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Activity of an Amazonian aerial insectivorous bat depends more of food resources than vegetation structural complexity

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more of food resources than vegetation structural complexity

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Sinopse:

Estudei o efeito da obstrução da vegetação do sub bosque e da disponibilidade de insetos voadores noturnos sobre a distribuição espacial da atividade de um morcego insetívoro aéreo (*Pteronotus Parnellii*) na Reserva Ducke, Manaus, Amazônia Central. Tanto a obstrução da vegetação quanto adisponibilidade de insetos afetaram a atividade da espécie *P. parnellii*. **Palavras chaves:** Acoustic, Chiroptera, Feeding zones, Insect composition, Mormoopidae, *Pteronotus parnellii*, Vegetation density.

Dedico essa dissertação a minha família

Especialmente a meu pai José Sergio e minha mãe Erica.

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"Mestre não é quem sempre ensina, mas quem de repente aprende"

Guimarães Rosa (Escritor e poeta sertanejo)

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RESUMO

1 - Muitos estudos têm mostrado que os morcegos insetívoros utilizam frequentemente zonas ripárias em torno de riachos, mas não é totalmente claro se os morcegos estão usando essas áreas para alimentação ou apenas para comutar entre ambientes usando os corredores de vegetação sobre os riachos. Nenhum estudo de morcegos neotropicais investigou o uso relativo de zonas ripárias e áreas distantes dos rios para forrageio dos morcegos.

2 – Estudei quais são os efeitos da estrutura da vegetação e disponibilidade de alimentos
 sobre a atividade do morcego insetívoro aéreo *Pteronotus parnellii* perto e longe de riachos
 na floresta tropical na Reserva Ducke, Manaus, Amazônia Central.

3 - Utilizei fotografias horizontais de vegetação rasteira entre 0 e 3m de altura para quantificar o grau de obstrução (desordem) provocado por folhas e ramos . A disponibilidade de alimentos foi avaliada com pequenas armadilhas luminosas projetadas para capturar insetos noturnos. A atividade dos morcegos foi monitorada com aparelhos de gravação de sons de alta frequência que operaram continuamente por 60 horas em cada unidade amostral.

4 - Em contraste com estudos anteriores, a maioria dos quais utilizaram redes de neblina, meus resultados sugerem que *P. parnellii* é mais ativo em locais com vegetação rasteira densa, mais comum fora das zonas ripárias. A disponibilidade de alimentos também foi maior em locais com vegetação mais obstruída.

5 - Generalizações na literatura sobre a morfologia indicam que *P. parnellii* deve ser mais ativo em locais com pouca obstrução da vegetação. No entanto, encontramos maior atividade em locais altamente obstruídos, indicando que a disponibilidade de alimentos pode ser mais importante do que a complexidade da vegetação para determinar onde os morcegos forrageiam.

ABSTRACT

1 – Many studies have shown that insectivorous bats frequently use riparian zones around streams, but it is often unclear whether the bats are using those areas for feeding or are just making use of the uncluttered areas over streams as movement corridors. No study of Neotropical bats has investigated the relative use of riparian zones and areas far from streams for foraging.

2 – We studied the effects of vegetation structure and food availability on the activity of the aerial insectivorous bat *Pteronotus parnellii* near and far from streams in tropical rainforest in Reserva Ducke, Central Amazonia.

3- We used horizontal photographs of understory vegetation to quantify the degree of obstruction (clutter) by leaves and branches. Food availability was evaluated with small light traps designed to catch nocturnal insects. Bat activity was monitored with high-frequency sound recorders that operated continually for 60 hours at each site.
4 – In contrast to previous studies, most of which used mist nets, we found *P. parnellii* to be more active in places with dense understory vegetation, which were more common outside riparian zones. Food availability was also higher in places with more vegetation clutter.
5 – Generalizations in the literature, based on morphology, indicate that *P. parnellii* should be more active in sites with little vegetation clutter. However, we found the species to be more active in cluttered sites, indicating that food availability may be more important than clutter in determining where the bats foraged.

Key words Acoustic, Chiroptera, Feeding zones, Insect composition, Mormoopidae, *Pteronotus parnellii*, Vegetation density.

INTRODUÇÃO GERAL

O uso do ambiente por animais está relacionado com a distribuição dos recursos alimentares e a características da paisagem que permitem o acesso dos organismos aos recursos (MacArthur & Pianka 1966). Em geral, locais que favorecem o deslocamento e disponibilizam maior quantidade de alimento são preferencialmente ocupados (Rosenzweig 1981). Nesses locais, a energia gasta para encontrar alimento é menor e existe um balanço energético positivo que possibilita o investimento da energia excedente em outras funções, como crescimento e reprodução (Pyke 1984). Contrariamente, locais com baixa quantidade de alimento e de difícil acesso são evitados pelos organismos, porque o deslocamento dentro destas áreas requer maior gasto de energia o que é desvantajoso para os animais em termos do balanço energético (MacArthur & Pianka 1996).

