Comparison between the chiropteran fauna from terra firme and mangrove forests on the Bragança peninsula in Pará, Brazil

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(Received 21 June 2006; accepted 16 June 2008)

The aim of this study is to compare the density and diversity of the chiropteran fauna of the terra firme and mangrove forests of the Bragança peninsula in the Brazilian state of Pará. Bats were captured using mist nets every 2 months, resulting in the collection of 217 specimens from the terra firme and 221 from the mangrove. There was no significant difference between sites in the number of individuals or diversity. Thus, while the terra firme forest is probably the principal source of fruit, the mangrove seems to be the secondary source for opportunistic species during the period of scarcity.

O objetivo deste estudo é comparar a densidade e a diversidade da fauna de quirópteros das florestas de terra firme e de manguezal da península bragantina no Estado do Pará, Brazil. Morcegos foram capturados com redes-neblina a cada dois meses, resultando na coleta de 217 espécimes provenientes da terra firme e 221 do manguezal. Não existe diferença significativa entre os sítios de trabalho no que se refere ao número de indivíduos ou diversidade. Por isso, enquanto a floresta de terra firme é provavelmente a fonte principal de fruto, o manguezal parece ser a fonte secundária para as espécies oportunistas durante o período de escassez.

Keywords: Amazon; Brazil; Chiropteran fauna; mangrove; terra firme

Introduction

Worldwide, according to Fernandes (2000), a total of 111 species of mammals belonging to 14 different orders are known to be associated with mangrove forests. These species represent 7.5% of the 1467 vertebrate species catalogued for this ecosystem. The order Chiroptera accounts for 12.6% of mangrove mammals, with 14 species from just two families (Pteropodidae and Molossidae), and is the fourth most diverse group found in the mangroves of Asia, east and west coasts of both Africa and the Americas, and Oceania. McKenzie and Rolle’s (1986) study of the mangroves of Kimberley, Australia, recorded a further 22 species of bats, of which 17 species can be added to Fernandes’ review on bats associated with this system.

The Brazilian coast has one of the most extensive areas of mangroves of any country (Kjerve & Lacerda 1993), with a total area of 10,713 km² (Schaeffer-Novelli et al. 1990; Vanucci 1999), 85% of which is located along the northern coast. No published data are available on the association between bats and mangroves in the Neotropical region, where the occurrence and ecological importance of these animals for the coastal forests is still poorly known. Given this, the present study is based on a comparative survey of the chiropteran fauna (with emphasis on the family Phyllostomidae) of terra firme and mangrove forests on the Bragança Peninsula in the Brazilian state of Pará.

Materials and methods

Study area

The study area is located on the Bragança Peninsula’s elevated coastal plain at the Fazenda das Salinas (1°55′26.7″S, 46°40′20.4″W), approximately 20 km from the town of Bragança, in the Brazilian state of Pará. The 166 km² of this peninsula contain a variety of landscapes (Lara 2003), such as beaches, dunes, salt marshes, and mangrove and terra firme forests. The study area comprises the latter three types of environments (Figure 1).

The terra firme forests are present in the form of fragments of vegetation, surrounded by mangroves. The largest of these fragments covers an area of 33 ha, with trees of up to 23 m in height (Abreu et al. 2008), and was chosen as the study site for the bat survey. The flora includes species belonging predominantly to the families Simaroubaceae, Myrtaceae, Arecaceae, Sapindaceae, Lecythidaceae, and Burseraceae. The mangrove forest is composed

**Fieldwork procedures**

Bats were captured bi-monthly over an annual cycle, on nights with a new moon, using mist nets. Six bi-monthly captures were conducted, each consisting of 7 h fieldwork per night (from 18:00 to 1:00 h) over three consecutive nights. Two additional captures were conducted at a 6-month interval, representing the rainy and dry seasons. These captures also took place over three nights, but in this case from 18:00 to 6:00 h.

Nocturnal captures was adopted in order to minimize the possibility of the bats memorizing the location of the mist nets, given that these animals have excellent spatial memory, and may thus avoid frequently sampled areas (Bernard 2002). The results of the nocturnal captures were included in most of the analyses described below, whereas the data from the 6-monthly captures were used only for the recording of new taxa, which are more active towards dawn.

The mist nets were set along four transects, each 400 m long (Figure 1). Transects T1 and T2 were located in the *terra firme* forest, and T3 and T4 in the mangrove. Four mist nets (3 m high by 7 m long) were set on each transect, suspended 3 m above the ground, representing a total of 112 m² of net area per night. All nets were checked at hourly intervals.

