Activity and foraging efficiency of the aerial insectivorous bat *Molossus molossus* (Molossidae) in Brazilian Atlantic Forest

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INTRODUCTION

Several factors influence the activity time of a species, such as food availability, predation risk, altitude, and climate (Jones & Rydell 1994, Kunz & Anthony 1996, Esbérard & Bergallo 2008, Dunn & Waters 2012). Among insectivorous bats, activity time outside the day roost can vary considerably (Racey & Swift 1985, Wai-Ping & Fenton 1989, Audet 1990, Rydell 1993), being influenced by temperature, wind (Fenton et al. 1998), rain (McClevey & Fairley 1988, Audet 1990, Carvalho et al. 2011), cloud cover (Kunz & Anthony 1996, Welbergen 2006), and moon phase (Esbérard 2007, Breviglieri 2011). Apart from these factors, activity time is related to feeding habits, with insectivorous bats tending to be more active soon after sunset and before sunrise and being less active in the intervening period, as well as throughout the day (Brown 1968, Esbérard & Bergallo 2010, Costa et al. 2011, Holland et al. 2011). This bimodal activity pattern has been linked to peak insect activity (Rautenbach et al. 1988, Chase et al. 1991, Jones & Rydell 1994).

The Molossidae and Vespertilionidae represent the primary insectivorous bat families in the Neotropics (see Nogueira et al. 2014, Reis et al. 2017). The Molossidae has the largest number of species (n = 31) (Nogueira et al. 2018), which commonly roost in human constructions, hollow trees, rock crevices, palm leaves, and caves (Nowak 1994, Pacheco et al. 2010, Biavatti et al. 2015, Lópeza-Baucells et al. 2017). Of the molossid bats in the Neotropics, *Molossus molossus* (Pallas 1766) is perhaps one of the best studied because it is relatively easy to capture upon emergence from its roosts and due to its abundance in urban areas and human constructions in forested areas (Esbérard 2011, Biavatti et al. 2015).

*Molossus molossus* is one of the most common bat species in the Neotropics (Esbérard & Bergallo 2010). This small species exhibits a bimodal foraging activity pattern, with greater activity being displayed soon after sunset and before sunrise (Dechmann et al. 2010, Esbérard & Bergallo 2010, Costa et al. 2011, Holland et al. 2011). Thus, more than one foraging flight can be taken in a given night, with durations of between 37.55 and 50 min in its first peak of activity (Dechmann et al. 2010, Holland et al. 2011), and averaging 82.2 min from dusk to dawn (Holland et al. 2011). *M. molossus* is an aerial insectivore (Barclay & Brigham 1994, MacDonald 2001), typically feeding on small and crepuscular insects, mainly Coleoptera (representing approximately 45%
of its diet) and Lepidoptera (~12%), followed by Hemiptera (9%), Hymenoptera (~3%), and Diptera (~2%) (Ramírez-Chaves et al. 2008). The species is known to forage in groups (Dechmann et al. 2010).

According to Biavatti et al. (2015) and Xavier et al. (2018), it occasionally roosts with other bat species such as Molossus aztecs Saussure, 1860, M. rufus E. Geoffroy, 1805, Eumops auripendulius (Shaw, 1800), Eumops perotis (Schinz, 1821), Myotis nigricans (Schinz, 1821), Eptesicus furinalis (D’Orbigny & Gervais, 1847), Histiotus velatus (L. Geoffroy, 1824), Phyllostomus hastatus (Pallas, 1767), and Tonatia bidens (Spix, 1823). Regarding its reproductive cycle, this species presents well-characterized polyestrous, with pregnant females and newborn young being recorded in the months of March-April and November in northeastern Brazil (Fabián & Marques 1989). In southeastern Brazil, pregnant and lactating females can be found between November and March (Freitas 2012). Sperm production is concentrated in the hottest and wettest period of the year (Barros et al. 2013, Christante et al. 2013, Arandas 2018), but males can be sexually active throughout the year (Fabián & Marques 1989, Freitas 2012).

Here, the aims of our study were to: (i) assess time of emergence, (ii) activity duration, and (iii) foraging efficiency for a population of M. molossus on an island in the southeastern Brazilian Atlantic Forest. In addition, (iv) we investigate if body mass gain is related to foraging amplitude and night length on capture nights. We expected the M. molossus population studied to display crepuscular activity, as previously reported elsewhere (Holland et al. 2011). As summer nights are warmer and shorter than winter nights, presenting a greater concentration of food availability, we expected M. molossus to exhibit greater body mass gain in the summer, coinciding with peak M. molossus reproductive activity (Esberard 2011).