Morcegos insetívoros aéreos são normalmente pouco ativos em locais altamente obstruídos por vegetação (Sleep & Brigham 2003; Ober, Hayes & Hall 2008; Jung *et al.* 2012). Este grupo de morcegos insetívoros difere de outros morcegos insetívoros, como os catadores, por serem capazes de capturar insetos em pleno voo (Kalko & Handley 2001), o que torna a obstrução da vegetação não somente um obstáculo para o deslocamento, mas também para a captura dos insetos. A redução da atividade dos morcegos insetívoros aéreos em sítios mais obstruídos pode estar relacionada ao maior risco de colisão com obstáculos da vegetação e maior dificuldade para realizar manobras durante o voo (Norberg & Rayner 1987; Schnitzler & Kalko 2001). A capacidade de localizar presas também fica comprometida em ambientes obstruídos pela vegetação, pois os ecos que retornam da vegetação se sobrepõem aos ecos que retornam dos insetos, mascarando a detecção e captura dos insetos pelos morcegos (Jones & Holderied 2007; Rainho, Augusto & Palmeirim 2010). Alguns morcegos com maior

capacidade de realizar manobras conseguem se deslocar em locais mais obstruídos (Schnitzler & Kalko 2001). No entanto, a maioria das espécies é mais ativa em ambientes com vegetação mais aberta (Siemers & Schnitzler, 2004; Ober, Hayes & Hall 2008; Hagen & Sabo 2011; Jung *et al.* 2012).

Pequenos riachos que cruzam o interior das florestas normalmente são locais pouco obstruídos por vegetação que favorecem o deslocamento dos morcegos que habitam o subosque (Fukui *et al.* 2006). A presença dos riachos no interior da floresta criam espaços com pouca vegetação sobre os canais dos corpos d'água, formando galerias ou corredores de vegetação usados para o deslocamento mais rápido (Fukui, Murakami & Hirakawa 2011; Hagen & Sabo 2011). Os morcegos podem usar os riachos para comutar entre um local e outro mais facilmente, evitando as áreas obstruídas no interior da floresta (Ober, Hayes & Hall 2008). Além disso, os riachos podem concentrar recursos utilizados pelos morcegos como água e insetos (Hagen & Sabo 2014; Fukui, Murakami & Hirakawa 2011; Jong & Ahlen 1991). A maior concentração de insetos e maior facilidade para voar, localizar e capturar presas pode resultar em maior atividade dos morcegos insetívoros aéreos sobre os canais dos riachos (Sleep & Brigham 2003; Llyoid, Law & Goldingay 2006; Ober, Hayes & Hall 2008; Hagen & Sabo 2011; Jung *et al.* 2012; Hagen & Sabo 2014).

Diversos estudos têm demonstrado o efeito da estrutura da vegetação, disponibilidade de insetos e dos corredores de vegetação das zonas ripárias sobre a distribuição espacial de morcegos insetívoros aéreos (Jung *et al.* 2012; Threlfall *et al.* 2011; Ober, Hayes & Hall 2008; Fukui *et al.* 2006, Grindal, Morissette & Brigham 1999). Contudo, a influência destes três fatores raramente tem sido avaliada simultaneamente (Hagen & Sabo 2011). A maioria dos estudos foi conduzida sobre ou próximo aos corredores de vegetação dos riachos, negligenciando a importância das

áreas não ripárias para esses morcegos (Sleep & Brigham 2003; Llyoid, Law & Goldingay 2006; Ober, Hayes & Hall 2008; Hagen & Sabo 2011; Jung *et al.* 2012; Hagen & Sabo 2014). Os resultados destes estudos provêm de morcegos de regiões temperadas e de áreas antropizadas, e pouco é conhecido sobre os morcegos neotropicais que habitam grandes extensões de floresta contínua. Por estes motivos, nós investigamos como o uso do ambiente pelo morcego insetívoro aéreo *Pteronotus parnellii* (Mormoopidae) é afetado pelas características estruturais da vegetação e pela disponibilidade de insetos em uma área de 25 km² de floresta contínua na Amazônia Central. Os morcegos foram monitorados por estações de gravação automáticas de ultrassom sobre pequenos riachos e em áreas não riparias para amostrarmos uma ampla variação na estrutura da vegetação e disponibilidade de insetos. Baseado nas generalizações na literatura e na morfologia da espécie, nós esperamos que a atividade dos morcegos esteja concentrada nos corredores de vegetação sobre os canais dos riachos com maior disponibilidade de insetos.

OBJETIVO GERAL

O presente estudo teve como objetivo principal investigar qual a distribuição espacial da atividade de uma espécie de morcego insetívoro aéreo *Pteronotus parnellii* em uma floresta tropical da Amazônia Central. Nos avaliamos a influencia que os ambientes ripários e não ripários desempenham sobre a distribuição da atividade dos morcegos. Avaliamos também como os níveis de obstrução da vegetação do sub-bosque e a disponibilidade de insetos voadores noturnos afetam a distribuição da atividade dos morcegos.