**Specimen processing and identification**

The biometry of each captured bat included the length of the forearm, nasal leaf, ear and tragus. These measurements were important for the identification of specimens, which was based on the catalogues of Handley (1987), Linares (1987), Marques-Aguiaar (1994), Emmons and Feer (1997), Eisenberg and Redford (1998), and Gregorin and Taddei (2002). Specimens that could not be identified reliably in the field were killed and later identified in the laboratory by comparison with the reference collection. The other specimens captured were released. Two voucher specimens were collected for each species. These specimens, together with individuals that were fatally injured during handling, were deposited in the scientific collection of the Goeldi Museum in Belém, Pará, Brazil, according to Appendix 1. These specimens were essential for the

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**Figure 1.** Map of the Bragança peninsula (A). It details the study area (B) with its transects in the *terra firme* “islands” (T1 and T2) and in the mangrove forest (T3 and T4), and the different habitats. Modified from Mehlig (2001).
confirmation of the taxonomic identification of animals captured during the present study.

Data analysis

The following basic parameters were calculated from the raw capture data (Bernard & Fenton 2002): individual density (ID), species density (SD), and the species:specimens ratio (RSS). Differences in ID values between ecosystems and transects were tested using the ANOSIM analysis of the Primer v5 program (Clarke & Gorley 2001). This test is based on a matrix of similarity generated from square-root transformed data, using the Bray–Curtis index of similarity.

Cumulative curves were then plotted for each ecosystem, and compared with the following estimates of species richness: Michaelis–Menten Mean (MMMean), ACE (Abundance-based Coverage Estimator), ICE (Incidence-based Coverage Estimator), Chao1 and Chao2, Jacknife 1 and Bootstrap (EstimateS 6.0b 1; Colwell 1997). The diversity of the two sites was estimated using the Shannon–Wiener ($H'$) and Simpson ($D$) indices, accompanied by Evenness (E) and the inverse Simpson (1/D), calculated by the program Species Diversity & Richness-v. 2.5 (Henderson & Seaby 1997). The number of species recorded per forest type was compared using the Jaccard ($C_J$) and Sørensen ($C_S$) quantitative indices (Magurran 1988).

Results

The bi-monthly nocturnal captures accumulated a total of 2016 net-hours, and a total of 438 specimens belonging to 23 taxa. Of this total, 217 individuals and 14 species were captured in the terra firme forest, while the mangrove forest returned a total of 221 individuals and 18 species (Table 1). In all, 97.6% of the bats captured (428 individuals belonging to 18 species) were Phyllostomidae, whereas the remaining 10 individuals (2.4% of the total) belonged to four different families (Figure 2).

The phyllostomids belong to five subfamilies, captured in both types of forest. Most of the specimens (62% in terra firme and 70% in mangrove) were members of the Stenodermatinae (Figure 3). The predominance of the stenodermatines was due primarily to the abundance of Artibeus planirostris and A. obscurus, with 29 and 25.6% of the specimens, respectively. Carollia perspicillata (Carollinae) was also relatively common, with 22% of the specimens, while the glossophagine Glossophaga soricina was responsible for 6.8% of the total sample (Table 1).

Overall ID was 0.22 individuals per net-hour (Table 2). The comparative analysis found no significant difference in the number of individuals captured in mangrove and terra firme forests (ANOSIM, $R=0.001; P>0.05$). The additional analysis of ID values among the four transects did reveal significant differences, however. Statistical differences were found between transects in the same forest type (T1 vs. T2: $R=0.014; P<0.001$), and between ecosystems (T1 vs. T3: $R=0.009; P<0.05$; T2 vs. T4: $R=0.006; P<0.05$). This is corroborated by the cluster analysis of the transects, which shows that transects T2 (terra firme) and T3 (mangrove) were the most similar in terms of the number of individuals captured (Bray–Curtis index=99.69), whereas T1 and T4 were the most distant from T2 (99.26 and 99.52, respectively).

Transects T1 and T3 also produced the same SD values of 0.026 species per net-hour (Table 2). While this was the highest value for the terra firme transects, the second mangrove transect (T4) resulted in a slightly higher value, 0.028. The mean RSS value for the terra firme forest was 0.064 species per capture, although it was much higher on T2 (0.15 species per capture). Mangrove presented the highest value of species captured per net-hour (0.018). This system has also reached 0.081 when the ratio between Ns and Ni (species:specimens) is considered (Table 2).

The cumulative capture curves indicate that the sampling effort may have been insufficient to record the full variety of species, given that neither curve has reached the asymptote (Figure 4). Estimates of species richness for the combined data predict the presence of between 23 and 38 species in the study area, which corresponds to between 61 and 100% of the species recorded, respectively (Table 3). By forest type, the results represent 78–100% of the species expected for the terra firme forest, and 60–90% of those expected for the mangrove.

