Phyllostomid bats flying in daylight: a case from the Neotropics

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ABSTRACT

Bats (Chiroptera), one of the most diverse groups in terms of taxonomy, morphology and ecology, are known for their nocturnal behaviour of flight and feeding. Although there is no consensus on the evolution of nocturnality in bats, many authors mention risk of predation, overheating, competition and mobbing by non-competitor species as arguments to justify nocturnality instead of daytime flight in bats. Herein we describe the first records of three genera of phyllostomid bats flying, foraging and drinking water during daytime in the Brazilian Amazon. All taxa were recorded drinking water, and some Phyllostomus sp. individuals were recorded foraging on termites, alongside birds. Risk of dehydration and overheating in roosts, as well as low competition in daytime, may explain the emergence of phyllostomid bats before sunset.

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Bats (Chiroptera), one of the most diverse groups in terms of taxonomy, morphology and ecology, are known for their nocturnal behaviour of flight and feeding. Given the difficulties in seeking food and navigating while flying in darkness, bats developed a complex system of orientation, the echolocation system (Grinnell and Griffin 1958). Many hypotheses on the rise of flight and echolocation in bats have been debated among ecologists and evolutionary biologists (Teeling et al. 2005; Jones and Teeling 2006). The recent discovery of two ‘pre-bat’ fossils from the early Eocene in North America supports the flight-first hypothesis over the echolocation-first or tandem hypotheses (Simmons et al. 2008).

Despite no consensus on the evolution of flight in Chiroptera, many authors mention risk of predation by visually oriented birds and hyperthermia during daylight incursions as evolutionary forces favouring nocturnal flight in the group (Speakman 2001, 2008). Echolocation ability and competition with aerial-feeding diurnal insectivorous birds are also known arguments to justify nocturnality in bats (reviewed by Speakman 1995).

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Although some species seem to be more sensitive to light, even to full moon light during bright nights (Saldaña-Vasquez and Munguía-Rosas 2013; Appel et al. 2017), studies in high latitudes recorded absence of lunar phobia, and daytime flight, in insectivorous bats (e.g. Speakman 1990; Rydell 1992; Speakman et al. 1994; Karlsson et al. 2002). Records of diurnal flight and emergence from roosts come from Oceania (Speakman et al. 1994; Bondarenco et al. 2014) Africa (Russo et al. 2011) and Europe (Speakman 1990; Speakman et al. 2000; Russo et al. 2009, 2011), evidencing this behaviour in some genera of insectivorous Yangochiroptera bats (e.g. *Rhinolophus* spp., *Myotis* spp., *Mormoops* spp.). Climatic factors such as lower temperatures, when compared to low-latitude regions, may be one of the reasons for the higher frequency of bat incursions in daytime (Speakman 1991).

Aside from some tropical species known for their activity in daily roosts (Miranda 2013), records of bats flying in daylight are outdated and dubious. These records are restricted to individuals of the haematophagous species *Desmodus rotundus* (É. Geoffroy, 1810) flying during the daytime while foraging on cattle and swine in Amazonian and Atlantic Forest environments (Carini 1911; Silva et al. 1967). The same authors’ studies are the only records of phyllostomid bats outside the roost in daylight. Considering the apparent rarity of this phenomenon, herein we describe the first records of three genera of Phyllostomid bats flying, foraging and drinking water outside the roost in daylight in a tropical region of Brazil.

We recorded bats flying during the daytime in midwest Brazil, state of Mato Grosso, Itaúba municipality. This region is located in the Brazilian Amazon and its vegetation is classified as highland forest, with no flooding events (IBGE 2012). The climate is dry tropical, according to Köppen’s climatic classification (Alvares et al. 2013). All visual records were made occasionally in forest remnants, while diurnal birds were sampled by mist nets installed at ground level and by acoustic and visual surveys throughout the area.