CAPÍTULO 1

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1	Activity of an Amazonian aerial insectivorous bat depends
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26 **SUMMARY**

1 – Many studies have shown that insectivorous bats frequently use riparian zones
around streams, but it is often unclear whether the bats are using those areas for feeding
or are just making use of the uncluttered areas over streams as movement corridors. No
study of Neotropical bats has investigated the relative use of riparian zones and areas far
from streams for foraging.

32 2 – We studied the effects of vegetation structure and food availability on the activity of
 33 the aerial insectivorous bat *Pteronotus parnellii* near and far from streams in tropical
 34 rainforest in Reserva Ducke, Central Amazonia.

35 3- We used horizontal photographs of understory vegetation to quantify the degree of

36 obstruction (clutter) by leaves and branches. Food availability was evaluated with small

37 light traps designed to catch nocturnal insects. Bat activity was monitored with high-

frequency sound recorders that operated continually for 60 hours at each site.

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40 to be more active in places with dense understory vegetation, which were more common

41 outside riparian zones. Food availability was also higher in places with more vegetation

42 clutter.

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should be more active in sites with little vegetation clutter. However, we found the

45 species to be more active in cluttered sites, indicating that food availability may be more

46 important than clutter in determining where the bats foraged.

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48 Key words Acoustic, Chiroptera, Feeding zones, Insect composition, Mormoopidae,

49 *Pteronotus parnellii*, Vegetation density.

50

51 **INTRODUCTION**

The use of habitat by animals is related to the distribution of food resources and characteristics of the landscape that permit access to those resources (MacArthur & Pianka 1966). In general, areas that favor movement and provide the most food are used more frequently (Chapman *et al.* 2011; Fukui *et al.* 2006; Rosenzweig 1981). In contrast, organisms generally avoid areas with little food and difficult access, because movement within them requires a larger expenditure of energy (Rainho, Augusto & Palmeirim 2010).

59 Aerially insectivorous bats normally show little activity in areas of cluttered vegetation (Sleep & Brigham 2003; Ober, Hayes & Hall 2008; Jung et al. 2012). This 60 group differs from other insectivorous bats, such as gleaners, because they can capture 61 62 insects in flight (Kalko & Handley 2001), which means that cluttered vegetation is not only an obstacle for movement, but also a potential barrier to food capture. A reduction 63 64 in activity of such bats in more cluttered sites may be related to the greater risk of 65 collision and the difficulty of achieving aerial maneuvers during flight (Norberg & 66 Rayner 1987; Schnitzler & Kalko 2001). The capacity to locate prey is also compromised in habitats obstructed by vegetation because echoes returning from plants 67 68 can interfere with those returning from insects, diminishing the detection and capture of prey (Jones & Holderied 2007; Rainho, Augusto & Palmeirim 2010). Though some bats 69 70 with greater capacity for aerial agility do manage to exploit closed habitats (Schnitzler & Kalko 2001), most aerially insectivorous bat species are more active in habitats with 71 72 more open vegetation (Siemers & Schnitzler, 2004; Ober, Hayes & Hall 2008; Hagen & 73 Sabo 2011; Jung *et al.* 2012).

Small streams that cross the forest are often located in areas with little vegetative
obstruction and may favor the movements of sub-canopy bats (Fukui *et al.* 2006). The

76 spaces with little vegetation above streams form open corridors in which more rapid 77 movement is possible (Fukui et al. 2011; Hagen & Sabo 2011). Bats can use the areas 78 above streams to commute more easily between sites, avoiding more cluttered regions 79 of the forest interior (Ober, Hayes & Hall 2008). In addition, such streams may concentrate resources used by bats, such as water and insects (Hagen & Sabo 2014; 80 81 Fukui et al. 2011; Jong & Ahlén 1991). A greater concentration of insects, easier and 82 more direct flight, and greater facility to locate and capture prey may result in higher activity levels by aerially insectivorous bat above streams courses (Sleep & Brigham 83 2003; Llyoid, Law & Goldingay 2006; Ober, Hayes & Hall 2008; Hagen & Sabo 2011; 84 85 Jung et al. 2012; Hagen & Sabo 2014).

Various studies have investigated the effect of vegetation structure, insect 86 availability and vegetation corridors in riparian areas on the spatial distribution of 87 88 aerially insectivorous bats (Jung et al. 2012; Threlfall et al. 2011; Ober, Hayes & Hall 2008; Fukui et al. 2006, Grindal, Morissette & Brigham 1999). However, the relative 89 90 impacts of these three factors were rarely evaluated simultaneously (Hagen & Sabo 91 2011). The majority of studies have been conducted in or near streamside vegetation 92 corridors, so potentially overlook the importance on non-riparian areas for the bats 93 (Sleep & Brigham 2003; Lloyd, Law & Goldingay 2006; Ober, Hayes & Hall 2008; Hagen & Sabo 2011; Jung et al. 2012; Hagen & Sabo 2014). Also, the majorities of 94 such studies have focused on bats of temperate regions and were carried out in habitats 95 96 strongly impacted by humans. Consequently, little is known about Neotropical bats in 97 continuous forest habitats, and how forest heterogeneity impacts their habitat use. According Schnitzler & Kalko (2001), P. parnellii is able to use highly clutter 98 environments, but no study has quantified the maximum clutter level tolerated by this 99 species. Clutter levels are high in the understory of the Amazon rainforest, and even 100

some areas above streams are cluttered. We undertook a study of how habitat use by the 101 102 aerially insectivorous bat Pteronotus parnellii (Mormoopidae) is affected by the 103 structural characteristics of vegetation and by the availability of insects. The study was undertaken in a 25 km² area of continuous forest in central Brazilian Amazonia, where 104 105 we monitored bats using automated ultrasound detectors located in streamside and in 106 non-riparian areas. Based on the general literature and on the morphology of the 107 species, we expected that *P. parnelli* would concentrate its activity in the riparian 108 corridors with ease flight and greater availability of insects and water. 109 110 MATERIALS AND METHODS STUDY SITE 111