MATERIALS AND METHODS

Study area

The study was conducted at Gato Beach (Praia do Gato) (22° 55’ 39” S and 43° 52’ 07” O), located on Itacuruça Island, within the municipalities of Itaguai and Mangaratiba, in the Mangaratiba Environmental Protection Area. Gato Beach is surrounded by Atlantic Forest, classified as dense submontane rainforest (IBGE 1992). This area has a tropical rainy AW climate (Köppen 1948). Average annual temperature is 23.7 °C, with February being the warmest month (average temperature of 26.8 °C) and August being the coldest (average temperature of 20.9 °C). Average annual rainfall is 1,239.7 mm, with 37% of rainfall occurring in the summer rainy season (October to March) and 15% in the winter dry season (April to September) (Matos 2005, André et al. 2008). In the study region, nights of the rainy season are shorter (average of 656 minutes, ~11 hours) than those of the dry season (average of 767 minutes, ~13 hours).

Data collection

We identified two diurnal roosts of M. molossus at Gato Beach, approximately 40 m apart from each other. One roost was located inside the roof lining of a house and the other was in a hollow mango tree (Mangifera indica, L., Anacardiaceae). Both roosts were adjacent to the beach and surrounded by primary Atlantic Forest vegetation. The roof lining covers approximately 190 m², and bats access the roost through an opening located ~5 m above ground. The mango tree is ~10 m tall, but the entrance to the roost is located ~2.5 m above ground. We considered these two roosts to be a single population due to their proximity and observed dual use by individuals (based on recaptures) throughout the sampling period. Mist-net sampling was conducted at roosts on 17 nights from September 2009 to August 2011, with a minimum interval of 40 days between capture nights to prevent bats from learning mist-net locations and to avoid excessive colony disruption (Esberard 2006). We set mist nets (9 x 2.5 m, mesh 19 mm) approximately 0.5 meters from and at the same height as roost access points. The mist nets remained open from ~1 hour before sunset to midnight. Captured bats were placed in cloth bags and released after the mist nets had been closed so they would not be caught twice on the same night. If we had released the bats while mist nets were still open, we would have generated a bias in our data due to the influence of capture. Animal handling and processing was in accordance with guidelines for the use of wild mammals in research from the American Society of Mammalogists (Sikes & ACUC 2016) and research permits issued by the Government of Brazil.

When we removed captured bats from the mist nets, we recorded the time and whether they were emerging from the roosts or returning to them. Captured bats were sexed (male or female), weighed (with an electronic weighing scale to within 0.1 g), classified as adult or juvenile [based on the degree of ossification of the phalangeal epiphyses (Kunz & Anthony 1982)], and their forearm length was measured (with calipers to within 0.1 mm). All captured adult bats were individually and permanently marked with a numbered plastic necklace (Esberard & Daemen 1999) to identify recaptures. Juvenile individuals were not marked and were removed from the analysis. Since all captured bats were released at midnight, they were still able to forage.

Data analyses

Differences in emergence and return times between males and females were initially assessed using a t test because, in some bat species, males can emerge later and return earlier than females (Kunz et al. 1998). However, as we detected no difference between the sexes for emergence ($t = -0.405; p = 0.69$) or return time ($t = -0.116; p = 0.91$), we pooled data from the sexes to carry out further analyses. We also assessed the difference in body mass between males and females upon roost emergence, as well as upon returning to roosts, but observed no significant differences (roost emergence: $t = 1.937; p = 0.07$; roost return: $t = 0.920; p = 0.36$). Thus, body mass data of males and females was pooled. We used t tests for these comparisons because the data distributions were normal (Shapiro-Wilk test, $p > 0.05$), and the variances were homogeneous (Levene test, $p > 0.05$).

We considered capture time of individuals emerging from the roosts to assess time of emergence. Since our data
is circular (hours over a day), we adopted circular statistics, which is a better approach than analyzing such data as linear or categorical (see Oliveira-Santos et al. 2013). Thus, we used Rayleigh’s test (R), which assesses the statistical significance of the average angle of a circular distribution (Zar 1996), to analyze bat emergence time.