Bats from three genera (Chiroptera, Phyllostomidae) were recorded flying during the daytime. On 6 April 2016, at 2:17 pm, two individuals of *Phyllostomus* sp. were recorded drinking water in a temporary pond on a dirt road located inside a forest remnant (Figure 1(a)). Another three individuals of *Phyllostomus* sp. were photographed at daylight on 11 April 2016 at 5:55 pm. These individuals were foraging on a swarm of termites (Isoptera, Termitidae – Figure 1(b)) alongside individuals of *Elanoideus forficatus* (Linnaeus, 1758). An individual of *Dermanura* sp. was the only species captured in a mist net, on 10 April 2016 at 9:45 am (Figure 1(c)). After being released from the net, the individual flew on to a pond to drink water. Additionally, an individual of *Artibeus* sp. was recorded resting in a day-roost on a tree on 12 April 2016 at 1:13 pm (Figure 1(d)) and as *Dermanura* sp. flew over a pond to drink water a few minutes later. After this short flight, the individual of *Artibeus* sp. came back to the same roost. According to data from the National Institute of Meteorology (INMET), the temperature during the daytime flight records ranged from 27.3 to 33.3°C, with solar radiation between 179.5 kJ/m² and 899.3 kJ/m² (Table 1).

These are the first records of non-haematophagous phyllostomid bats flying during the daytime in the Neotropics. Former studies of Carini (1911) and Silva et al. (1967) reported ill individuals of *Desmodus rotundus* flying in daylight, based on personal or laypersons’ experiences. These studies did not focus on bats and both lack a full
Figure 1. Diurnal foraging and drinking activities in phyllostomid non-haematophagous bats in an Amazon Forest remnant, midwest Brazil. (a) *Phyllostomus* sp. drinking water in a temporary pond on a dirty road inside a forest remnant; (b) *Phyllostomus* sp. feeding on termites in flight; (c) *Artibeus* sp. roosting in tree foliage, in the vicinity of a pond; and (d) *Dermaptera* sp. captured in a mist net. Photographs by the authors.

Table 1. Meteorological data of the events when bats were recorded flying during daytime in an Amazon Forest remnant, midwest Brazil. Each line represents one event recorded, with its respective date, time, taxon, maximum diel temperature and instant solar radiation. Source of temperature and radiation data: INMET (2016).

<table>
<thead>
<tr>
<th>Date</th>
<th>Time</th>
<th>Taxon</th>
<th>Max. temperature (°C)</th>
<th>Radiation (kW/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>06 April 2016</td>
<td>2:17 pm</td>
<td><em>Phyllostomus</em> sp.</td>
<td>33.3</td>
<td>822.8</td>
</tr>
<tr>
<td>11 April 2016</td>
<td>5:55 pm</td>
<td><em>Phyllostomus</em> sp.</td>
<td>28.9</td>
<td>179.5</td>
</tr>
<tr>
<td>10 April 2016</td>
<td>9:45 am</td>
<td><em>Dermaptera</em> sp.</td>
<td>27.3</td>
<td>511.8</td>
</tr>
<tr>
<td>12 April 2016</td>
<td>1:13 pm</td>
<td><em>Artibeus</em> sp.</td>
<td>29.3</td>
<td>899.3</td>
</tr>
</tbody>
</table>

description of the bat diurnal events or even photographs, which makes species identification not completely trustful.

Studies on daytime flight by bats in Europe, Oceania and Africa (e.g. Speakman 1990, 1991, 1995; Speakman et al. 1994, 2000; Russo et al. 2009, 2011; Bondarenco et al. 2014) are associated with insectivorous bat species. In our study, *Phyllostomus* sp. was recorded drinking water and feeding on arthropods. This way, similar events can occur, mainly for energy intake. The other records here described are mainly from frugivorous taxa, another difference from records from other continents. In tropical regions, diurnal flight seems to be more related to thermoregulatory functions to avoid hyperthermia and increasing of energy intake, both related to the individual’s physiological state.
Individuals of *Artibeus* sp. and *Phyllostomus* sp. were recorded in periods with greater temperature and insolation, which supports hypothesis that this behaviour is related to thermoregulatory functions and energy intake. Endothermic animals deal with the heat produced by metabolism and also from the environment, which can be critical for their capacity of thermoregulation (Schmidt-Nielsen 1972), mainly in higher temperatures. Difficulties in thermoregulation for bats may be more likely to occur in individuals of species that roost in foliage (e.g. Nowak 1991), considering these sites are less thermally stable than caves or tree trunk cavities (Kunz et al. 2003; Turbill 2006; Phelps et al. 2016). Additionally, higher temperatures in roosts may induce greater water loss by individuals (Webb et al. 1995). Increases in body temperature and water loss are consequences that can force bats to leave roosts for drinking water, aiming to restore body temperature and water balance.