112 The study was conducted in the Adolpho Ducke Forest Reserve (2°58'S, 59°55'W)

113 (Reserva Ducke), located to the north of the city of Manaus, at Km 26 of the AM-110

114 Highway, Amazonas State, Brazil. The reserve forms part of the Brazilian Long-term

115 Ecological Research Program of the Brazilian National Research Council (Programa de

116 Pesquisas Ecológicas de Longa Duração: PELD/CNPq) and covers 10,000 ha of

117 lowland rainforest. Annual rainfall varies between 1,800 and 2,800 mm, with highest

rainfall occurring between November and May and a drier period between June and

119 October (Deciso *et al.* 1975). Mean relative humidity is 86%, and the mean annual

temperature is 26° C (Deciso *et al.* 1975). The region's relief is undulating with small

121 plateaus, slopes and valleys that vary between 45 and 140 m in height. Small streams

are found in the valley bottoms. The canopy reaches 30 to 35 m, though emergents may

123 exceed 50m (Oliveira *et al.* 2008).

Within the reserve, there is a 25 km² (5 x 5 km) trail system, installed when the
Biodiversity Research Program (Programa de Pesquisa em Biodiversidade: PPBio)

126 began its long-term biodiversity research program in the area (Magnusson et al. 2005, 127 Magnusson et al. 2013). The system consists of a grid of six trails oriented north-south and six trails oriented east-west (Fig. 1). The trails give access to 30 uniformly 128 129 distributed study plots, each separated from the next by 1000 m. Within the grid there 130 are also 15 riparian plots, located along streams (Fig. 1). All plots are 250 m long and, 131 since characters such as soil type and humidity often vary with altitude, the central line 132 of the uniformly distributed plots follow topographical contours, which reduces 133 variation in environmental characteristics within plots (Magnusson et al. 2005). Riparian plots follow the banks of streams. 134

135

136 STUDY SPECIES

137 Pteronotus parnellii is a medium-sized understory-dwelling Neotropical bat with body

138 length 7.3-10.2 cm, wingspan 30-35 cm, and mass 10-20 g (Herd 1983). The species

ranges 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 the state of Matto

141 Grosso, in central Brazil (Smith 1972). The species occurs in a variety of forest types,

142 from lowland rainforest to drier forest types at 3000 m on the coastal slopes of the

143 Andes (Handley 1976; Smith 1972). The non-feeding echolocation call of *P. parnellii*

144 (Fig, S1) is short and composed of two principle components (CF-FM). Spectrographic

145 analysis of this characteristic signal permits unequivocal identification of this species,

146 as it is unlike the call of any other Amazonian bat species (Vater *et al.* 2003).

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148 BAT ACTIVITY ESTIMATION

149 Bat vocalizations were sampled from January to May 2013, during the local rainy

season. We sampled 22 plots, 12 in non-riparian and 10 in riparian localities (Fig. 1).

The non-riparian plots were separated by a minimum distance of 1 km and a maximum 151 of 6 km, and the riparian plots were separated by a minimum distance of 560 m and a 152 maximum of 5.2 km. The minimum distance between the riparian and non-riparian plots 153 154 was 400 m and the maximum 8.1 km. Each plot was sampled for five consecutive nights between 18:00 and 06:00 hrs (12 hours per night), resulting in a total of 60 hours of 155 recordings per plot. To record *P. parnellii* activity, we used Song Meter SM2+ 156 recording stations (Wildlife Acoustics, USA), each coupled to an omnidirectional 157 158 ultrasonic microphone (model SMX-US: Wildlife Acoustics, USA). We programed each SM2+ to record in real time with a sampling frequency of 384 Hz, a full-spectrum 159 resolution of 16 bits, with a 1-second pre-trigger and a 0.1 second post-trigger, with Dig 160 HPF and Dig LPF deactivated and Trigger Level 0 dB. The recording units were placed 161 162 in the center of each plot. In the riparian plots we used 3 m-long cables to position the 163 microphones over the center of the stream.