Indices of species diversity were relatively similar for the two ecosystems, with $H'=1.84$ and $1-D=0.80$ for the terra firme and $H'=1.80$ and $1-D=0.76$ for the mangrove. Overall diversity for the study area was $H'=1.90$ and $1-D=0.79$. The two ecosystems were relatively similar, according to both Jaccard’s $C_J$ (64.28%) and Sørensen’s $C_S$ (78.26%).

During the day bats were seen roosting in the hollows of a mangrove tree (A. germinans) 10 m above the ground but identification was impossible.

During the nocturnal all-night captures conducted at 6-monthly intervals more specimens (65.5%) were collected in the mangrove. The most common species captured during the main study made a similar contribution here, with A. planirostris (44%), A. obscurus (23%), and C. perspicillata (12%)
contributing most to the total sample. However, this complementary sampling did provide the record of one more species, *Myotis nigricans*, represented by a single individual for mangrove forest.

**Discussion**

One primary result of the present study was the addition of 18 species to the list of mangrove-dwelling mammals compiled by Fernandes (2000). Despite this, the estimators of species richness indicated that the expected number of bat species present in the mangrove forest was not recorded during the present study.

Reinforcing this conclusion, neither of the cumulative species curves stabilized, although most of the observed values of species richness were closer to the estimated values either for *terra firme* forest or mangrove.

Despite the lower sampling effort and lower ID values in comparison with, for example, Bernard and Fenton (2002), SD values recorded in the present study in both ecosystems were similar to those recorded by these authors for fragmented forest and savanna (Table 2). It thus seems reasonable to conclude that, while increased sampling effort may result in the capture of a larger number of species, this does not necessarily guarantee the higher species density (SD).

Table 1. Characterization of the Chiropterofauna at the Fazenda das Salinas including information on taxonomy (Silva 1994; Wilson et al. 1996; Emmons & Feer 1997), guilds (Hill & Smith 1986; Findley 1993; Wilson et al. 1996; Emmons & Feer 1997), conservation status (Fundação Biodiversitas 2002; Ministério do Meio Ambiente 2003), occurrence status in the study area (Marques-Aguiar et al. 2002), and number of individuals per species captured in both habitats by using mist nets from 18:00 to 01:00 h.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Guild</th>
<th>Conservation status</th>
<th>Occurrence status</th>
<th>Habitats&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Relative abundance (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>EMBALLONURIDAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Saccopteryx leptura</em> (Schreber, 1774)</td>
<td>Insectivorous</td>
<td>Stable (+)</td>
<td>– 1 1 1</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td><strong>MOLOSSIDAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Molossus melolosus</em> (Pallas, 1766)</td>
<td>Insectivorous</td>
<td>Stable (+)</td>
<td>3 – 3</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td><strong>NOCTILIONIDAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Noctilio leporinus</em> (Linnaeus, 1758)</td>
<td>Piscivorous</td>
<td>Stable (+)</td>
<td>5 – 5</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td><strong>PHYLLOSTOMIDAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caroliniae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Carollia perspicillata</em> (Linnaeus, 1758)</td>
<td>Omnivorous</td>
<td>Stable (+++)</td>
<td>36 61 97</td>
<td>22.2</td>
<td></td>
</tr>
<tr>
<td>Desmodontinae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Desmodus rotundus</em> (E. Geoffroy, 1810)</td>
<td>Sanguivorous</td>
<td>Stable (+)</td>
<td>3 2 5</td>
<td>1.1</td>
<td></td>
</tr>
<tr>
<td>Glossophaginae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Glossophaga soricina</em> (Pallas, 1766)</td>
<td>Nectarivorous</td>
<td>Stable (+++)</td>
<td>14 16 30</td>
<td>6.8</td>
<td></td>
</tr>
<tr>
<td>Phyllostominae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Choeropus auritus</em> (Peters, 1856)</td>
<td>Carnivorous</td>
<td>Stable (+)</td>
<td>2 2 2</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Micronycteris megalotis (Gray, 1842)</td>
<td>Insectivorous</td>
<td>Stable (+)</td>
<td>1 – 1</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td><em>M. schmidtorum</em> Sanborn, 1935</td>
<td>Insectivorous</td>
<td>Stable (+)</td>
<td>2 2 2</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Mimom crenulatum (E. Geoffroy, 1803)</td>
<td>Insectivorous</td>
<td>Stable (+)</td>
<td>2 2 2</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>Phyloderma stenops Peters, 1865</td>
<td>Omnivorous</td>
<td>Stable (+)</td>
<td>5 2 7</td>
<td>1.6</td>
<td></td>
</tr>
<tr>
<td>Tonatia saurophila Koopman and Williams, 1951</td>
<td>Insectivorous</td>
<td>Stable (+)</td>
<td>1 2 3</td>
<td>0.7</td>
<td></td>
</tr>
<tr>
<td>Stenodermatinae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Artibeus obscurus</em> (Schinz, 1821)</td>
<td>Frugivorous</td>
<td>Not stable (+++)</td>
<td>58 54 112</td>
<td>25.6</td>
<td></td>
</tr>
<tr>
<td><em>A. cinereus</em> (Gervais, 1856)</td>
<td>Frugivorous</td>
<td>Stable (+++)</td>
<td>4 22 26</td>
<td>5.9</td>
<td></td>
</tr>
<tr>
<td><em>A. planirostris</em> (Spix, 1823)</td>
<td>Frugivorous</td>
<td>Stable (+++)</td>
<td>82 45 127</td>
<td>29.0</td>
<td></td>
</tr>
<tr>
<td><strong>VESPERTILIONIDAE</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Myotis albescens</em> (E. Geoffroy, 1806)</td>
<td>Insectivorous</td>
<td>Stable (+)</td>
<td>1 – 1</td>
<td>0.2</td>
<td></td>
</tr>
<tr>
<td>Individuals</td>
<td>221 217 438</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>18 14 23</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exclusive species</td>
<td>9 5</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<sup>a(+)=rare, from one to five individuals; (++)=low, from six to 10 individuals; (+++)=common, more than 10 (Marques-Aguiar et al. 2002).</sup>