To assess foraging time, we considered foraging amplitude (flight time or duration of foraging flight, Winter 1999), i.e., the difference between the time of capture of the first individual emerging from the roost and the time of capture of the last individual returning to the roost. To analyze foraging efficiency, we compared the average total body mass of animals entering the roost with those leaving the roost (representing body mass gain). For this, we used a t test because the data distribution was normal (Shapiro-Wilk test, p > 0.05) and the variance was homogeneous (Levene test, p > 0.05).

To establish if body mass gain on capture nights (response variable) was related to foraging amplitude and night length up to midnight (explanatory variables), we performed a generalized linear model (GLM) selection with a gaussian error distribution and considering Akaike’s Information Criterion corrected for small sample size (AICc, Burnham & Anderson 2002), where the best candidate model was that with the smallest AICc value to predict body mass gain. For model selection, we disregarded capture nights on which fewer than five individuals were captured entering or leaving the roosts. Consequently, only 13 of 17 capture nights were assessed (i.e., excluding the 8th, 15th, 16th and 17th capture nights). Data are presented as mean values with standard deviations. A Spearman correlation matrix was generated to exclude possible bias from collinearity between foraging amplitude and night length on capture nights, as well as temporal autocorrelation within each of the explanatory variables, with values >0.7 weakening the power of model selection to identify relevant factors (Tabachnick & Fidell 1996). However, all Spearman correlations had values <0.7.

We performed Rayleigh’s test using the package CircStats (Agostinelli 2009), model selection was performed in AlCcmodavg version 2.0-1 (Mazerolle 2013), and t tests were conducted in Rcmr (Fox 2005) for R (R Development Core Team 2010). Time of capture for each bat was transformed into “minutes after sunset” using the program Moonphase 3.2 (see Esbérard 2012).

RESULTS

Foraging activity of Molossus molossus

We captured 248 adult individuals of M. molossus, with a sex ratio (male/female) of 0.36, so we considered the studied population to represent a reproductive colony. We achieved 592 captures/recaptures, with 158 for males and 434 for females, and of which 405 represented roost emergence and 187 were roost return. Pregnant or lactating females were captured/recaptured on 40 or 47 occasions, with 24 pregnant or 36 lactating females leaving the roosts and 16 pregnant or 11 lactating females entering roosts. For males, 100 and 58 individuals were captured/recaptured leaving or entering the roosts, respectively. As expected, the bats were predominantly crepuscular (R = 0.76; p < 0.01), with only 31 captures/recaptures (5.24%) being recorded before sunset (Fig. 1). Most capture events...
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Table 1 - Results of our generalized linear model showing variation in night length and foraging amplitude as a function of average body mass of bats upon returning to the roost. K – the number of covariates in the model; ΔAIC – difference in AIC; AICcWt – the AIC weight.

<table>
<thead>
<tr>
<th>Model</th>
<th>K</th>
<th>AICc</th>
<th>ΔAICc</th>
<th>AICcWt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model 1 - Night length</td>
<td>3</td>
<td>54.854</td>
<td>0.000</td>
<td>0.839</td>
</tr>
<tr>
<td>Model 2 - Night length + Foraging amplitude</td>
<td>4</td>
<td>58.216</td>
<td>3.363</td>
<td>0.156</td>
</tr>
<tr>
<td>Model 3 - Foraging amplitude</td>
<td>3</td>
<td>65.221</td>
<td>10.367</td>
<td>0.005</td>
</tr>
</tbody>
</table>

DISCUSSION

Activity of Molossus molossus

Molossus molossus exhibited a crepuscular activity pattern in the studied area, mirroring data for this species in Central America (Chase et al. 1991, Holland et al. 2011) and for another species of the same genus, M. rufus (Brown 1968), in North America (Fenton et al. 1998). This crepuscular activity coincides with the timing of greatest food availability, i.e., flying insects (Rautenbach et al. 1988, Chase et al. 1991, Jones & Rydell 1994, Jung & Kalko 2010, 2011). Typically, the activity peak for M. molossus that occurs close to sunset is more intense than the peak that occurs close to sunrise (Esberard & Bergallo 2010, Costa et al. 2011, Holland et al. 2011, perhaps reflecting activity peaks for the dipteran insects on which these bats prey (Chase et al. 1991, Jones & Rydell 1994).