The SM2+ units were programed to create audio files in WAC format at 164 165 intervals of 30 minutes, giving 24 files for each 12 h sampling period. Each WAC file 166 was then converted to WAV format and divided into segments of 5 seconds maximum duration using the program Kaleidoscope (Wildlife Acoustics, USA). The acoustic 167 signals were visualized with the AVISOFT SASLAB PRO program, version 4.34 168 169 (Raimund Specht, Avisoft, Germany). Spectrogram resolution characteristics were set to a hamming evaluation window, with a FFT (Fast Fourier Transformation) of 512 170 points and a frame size of 100%. We considered each five-second segment that 171 172 contained two or more P. parnellii acoustic signals to be indicative of one pass of the species through the plot. To quantify P. parnellii activity per plot, we used the medium 173 number of passes per night (total number of passes/5 nights). 174

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176 QUANTIFYING UNDERSTORY VEGETATIVE CLUTTER LEVELS

Vegetative clutter was measured using horizontal photographs of vegetation, adapted 177 from the method of Marsden et al. (2002). We used a white cloth mounted in a 3 x 3 m 178 179 aluminum frame to create a panel that contrasted with the vegetation. The white panel 180 was positioned perpendicular to a digital camera positioned 8m from the panel. In each 181 non-riparian plot, the vegetation was photographed at points each 10m along 100m of 182 the central line of the plot, giving 10 vegetation photographs per plot (Fig. S2a). In 183 riparian plots, the photographs were made above the stream, and we positioned the white panel perpendicular to the central channel at distances of 10m along a 180 m 184 185 transect of the stream course, giving 10 vegetation photographs per plot (Fig. S2b). In each plot we positioned the SM2+ unit in the mid-point of the line used to quantify the 186 187 vegetation clutter levels.

188 Clutter levels were quantified by transforming the photographs into black-and-189 white images to increase the contrast between the vegetation and the white panel, so that 190 black areas represented vegetation and white areas represented open space. The white 191 areas for each of the 10 images from each plot were summed to quantify the percentage 192 of the area covered by vegetation, equivalent to one large photograph per plot. We used 193 the program ImageJ 1.38x (National Institutes of Health, USA) to calculate the 194 percentages of black and white and quantify the vegetation clutter levels.

195

196 QUANTIFYING INSECT ABUNDANCE AND COMPOSITION

Flying nocturnal insects were collected in light traps, consisting of a 20 cm diameter
plastic cone attached to a 100 ml insect collecting pot containing 70% alcohol. A 25 cm
diameter plate was suspended above the cone to protect against rain (Fig. S3). To attract
insects, a lantern with 10 LED lights was positioned beneath the plate and pointed

towards the cone. Two such light traps were installed per plot, each a distance of 70 m
from the SM2+ unit. The light traps remained lit for a 48 h period during the time when
bat ultrasonic vocalizations were being recorded.

204 The trapped insects were identified to order, and only those orders known to be eaten by P. parnellii were included in analyses. Rolfe & Kurta (2012) analyzed the diet 205 206 of the species and recorded the following taxa: Coleoptera (40.4%), Lepidoptera (27.4%), Hymenoptera (18%), Odonata (1.8%), Diptera (1.6%) e Orthoptera (0.7%). 207 208 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, USA) to quantify 209 210 the total mass of insects captured in each plot. The insects were preserved in 70% alcohol and deposited in the Invertebrate Collections of the Instituto Nacional de 211 212 Pesquisas da Amazônia (INPA), Manaus.

213

214 DATA ANALYSIS

215 We compared vegetation clutter levels, mass of insects in the diet of P. parnellii 216 between riparian and non-riparian plots using a Student's *t*-test. To evaluate the effect of vegetation clutter on the mass of diet insects we used a Poisson General Linear Model 217 218 (GLM) to correct for the overdispersion produced by the variance exceeding the mean 219 (Zuur et al. 2009). The composition of insect orders in the samples was evaluated using 220 the mass of each order as a measure of abundance that was used to create a non-metric 221 multidimensional scaling axis (NMDS) based on the Bray-Curtis Dissimilarity Index 222 (Legendre & Legendre 1998). The NMDS axis was regressed against vegetation clutter in a Gaussian GLM model. 223

We compared the activity of bats in riparian and non-riparian plots using a *t*-test.
To examine the effect of vegetation-clutter levels and insect mass on the activity of *P*.

226	parnellii (measured as numbers of passes per night), we used a multiple Poisson GLM
227	model (Zuur et al. 2009). Vegetation-clutter levels and insect mass had little correlation.
228	To examine the effect of insect composition on bat activity, we use a simple Poisson
229	GLM, because this variable is correlated with vegetation clutter and insect mass. All
230	analyses were conducted using Vegan 2.1-16 (Oksanen et al. 2012) in the R program,
231	version 2.12.1 (R Core Team, 2012).
232	
233	RESULTS
234	INSECT AVAILABILITY AND VEGETATION-CLUTTER LEVELS
235	The light traps captured a total of 1006 insects from 12 orders. Their total mass was
236	4.2 g (Table 1). In terms of mass, the most abundant orders were Coleoptera
237	(64.5%; 2.7 g), Hymenoptera (13.4%; 0.6 g), Ephemeroptera (5.0%; 0.2 g),
238	Tricoptera (4.3%; 0.2 g) and Diptera (4.1%; 0.2 g). These orders constituted 91.2%
239	of the collected insect mass. The mass of the orders known to be eaten by <i>P</i> .
240	parnellii comprised 86.3% of the total mass of insects captured. The median mass
241	of insect orders known to be eaten by P. parnellii captured in non-riparian plots
242	was greater than that in riparian plots (<i>t</i> -test, $t = -2.04$; $P = 0.06$).
243	Vegetation clutter varied between 43-63.8% (mean 54.9 \pm 6.0 SD) in non-
244	riparian plots, and between 13.6% and 42.8% (mean 27.5 \pm 12.6 SD) over the stream
245	channels of riparian plots. The non-riparian plots had twice as much cluttering
246	vegetation as riparian plots (<i>t</i> -test, $t = -6.29$; $P < 0.001$). The distribution of insect orders
247	indicated structuring of insect assemblages as a function of vegetation clutter and
248	habitat type (riparian, non-riparian; Fig. 2). The insect-order composition (NMDS axis)
249	using mass as an index of abundance (Fig. 3), was related to vegetation clutter (GLM, t

