered plots by *P. parnellii* may have been compensated for by choosing sites containing more large prey. Energy gained per individual prey is higher for large insects (Akasaka et al. 2009). These findings suggest that foraging activities of *P. parnellii* in nonriparian zones may be attributable to both quantity and quality of insect prey.

Many studies of aerial insectivorous bats have been conducted in areas subjected to strong human impacts. These studies have found higher levels of bat activity in riparian zones (e.g., Law and Chidel 2002; Fukui et al. 2006; Dodd et al. 2008; Stahlschmidt et al. 2012). However, few studies of bat activity in riparian zones have included closed adjacent undisturbed forest (Grindal et al. 1999; Hagen and Sabo 2011). Riparian forests in a landscape subject to human modification could be functioning as refuges in an otherwise highly degraded habitat (Robinson

et al. 2002). This can hinder the understanding of the biotic and abiotic factors that influence habitat selection by bats as the bats do not have alternative areas in which to forage. *Pteronotus parnellii* is a forest specialist that avoids highly degraded areas (Bernard and Fenton 2007; Bobrowiec and Gribel 2010) and seems to choose closed vegetation to naturally open environments. In degraded landscapes, this bat may use riparian areas merely as a refuge. More studies need to be conducted in relatively undisturbed areas, with simultaneous monitoring of bat activity in riparian and nonriparian areas, to make generalizations about the need for riparian zones by insectivorous bats.

SUPPORTING INFORMATION

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Method used to quantify vegetation clutter using digital photographs in nonriparian and riparian plots.

LITERATURE CITED

AKASAKA, T., D. NAKANO, AND F. NAKAMURA. 2009. Influence of prey variables, food supply, and river restoration on the foraging activity of Daubenton's bat (*Myotis daubentonii*) in the Shibetsu River, a large lowland river in Japan. Biological Conservation 142:1302–1310.

ALDRIDGE, H. D. J. N., AND I. L. RAUTENBACH. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. Journal of Animal Ecology 56:763–778.

BERNARD, E., AND M. B. FENTON. 2007. Bats in a fragmented landscape: species composition, diversity and habitat interactions in savannas of Santarém, Central Amazonia, Brazil. Biological Conservation 134:332–343.

Bobrowiec, P. E. D., and R. Gribel. 2010. Effects of different secondary vegetation types on bat community composition in Central Amazonia, Brazil. Animal Conservation 13:204–216.

Clare, E. L., A. M. Adams, A. Z. , J. L. Eger, P. D. Hebert, and M. B. Fenton. 2013. Diversification and reproductive isolation: cryptic species in the only New World high-duty cycle bat, *Pteronotus parnellii*. BMC Evolutionary Biology 13:1–26.

Dodd, L. E., M. J. Lacki, and L. K. Rieske. 2008. Forest ecology and management variation in moth occurrence and implications for foraging habitat of Ozark big-eared bats. Forest Ecology and Management 255:3866–3872.

Emrich, M. A., E. L. Clare, and W. O. C. Symondson. 2014. Resource partitioning by insectivorous bats in Jamaica. Molecular Ecology 23:3648–3656.

Fenton, M. B. 1990. The foraging behaviour and ecology of animal-eating bats. Canadian Journal of Zoology 68:411–422.

Fenton, M. B., P. A. Faure, and J. M. Ratcliffe. 2012. Evolution of high duty cycle echolocation in bats. Journal of Experimental Biology 215:2935–2944.

Fukui, D., M. Murakami, S. Nakano, and T. Aoi. 2006. Effect of emergent aquatic insects on bat foraging in a riparian forest. Journal of Animal Ecology 75:1252–1258.

Grindal, S. D., J. L. Morissette, and R. M. Brigham. 1999. Concentration of bat activity in riparian habitats over an elevational gradient. Canadian Journal of Zoology 77:972–977.

Hagen, E. M., and J. L. Sabo. 2011. A landscape perspective on bat foraging ecology along rivers: does channel confinement and insect availability influence the response of bats to aquatic resources in riverine landscapes? Oecologia 166:751–60.

Hagen, E. M., and J. L. Sabo. 2014. Temporal variability in insectivorous bat activity along two desert streams with contrasting patterns of prey availability. Journal of Arid Environments 102:104–112.

Handley, C. O. J. 1976. Mammals of the Smithsonian Venezuelan project. Brigham Young University Science Bulletin - Biological Series 20:1–89.

Herd, R. M. 1983. *Pteronotus parnellii*. Mammalian Species 209:1–5.

Jones, G. 2005. Echolocation. Current Biology 15:R484–R488.

Jones, G., and M. W. Holderied. 2007. Bat echolocation calls: adaptation and convergent evolution. Proceedings of the Royal Society B 274:905–912.

Jones, G., and E. C. Teeling. 2006. The evolution of echolocation in bats. Trends in Ecology and Evolution 21:149–156.

Jong, J., and I. . 1991. Factors affecting the distribution pattern of bats in upland, central Sweden. Holarctic Ecology 14:92–96.

Jung, K., S. Kaiser, S. , J. Nieschulze, and E. K. V. Kalko. 2012. Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. Journal of Applied Ecology 49:523–531.

Kusch, J., C. Weber, S. Idelberger, and T. Koob. 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.

Law, B., and M. Chidel. 2002. Tracks and riparian zones facilitate the use of Australian forest by insectivorous bats. Journal of Applied Ecology 39:605–617.