We found that the duration of activity outside roosts during the first half of the night (35.93 min) is close to the values reported for M. molossus by Dechmann et al. (2010) (37.55 min) and Holland et al. (2011) (50 min). We also note concordance in activity patterns between M. molossus and M. rufus, with these two species exhibiting similar preferences for habitat and roost sites (Esberard 2011). Fenton et al. (1998) reported average M. rufus flight durations of 26.8 min in North America, whereas Marques (1986) cited average flight durations of 50.5 min for M. rufus in South America. These relatively short bouts of activity may be attributable to the considerable foraging efficiency of M. molossus (Fenton et al. 1998, Holland et al. 2011) and the bimodal activity pattern that allows these bats to return to their roosts to rest before engaging in a second flight near sunrise to forage again.

Insect consumption by Molossus molossus

Animals captured emerging from the roosts had an average body mass of 14.70 ± 1.50 g. Individuals captured returning to the roosts had an average body mass of 15.50 ± 1.90 g, representing a significant increase in mass (0.80 g or 6.37 ± 7.03%; t = -3.30; p < 0.005). The model selection showed that only night length (up to midnight) was important to explain the variation in average body mass of bats returning to the roost (Table 1). The average body mass of bats returning to the roost was negatively influenced by night length (Fig. 2). Estimate = -0.04, SE = 0.01, Confidence Intervals = -0.07 to -0.02, t value = 3.63, p = 0.003, Line equation – y = -11.032x + 520.85; R² = 0.52). We found that the difference in body mass between emerging and returning individuals was smaller on longer nights and that the difference in body mass between emerging and returning individuals was smaller on longer nights and that the difference in body mass between emerging and returning individuals was smaller on longer nights and that the difference in body mass between returning and returning individuals was smaller on longer nights and vice versa. Considering that the average time bats spent outside the roosts in their first of two peaks of activity was 35.93 min and that they consumed, on average, 0.80 g during this period, we estimate that each individual M. molossus consumed an average of 22 mg/min of insects during that initial activity period.

Fig. 2 - Relationship between capture night length until midnight (measured in minutes after sunset) and average body mass (in grams) of Molossus molossus returning to the roost. The bat colony was located at Gato Beach, Itacuruçá Island, Rio de Janeiro, southeastern Brazil, and it was monitored from August 2009 to August 2011.

(n = 408, 68.92%) occurred within 60 min of sunset. Initial emergence time varied from 7 min before sunset to 25 min after sunset on capture nights (4.81 ± 8.94 min). On average, bats emerged 37.37 ± 51.71 min after sunset and returned to their roosts 73.30 ± 59.66 min after sunset. Mean activity time outside the roosts was 35.93 ± 9.92 min.

Insect consumption by Molossus molossus

Although pregnant and lactating females exhibit differences in terms of amounts of food ingested (Kunz et al. 1995), we did not factor this aspect into our analysis because of the low numbers of pregnant/lactating females we captured. Amounts of food consumed by M. molossus we present here (0.80 g per individual or 22 mg/min) are similar to data on M. rufus by Marques (1986), who reported insect consumption ranging from 10.67 to 19.00 mg/min. However, Fenton et al. (1998) calculated average insect consumption for M. rufus of approximately 4.4 g in 26.8 min of activity, equating to a rate of 164.2 mg/min. However, such comparisons should be interpreted with caution because despite having a similar biology to M. molossus...
(Esbérard 2011), M. rufus has a higher body mass and so requires greater food consumption.

We found a relationship between the increased average body mass upon returning to the roost and night length (to midnight) on capture nights, suggesting that these bats eat more when nights are shorter. Shorter nights occur in the period of year when environmental conditions (e.g., higher temperatures and rainfall) favor greater food availability and, consequently, higher bat activity (Williams 1940, Taylor 1963), i.e., corresponding to summer at our study site at 23° southern latitude. Findings by Barros et al. (2014) corroborate this supposition through observations that in winter, on colder days, bats in southern Brazil exhibit reduced activity.

CONCLUSIONS

Here, we show that M. molossus in Brazilian Atlantic Forest exhibits greater activity soon after sunset during the first half of the night, representing a crepuscular activity pattern. Our study bats spent approximately 36 min outside of the roost and each individual bat consumed, on average, 22 g/min of insects, with greater activity on short nights. Although we only sampled the first half of the total activity period of M. molossus, our data indicate higher insect consumption in summer during peak insect abundance. Our findings can contribute to further studies of bats as biological controls, which are warranted in Brazil because it is an important producer and exporter of agricultural products.

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REFERENCES