250 = -2.28; P = 0.03), and differed between riparian and non-riparian plots. This structuring

probably resulted from the greater mass of insects in orders eaten by *P. parnellii* (Fig. 4)

in areas with higher vegetative clutter (GLM, t = 2.07; P = 0.05).

253

254 BAT ACTIVITY

255 We monitored the activity of *P. parnellii* for 110 nights, and successfully recorded

- ultrasound on 99 (90% of recording nights). In 1320 hours of recordings, we registered
- a total of 3648 passes by *P. parnellii*, of which 3433 passes were in non-riparian plots
- (mean 278.6 \pm 260.8 SD), and 305 in riparian plots (mean 30.5 \pm 30.8 SD). *Pteronotus*
- 259 *parnellii* was recorded in all 22 non-riparian plots, and activity varied between three and
- 260 347 passes per plot. Mean activity in non-riparian plots was 10 times greater than in
- riparian plots (*t*-test, t = -3.26; P = 0.007). Activity of *P. parnellii* was significantly
- 262 (GLM, t = 4.43; P < 0.001) and positively (Fig. 5a) related to insect mass and
- significantly (GLM, t = 2.46; P = 0.02) and positively (Fig. 5b) related to vegetation
- clutter. The composition of insects was associated significantly (GLM, t = -5.74; P < -5.74
- 265 0.001) with the activity of *P. parnellii* (Fig. 6).
- 266

267 DISCUSSION

As has been recorded in other regions (Hagen & Sabo 2011; Fukui *et al.* 2006),

269 vegetation clutter is greater in non-riparian habitats than in riparian zones. This

270 indicates that streams may facilitate bat movements within forests (Ober, Hayes & Hall

271 2008). However, unexpectedly, the activity of *P. parnellii* was greater in habitats with

- 272 greater levels of vegetation clutter. Insect availability was also greater in more
- obstructed areas, and this could explain the greater levels of activity by *P. parnellii* in
- areas with more closed vegetation.

The increase in *P. parnellii* activity in the areas with denser vegetation is not in 275 276 line with the results of most studies of activity patterns by aerially insectivorous bats, which reported greater activity above streams (Bendix 2012; Akasaka, Nakano & 277 278 Nakamura 2009; Fukui et al. 2006; Camporeale & Ridolfi 2006). A study by Grindal, Morissette & Brigham (1999) about habitat use by bats in British Columbia, indicated 279 280 that the activity was three times higher over streams than in neighboring, denser, 281 vegetation. The authors of those studies concluded that riparian areas are favored by 282 bats because vegetation structure is more open and so facilitates flight passage (Fukui et al. 2006), and because there is both water and more adult insects with aquatic larvae 283 284 (viz. Ephemeroptera, Trichoptera and various dipteran families such as Curculidae) near streams (Hagen & Sabo 1014; Fukui et al. 2006). However, Hagen & Sabo (2011) 285 286 showed that aerially-available food resources were most abundant in those parts of 287 streams where vegetation density was greatest. In our study, P. parnellii activity was lowest over streams and highest in non-riparian areas with dense vegetation. 288 289 Availability of insects consumed by P. parnellii was greater in areas with densest 290 vegetation, indicating that these bats are probably selecting cluttered places as feeding sites, concentrating their activities in those areas with higher prey density. Within the 291 292 riparian zone, the bats showed more activity in plots with denser vegetation and higher 293 insect abundances. This suggests that the amount of cluttering vegetation encountered in 294 this study did not restrict the activity of P. parnellii, and indicates that the availability of 295 insects had more influence on the distribution of this bat species than did the density of 296 understory vegetation.