Lazure, L., and M. B. Fenton. 2011. High duty cycle echolocation and prey detection by bats. Journal of Experimental Biology 214:1131–1137.

Legendre, P., and L. Legendre. 1998. Numerical ecology. Elsevier, Amsterdam, The Netherlands.

Lloyd, A., B. Law, and R. Goldingay. 2006. Bat activity on riparian zones and upper slopes in Australian timber production forests and the effectiveness of riparian buffers. Biological Conservation 9:207–220.

Mac Nally, R. 2002. Multiple regression and inference in conservation biology and ecology: further comments on identifying important predictor variables. Biodiversity and Conservation 11:1397–1401.

Mac Nally, R., and C. J. Walsh. 2004. Hierarchical partitioning public-domain software. Biodiversity Conservation 13:659–660.

Magnusson, W. E., et al. 2005. RAPELD: a modification of the Gentry method for biodiversity surveys in long-term ecological research sites. Biota Neotropica 5:19–24.

Magnusson, W. E., et al. 2014. Multi-taxa surveys: integrating ecosystem processes and user demands. Pp. 177–187 in Applied ecology and human dimensions in biological conservation (L. M. Verdade, M. C. Lyra-Jorge, and C. I. Piña, eds.). Springer Berlin Heidelberg, Berlin, Germany.

Marinello, M. M., and E. Bernard. 2014. Wing morphology of Neotropical bats: a quantitative and qualitative analysis with implications for habitat use. Canadian Journal of Zoology 92:141–147.

Marsden, S. J., A. H. Fielding, C. Mead, and M. Z. Hussin. 2002. A technique for measuring the density and complexity of understory vegetation in tropical forests. Forest Ecology and Management 165:117–123.

Norberg, U. M., and J. M. V. Rayner. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London 316:335–427.

Ober, H. K., and J. P. Hayes. 2008. Influence of vegetation on bat use of riparian areas at multiple spatial scales. Journal of Wildlife Management 72:396–404.

Oksanen, J., et al. 2013. Vegan: community ecology package. R package version 2.0-10. http://CRAN.R-project.org/package=vegan. Accessed 26 January 2015.

Oliveira, M. L., F. B. Baccaro, R. Braga-Neto, and W. E. Magnusson. 2008. Reserva Ducke a Biodiversidade Amazônica através de uma grade. Áttema Editorial, Manaus, Brazil.

Patton, J. L., and A. L. Gardner. 2007. Family Mormoopidae. Pp. 376–384 in Mammals of South America. 1. Marsupials, xenarthrans, shrews, and bats (A. L. Gardner, ed.). University of Chicago Press, Chicago, Illinois.

R Development Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.Rproject.org/. Accessed 16 December 2014.

Rainho, A., A. M. Augusto, and J. M. Palmeirim. 2010. Influence of vegetation clutter on the capacity of ground foraging bats to capture prey. Journal of Applied Ecology 47:850–858.

Rasband, W. S. 2007. ImageJ. Ver. 1.38x. National Institutes of Health, Bethesda, Maryland.

Ribeiro, J. E. L. S., et al. 1999. Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia Central. Editora INPA, Manaus, Brazil.

Robinson, C. T., K. Tockner, and J. V. Ward. 2002. The fauna of dynamic riverine landscapes. Freshwater Biology 47:661–677.

Rolfe, A. K., and A. Kurta. 2012. Diet of Mormoopid bats on the Caribbean island of Puerto Rico. Acta Chiropterologica 14:369–377.

RYDELL, J., H. T. ARITA, M. SANTOS, AND J. GRANADOS. 2002. Acoustic identification of insectivorous bats (Order Chiroptera) of Yucatan, Mexico. Journal of Zoology (London) 257:27–36.

SCHNITZLER, H. U., AND E. K. V. KALKO. 2001. Echolocation by insect-eating bats. Bioscience 51:557–569.

SCHNITZLER, H. U., C. F. MOSS, AND A. DENZINGER. 2003. From spatial orientation to food acquisition in echolocating bats. Trends in Ecology and Evolution 18:386–394.

SLEEP, D. J. H., AND R. M. BRIGHAM. 2003. An experimental test of clutter tolerance in bats. Journal of Mammalogy 84:216–224.

SMITH, J. D. 1972. Systematics of the chiropteran family Mormoopidae. Museum of Natural History University of Kansas 56:1–132.

SPECHT, R. 2005. Avisoft-SASLab Pro. Ver. 4.34. Avisoft, Berlin, Germany.

STAHLSCHMIDT, P., A.   , L. RESSL, R. SCHULZ, AND C. A.   . 2012. Constructed wetlands support bats in agricultural landscapes. Basic and Applied Ecology 13:196–203.

THOISY, B. D., ET AL. 2014. Cryptic diversity in common mustached bats Pteronotus cf. parnellii (Mormoopidae) in French Guiana and Brazilian Amapa. Acta Chiropterologica 16:1–13.

VATER, M., M. KOSSL, E. FOELLER, F. CORO, E. MORA, AND I. RUSSELL. 2003. Development of echolocation calls in the mustached bat, Pteronotus parnellii. Journal of Neurophysiology 90:2274–2290.

WICKRAMASINGHE L. P., S. HARRIS, G. JONES, AND N. VAUGHAN. 2003. Bat activity and species richness on organic and conventional farms: impact of agricultural intensification. Journal of Applied Ecology 40:984–993.

ZUUR, A. F., E. N. IENO, N. J. WLAKE, A. A. SAVELIV, AND G. M. SMITH. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.