<sup>bM, mangrove; TF, terra firme.</sup>
Bergallo et al. (2003) argued that an increase in sampling effort (net-hours) at a given site would be a less efficient strategy for increasing the reliability of estimates of species richness than an increase in capture locations (netting sites). This conclusion was confirmed in the present study, given that the ratio of species to individuals captured differed considerably between transects and because transects T3 and T4, even though species:specimens ratios were similar, yielded different species resulting in a higher overall richness. This suggests that the number of species recorded in the present study might have been larger if the nocturnal captures had been more amply distributed within each ecosystem, even without any increase in sampling effort (net-hours).

On the other hand, the considerable similarities in the numbers of individuals captured, whether per transect or per ecosystem, suggest that the bats visit these environments at similar frequencies. The flight capabilities of two of the most common species recorded, A. planirostris and C. perspicillata, are well known (Morrison 1979; Bernard & Fenton 2003), and both are well able to cross the approximately 500 m that separate the two sites. In fact, bats of either species would be capable of visiting all four transects a number of different times on a given night. It is thus reasonable to conclude that the

Figure 2. Percentage of bats captured per family in mangrove and *terra firme* at the Fazenda das Salinas, Bragança, Pará, Brazil. P, Phyllostomidae; V, Vespertilionidae; E, Emballonuridae; M, Molossidae; N, Noctilionidae.

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Figure 3. Percentage of bats captured by subfamilies of the family Phyllostomidae in mangrove and *terra firme* at the Fazenda das Salinas, Bragança, Pará, Brazil.

Table 2. Mist net sampling in both habitats considering transects at the Fazenda das Salinas, Bragança, Pará, Brazil.

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Transect</th>
<th>Net-hours</th>
<th>Individuals (NI)</th>
<th>Species (NS)</th>
<th>Individuals/ net-hour (ID)</th>
<th>Species/ net-hour (SD)</th>
<th>Species:specimens (RSS)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fazenda das Salinas</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terra firme</td>
<td>T1</td>
<td>504</td>
<td>142</td>
<td>13</td>
<td>0.28</td>
<td>0.026</td>
<td>0.15</td>
</tr>
<tr>
<td></td>
<td>T2</td>
<td>504</td>
<td>75</td>
<td>10</td>
<td>0.15</td>
<td>0.020</td>
<td>0.15</td>
</tr>
<tr>
<td>Mangrove</td>
<td>T3</td>
<td>504</td>
<td>99</td>
<td>13</td>
<td>0.20</td>
<td>0.026</td>
<td>0.13</td>
</tr>
<tr>
<td></td>
<td>T4</td>
<td>504</td>
<td>122</td>
<td>14</td>
<td>0.24</td>
<td>0.028</td>
<td>0.12</td>
</tr>
<tr>
<td>Central Amazonia*</td>
<td>Forest</td>
<td>1523</td>
<td>1129</td>
<td>44</td>
<td>0.74</td>
<td>0.028</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>Savanna</td>
<td>2146</td>
<td>1183</td>
<td>41</td>
<td>0.74</td>
<td>0.023</td>
<td>0.03</td>
</tr>
<tr>
<td></td>
<td>Forest fragments</td>
<td>2445</td>
<td>1605</td>
<td>50</td>
<td>0.48</td>
<td>0.016</td>
<td>0.03</td>
</tr>
</tbody>
</table>