297 Several studies have reported associations between plant and insect composition 298 (Dinnage *et al.* 2012; Andow 1991). Schietti *et al.* (2013) showed that there are changes 299 in plant composition along the hydrological gradient that starts in the streams and

300 continues into the non-riparian areas in Reserva Ducke. This change in plant 301 assemblages between riparian and non-riparian sites may explain the differences in insect orders we captured at different distances from the streams. In the same study site, 302 303 Bueno et al. (2012) found a similar pattern of composition change in bird species with distance from streams. As in other groups, the insectivorous bat P. parnellii was 304 305 apparently strongly affected by the composition of insects along a clutter gradient, 306 concentrating its activity in environments with more insect diet. Although riparian 307 zones are also used, areas away from streams may be important for bats, because they provide food resources that are scarce near streams. 308

309 The use of cluttered environments requires energetically costly levels of high maneuverability to successfully avoid obstacles in the understory (Norberg & Rayner 310 311 1987; Schnitzler & Kalko 2001). Flying in more cluttered environments could be 312 advantageous when they contain more food or if the food they contain is especially 313 energy-rich (MacArthur & Pianka 1966). The energetic expenditure accompanying the 314 use of more cluttered areas by *P. parnellii* may be compensated by the greater 315 availability of insect prey. In addition, the species may possess ecomorphological adaptations that reduce the energetic expenditure when foraging in cluttered habitats. 316 317 The signal type used by *P. parnellii* is CF-FM, and the second harmonic of the 318 frequency of the CF component is modulated to compensate for Doppler effects as the species closes in on prey or vegetative obstacles (Jen & Kamada 1982). Such 319 320 adaptations in signal characteristic are common in bats, such as Rhinolophus 321 ferrumequinum and P. parnellii, which commonly forage in cluttered areas (Schnitzler & Kalko 2001). The wing morphology of *P. parnellii* is that of a generalist, so that it 322 may exploit a variety of different habitats and foraging modalities (Marinello & Bernard 323 324 2014), including, highly cluttered habitats.

Many of the studies conducted in areas subjected to strong human impacts have 325 326 found higher levels of bat activity in riparian zones (e.g. Law & Chidel 2002; Dodd, Lacki & Rieske 2008; Threlfall et al. 2011; Fukui et al. 2011; Stahlschmidt et al. 2012). 327 328 However, few studies of bat activity in riparian habitats have simultaneously evaluated the use by bats of closed adjacent forest (Grindal, Morissette & Brigham 1999; Hagen 329 & Sabo 2011). Pteronotus parnellii is a forest specialist (Bernard & Fenton 2007) that 330 331 avoids highly degraded areas (Bobrowiec & Gribel 2010), and seems to prefer closed 332 vegetation, compared with naturally open environments. Therefore, riparian forests in areas subject to human modification could be functioning as a refuge in an otherwise 333 334 highly degraded habitat (Robinson, Tockner & Ward 2002), and not as a prefered feeding habitat for bats. More studies need to be carried out in relatively undisturbed 335 336 areas, with simultaneous monitoring of bat activity in riparian and non-riparian zones 337 before it will be possible to make generalizations about the importance of riparian zones 338 for insectivorous bats.

339

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Fig. 1. Location of study plots within Reserva Ducke, Central Amazon, Brazil. The open

480 circles represent terrestrial (non-riparian) plots, with uniform inter-plot separation of 1 km.

- 481 The open squares represent riparian plots adjacent to streams.
- 482
- 483



Fig. 2. Distribution of insect orders as a function of a gradient of obstruction of vegetation
(clutter) in Reserva Ducke, Central Amazonia, Brazil. The vertical bars indicate the
relative masses of the insect orders in the two habitats. Asterisks indicate those orders
known (according to Rolfe *et al.* 2012) to form part of the diet of *Pteronotus parnellii*.





Fig. 3. Relationship between vegetation obstruction levels (clutter) and insect order
composition represented by a one-dimensional NMDS ordination at Ducke Reserve, Central
Amazonia, Brazil. The black dots represent non-riparian (terrestrial) plots and open points
represent riparian plots.



Vegetation obstruction (%)

Fig. 4. Relation between vegetation obstruction (clutter) and the masses of insect orders in the
diet of *Pteronotus parnellii* in Reserva Ducke, central Amazonia, Brazil. The closed circles
represent non-riparian plots and the open circles represent riparian plots.



Fig. 5. Partial regression results from a multiple regression of *Pteronotus parnellii* activity
against mass of insects known to be part of its diet (a) and level of vegetation obstruction
(clutter) (b). The black line represents a least-squares regression. The closed circles
correspond to non-riparian (terrestrial) plots and the open circles to riparian plots in Reserva
Ducke, Central Amazonia, Brazil.



Fig. 6. Relationship between Pteronotus parnellii activity and the a one-dimensional NMDS axis representing insect assemblage composition in Reserva Ducke, central Amazonia, Brazil. The closed circles represent non-riparian plots and the open circles represent riparian plots.