Other factors can also alter water demand, such as an individual’s sex and reproductive condition. It is known that females in lactation consume more water, due to milk production and lactation maintenance during this period (Adams and Hayes 2008). Flight is energetically very costly mainly during the pregnancy period, when females increase in body mass due to foetal mass (Kunz et al. 1995). Considering bats should benefit from minimising the time spent in this activity (Schmidt-Nielsen 1972; Speakman et al. 2003), the individuals recorded here could have been induced to fly during the daytime to keep homeostasis. Beyond this, the explanation for the records we present here is uncertain due to the absence of information on the individuals’ sex and physiological state.

Even in the same family, small species have low body temperature (e.g. 34.7°C for *Demanura cinerea*) when compared to bigger ones (e.g. 37.3°C for *Artibeus lituratus*) (McNab 1982). The thermoneutral zone is narrower and occurs at lower temperatures for small species, which can acquire and dissipate heat more rapidly. Given that body temperature is related to the volume/surface relation, *Phyllostomus* and *Artibeus* species could fly during the daytime due to their upper critical maximum temperature and to the slow rate with which they acquire ambient heat. Therefore, large-sized species are less likely to die by overheating or dehydration, with the diurnal emergence of *Demanura* sp. being the most problematic event for survival.

Records from Europe have shown emergence by insectivorous bats before sunset in forests with dense canopy structures (Russo et al. 2007). The same occurred with all individuals recorded here, except for the *Phyllostomus* sp. individuals foraging on termites. Individuals of *Phyllostomus* sp. seem to emerge early from roosts to avoid inraspecific, but not interspecific, competition, as birds were also foraging on termites. By advancing the time they start foraging, these individuals may extend the time spent on foraging activities, thereby increasing energy intake while other bats are still in their roosts. The physiological state of certain individuals, such as those we recorded here, may be the reason for this phenomenon not occurring in the whole population. For those individuals, there may exist a trade-off between a greater energy intake and the risk of flying during the daytime.

Mobbing by diurnal predators constitutes another great risk of daytime flight in bats (Mikula et al. 2016). Diurnal birds of prey are commonly opportunistic, attacking easy prey such as bats out of their roosts. Smaller individuals such as those of the genus *Demanura* are commonly recorded in many animals’ diets (Gardner et al. 1991; Sutter
and even larger individuals of *Phyllostomus* and *Artibeus* can be prey for mammals and birds (Boughman 2006). According to Mikula et al. (2016), Phyllostomidae are the fourth most attacked and preyed upon family by raptorial and non-raptorial diurnal birds, but there is no evidence of attacks on bats out of their roosts during the daytime. Given this, we believe that only individuals of *Phyllostomus* sp. advanced their emergence of the roost and maintained a non-stop foraging until night. All other individuals seemed to have the same behaviour as *Artibeus* sp., only flying to hydrate in order to keep homeostasis and then coming back to the roost soon.

Therefore, it is possible that more individuals from the Phyllostomidae family are complementing their nocturnal foraging activity with some diurnal incursions to forage and ingest water. This is apparently an opportunistic way to meet energetic costs rapidly while avoiding the lethal consequences of overheating. Although very specific, the events reported here are important information on the biology and ecology of neotropical bats. Studies focusing on the diurnal activity of bats are necessary to detail the whole period of daytime incursions, as well as the biology of the individuals (e.g. sex, age, reproductive period and physiological parameters) in order to assess the reasons for this uncommon behaviour in Neotropical bat species.

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