aData for forest, savannas and forest fragments calculated from Bernard & Fenton (2002).
The chiropteran fauna of the two ecosystems would be effectively the same, in terms of both density and diversity. The highest numbers of frugivorous bats were collected along the transects T1 and T4 in both forest types, where trees formed a less closed canopy providing easy access for bats of this guild. This type of situation appears to be consistent with previous studies. Fleming (1986) and Mikich (2002), for example, pointed out that most frugivorous bats have generalist diets, and prefer fruits that are easily accessible on the plant and seasonally abundant. In general, open areas are more appropriate environments for plant species of families such as Cecropiaceae and Moraceae. According to Passos et al. (2003), these families are preferred by many frugivorous bat species, such as those of the genus *Artibeus*, just as species of the family *Piperaceae* are appreciated by *C. perspicillata*.

Neotropical mangroves are forests with high primary productivity (Fernandes 2003), but low diversity of plant species. In addition, the fruit and propague of the three tree genera found in these forests (*Rhizophora, Avicennia*, and *Laguncularia*) have no pulp or attractive odor, but many secondary compounds (Tomlinson 1986). According to Charles-Dominique (1986), frugivorous bats are most attracted to fleshy fruits with a strong odor. Given this, the presence of large numbers of bats in the mangrove forest is more likely related to the presence of contiguous *terra firme* forest than to the availability of edible fruit.

The higher number of bat species recorded in the mangrove forest was due to the capture of rare species (less than five individuals collected), primarily those belonging to insectivorous, carnivorous, piscivorous and sanguivorous guilds. Insects are relatively abundant in mangrove forests (Hogarth 1999), mainly during the rainy season. In contrast the *terra firme* forest constitutes the primary source of fruit, but even many frugivorous bats will shift to an insectivorous diet during periods when fruit are scarce. Thus the abundance of frugivorous bats in the mangrove forest may have been related to the exploitation of arthropods in this system. At last, the

**Table 3.** Expected numbers of bats at Fazenda das Salinas, based on different species-richness estimators.

<table>
<thead>
<tr>
<th></th>
<th>Bat species richness</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td><em>Terra firme</em></td>
</tr>
<tr>
<td></td>
<td>Richness</td>
</tr>
<tr>
<td>Captured</td>
<td>14</td>
</tr>
<tr>
<td>ACE</td>
<td>16</td>
</tr>
<tr>
<td>ICE</td>
<td>18</td>
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<td>Chao1</td>
<td>15</td>
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<tr>
<td>Chao2</td>
<td>14</td>
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<tr>
<td>Jackknife1</td>
<td>17</td>
</tr>
<tr>
<td>Bootstrap</td>
<td>16</td>
</tr>
<tr>
<td>MMMean</td>
<td>16</td>
</tr>
</tbody>
</table>

ACE, Abundance-based Coverage Estimator; ICE, Incidence-based Coverage Estimator; MMMean, Michaelis–Menten Mean.
mangrove forest may simply serve as a “corridor” for the frugivorous bats on their way between patches of terra firme forest.

Acknowledgements

We are grateful to the bilateral project MADAM (Mangrove Dynamics and Management) between Brazil (CNPq) and Germany (ZMT) and to the project Instituto do Milênio for financial support. We also want to thank the Laboratory of Mangrove Ecology of the Federal University of Para (UFPA) for logistic support and Nêlio Salanha for technical advice. The first author was supported by a fellowship from the Brazilian Scientific and Technological Council (CNPq: process no. 390007/2004-8).

References


Appendix 1. Specimens collected during fieldwork at the Fazenda das Salinas

Specimens were collected from 18:00 to 06:00 h during fieldwork at the Fazenda das Salinas and deposited at the mammal collection of the Museu Paraense Emílio Goeldi (MPEG), Belém, Pará, Brazil (curator: Suely Marques-Aguiar). The following data are presented: MPEG number, species, habitat (FS, Fazenda Salinas; M, mangrove; TF, “island” of terra firme), collector (F.A.G.A., Fernanda A.G. de Andrade; G.B.L., Geovanny B. Lima; S.A.C.B., Stélio Ângelo C. Brito), and date.