	N	Ion-riparian	areas		Streams			Total	
	N	Mass (g)	% mass	Ν	Mass (g)	% mass	Ν	Mass (g)	% mass
Hymenoptera*	155	0.4	14.0	101	0.2	11.9	256	0.6	13.4
Coleoptera*	110	2.1	73.2	48	0.6	44.4	158	2.7	64.5
Diptera*	74	0.2	5.5	79	0.0	0.8	153	0.2	4.1
Homoptera*	23	0.1	2.2	8	0.0	0.8	31	0.1	1.7
Lepidoptera*	10	0.1	1.7	44	0.1	4.0	54	0.1	2.4
Isoptera	5	0.0	0.3	48	0.1	4.0	53	0.1	1.4
Blattodea	2	0.0	0.3	5	0.0	0.2	7	0.0	0.3
Ephemeroptera	1	0.0	0.0	184	0.2	16.7	185	0.2	5.0
Orthoptera*	0	0.0	0.0	36	0.0	0.8	36	0.0	0.2
Mantodea	0	0.1	2.7	2	0.0	0.0	2	0.1	1.9
Plecoptera	0	0.0	0.0	8	0.0	2.4	8	0.0	0.7
Trichoptera	0	0.0	0.0	63	0.2	14.3	63	0.2	4.3
Total	380	2.9	100	626	1.3	100	1006	4.2	100
529									
530									
531									
532									
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534									

Table 1. Number of individuals, mass (g), and the relative percentage of the insects mass collected in Ducke Reserve, Central Amazonia. Asterisks indicate taxa known to be part of the diet of *Pteronotus parnellii*.

536 SUPPORTING INFORMATION





Fig. S1. Spectrogram of the navigation pulses of Pteronotus parnellii. The signal has a narrow 538 539 frequency range and is composed of two principle components (CF-FM). The first component is frequency modulated (FM) and appears at the beginning and end of the spectrogram. The 540 start of the FM signal is short (less than 1 millisecond - ms) and that at the end is longer 541 542 (varying between 2 and 3 ms). Between the two FM components there is a longer element of 543 constant frequency CF) ranging from 16 to 28 ms in duration. The call is of high frequency and is composed of 4 to 5 harmonics, with the second harmonic (61 - 62 KHz) being the most 544 545 intense (28 dB). Pteronotus parnellii normally emits more than one call during each wing-546 beat and will adjust the frequency of the second harmonic to compensate for the Doppler effect that occurs when the bat approaches prey or obstructing vegetation. 547 548



Fig. S2. The method used to quantify levels of vegetation clutter in non-riparian vegetation
plots using digital photographs (a), and in riparian plots (b). We used a white cloth tied to a 3
x 3 m aluminum frame to create a panel that would contrast with the vegetation. The panel
was positioned perpendicular to a digital camera placed at a distance of 8 m from the panel.



Fig. S3. Light traps for collecting nocturnal insects. The trap consisted of a 20 cm diameter

plastic cone attached to a removable 100 ml insect collecting pot containing 70% alcohol.

563 Above the cone we placed a 25 cm diameter dish to protect the collector from rain. A lantern

of with 10 LED lamps was fixed to the plate to attract insects.

CONCLUSÃO

A distribuição da atividade de *P. parnellii* em nossa área de estudo foi concentrada nos ambientes com maior obstrução da vegetação e a seleção por este tipo de ambiente foi associada mais com a disponibilidade de insetos do que a estrutura da vegetação. Diferente de outras espécies de insetívoros aéreos, *P. parnellii* utilizou pouco os canais dos riachos para o deslocamento e alimentação, provavelmente porque os riachos apresentaram poucos insetos que fazem parte da sua dieta. A obstrução da vegetação da reserva Ducke não foi um fator capaz de limitar a atividade de *P. parnellii*. Esta espécie de morcego possui adaptações no sinal acústico e forma das asas que possibilitam o deslocamento e acesso aos recursos alimentares em ambientes altamente obstruídos do subosque da floresta.

APENDICES

ATAS DAS BANCAS DE QUALIFICAÇÃO E DEFESA









ATA DA DEFESA PÚBLICA DA DISSERTAÇÃO DE MESTRADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA.

Aos 17 dias do mês de março do ano de 2014, às 09:00 horas, no Auditório do PG CLIAMB, prédio do LBA, Campus II, INPA/Aleixo., reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Fabricio Beggiato Baccaro** da Universidade Federal do Amazonas - UFAM, o(a) Prof(a). Dr(a). Pedro Ivo Simões do Instituto Nacional de Pesquisas da Amazônia - INPA e o(a) Prof(a). Dr(a). Igor Luis Kaefer, da Universidade Federal do Amazonas - UFAM, tendo como suplentes o(a) Prof(a). Dr(a). Marcelo Gordo, da Universidade Federal do Amazonas - UFAM, tendo como suplentes o(a) Prof(a). Dr(a). Claudia Keller do Instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **DISSERTAÇÃO DE MESTRADO** de **LEONARDO QUEIROZ DE OLIVEIRA**, intitulado ""Activity of an Amazonia depends more of food resources than the structural complexity of vegetation", orientado pelo(a) Prof(a). Dr(a). Paulo Estefano Bobrowiec do Instituto Nacional de Pesquisas da Amazônia de Amazonia de Pesquisas da Amazônia - INPA.

Após a exposição, o(a) discente foi arguido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

APROVADO(A)	REPROVADO(A)				
POR UNANIMIDADE	POR MAIORIA				

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Fabricio Beggiato Baccaro

Prof(a).Dr(a). Pedro Ivo Simões

Prof(a).Dr(a). Igor Luis Kaefer

Coordenação PPG-ECO/INPA