

Bats got a place in the sun: new findings of daytime flight in Brazil

Los murciélagos ganan un lugar bajo el sol: nuevos descubrimientos de vuelo diurno en Brasil

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Most bats species are small and nocturnal. The nocturnal habit evolved mainly to avoid predators and competition. Recently, bats of the suborder Yangochiroptera have been recorded flying during daytime in Amazonia and Peninsular Malaysia. We described new events of neotropical bats flying during daytime in tropical and subtropical regions of Brazil. All records were made occasionally during bat and bird sampling with mist nets and visual searching. We provided information about the records' time, respective solar radiation, air temperature, humidity, nebulosity, and wind velocity measurements taken from the nearest available meteorological stations from the National Institute of Meteorology (INMET). In northeastern and southern Brazil, we recorded 6 species/taxa of bats from 4 families (Molossidae, Noctilionidae, Phyllostomidae and Vespertilionidae) flying at daytime in air temperatures varying from 23.5 to 35.1 °C. Bats flying in the daytime are poorly documented in rainforests. We recorded bats flying at daytime in warm sites of Brazil, from Caatinga scrublands to the Ombrophilous Atlantic Forest, from 7° to 28° S of latitude. The size of the individuals, the characteristics of the roost and the air temperature can possibly explain the causes of these diurnal records. These records reinforce the need for studies on thermoregulatory mechanisms in bats near the equator, evidencing data on natural history, as these are essential to assess how chiropteran species will be influenced by climate change in the future.

Key words: Chiroptera; diurnal behavior; flight; Neotropics; overheating.

La mayoría de las especies de murciélagos son pequeños y nocturnos. El hábito nocturno evolucionó principalmente para evitar depredadores y la competencia. Recientemente, se han registrado murciélagos del suborden Yangochiroptera volando durante el día en la Amazonía y Malasia peninsular. Describimos nuevos registros de murciélagos neotropicales volando durante el día en regiones tropicales y subtropicales de Brasil. Todos los registros se realizaron ocasionalmente durante el muestreo de aves y murciélagos con redes de niebla y búsqueda visual. Proporcionamos información sobre el tiempo de los registros, las respectivas medidas de radiación solar, temperatura del aire, humedad, nebulosidad y velocidad del viento tomadas de las estaciones meteorológicas disponibles más cercanas del Instituto Nacional de Meteorología (INMET). En el noreste y sur de Brasil, registramos 6 especies/taxones de murciélagos de 4 familias (Molossidae, Noctilionidae, Phyllostomidae y Vespertilionidae) volando durante el día con temperaturas del aire que varían de 23.5 a 35.1 °C. Las causas de estos registros diurnos posiblemente pueden explicarse por el tamaño de los individuos, las características de su sitio de descanso y principalmente por la temperatura del aire. Estos registros refuerzan la necesidad de estudios sobre los mecanismos de termorregulación en murciélagos cerca del ecuador, evidenciando datos sobre su historia natural, ya que estos son esenciales para evaluar cómo las especies de quirópteros se verán influenciadas por el cambio climático en el futuro.

Palabras clave: Calentamiento excesivo; comportamiento diurno; neotrópicos; quirópteros; vuelo.

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Diurnal flight is commonly known for some insectivorous bats in temperate zones and pteropodid bats ([Moore 1975](#); [Speakman et al. 1994](#); [Russo et al. 2011](#)). This behavior is associated with a lack or low number of predators, sunlight for a long period in the circadian cycle, and a higher abundance of food resources during the nighttime period ([Speakman et al. 1994](#)). More recently, bats flying under sunlight or inside forests during the day were recorded in tropical regions for Brazilian Amazon ([Bólla et al. 2017](#)), Peninsular Malaysia ([Chua and Aziz 2018](#)) and in a rainforest of Colombia ([Vivas-Toro and Murillo-García 2020](#)). Conversely to most temperate regions, tropical areas shelter lots of

avian predators ([Willig et al. 2003](#)), feature high air temperatures with small seasonal variation ([Feng et al. 2013](#)), and have a high abundance of food items as insects ([Bale 2002](#)).

High air temperatures and predators' abundance seems to be the most important reasons which make bats avoid sunlight in the tropics ([Rydell and Speakman 1995](#)). However, diurnal flight in tropical bats may be due higher evapotranspiration rates and the consequent need to replenish body water since some individuals have already been recorded drinking water in ponds and streams ([Bólla et al. 2017](#)). Additionally, some Neotropical bat species may emerge earlier

than others to reach the required energy intake, diminishing competition by shifting foraging time (Bólla *et al.* 2017).

Herein we describe 6 events of bats flying in daytime during bat and bird sampling expeditions for a decade (2010 to 2020) in 2 Brazilian biomes, Caatinga and Atlantic Forest.

The Caatinga climate is classified as Köppen's BSh (semi-arid climate with annual rainfall dropping on average to less than 800 mm), and the vegetation type is Forested Steppe Savannah (IBGE 2012; Alvares *et al.* 2013). The Atlantic Forest from southeastern and southern Brazil's climate is classified as Aw (markedly seasonal with annual rainfall ranging from 1,300 to 1,900 mm), and Cfa (subtropical climate with hot summers and no dry season) respectively, and vegetation type is Dense Ombrophilous Forests (IBGE 2012; Alvares *et al.* 2013).

Weather data was extracted from the National Institute of Meteorology (INMET) website, which has stations in most Brazilian municipalities that upload meteorological data measured in 15-minute intervals. Then we accessed the time series to extract the data from the exact or nearest time we observed the bats from the nearest station with the area where records were made. The heat index was calculated by the Agricultural Research and Rural Extension Company from Santa Catarina (EPAGRI 2023). This index takes air temperature and humidity to calculate how the air temperature feels for a human body. It is a way to measure how hot a day feels like for a mammal.

All records were made before the bat sampling that would be carried out during the same night and area. We noticed the bats flying during the daytime and captured them with the same mist nets that would be opened at night. The two exceptions were the fourth and sixth records. The fourth record was made with the capture of the bat using an improvised insect net with cotton fabric, and the sixth record was during a bird sampling using binoculars. The individuals from the last record were not captured, then they could not be identified at the species level.

The first record was made on June 23 (during the dry season) 2010, in the Serra da Jitirana, São João do Piauí, Piauí (08° 18' 28" S, 42° 01' 19" W). Using mist nets, we captured a female *Neoplatymops mattogrossensis* (family Molossidae) leaving the roost at around 15:30 hr. This

individual belonged to the colony roosting in a sandstone outcrop crevice we found beforehand. The bats from this colony emerged from the roost between around 15:00 and 17:00 hr, in broad daylight, and did not return until the 21:00 hr, when we captured 6 individuals returning to the roost with mist nets.

The second record was made in Piauí River, São João do Piauí, Piauí (08° 26' 48" S, 42° 10' 59" W) on October 3 (during the dry season) 2011. We recorded many individuals of *Noctilio albiventris* (family Noctilionidae) flying over a river from around 14:50 hr. These bats flew in semicircles and very close to the water's surface. The bats emerged from cavities in the sandstone outcrops on the riverbank. However, it was not possible to find the roost or count the number of individuals, since there were plenty of them simultaneously.

The third record was made on December 24 (during the summer) 2012, at Pedras Grandes, Santa Catarina (28° 26' 58" S, 49° 11' 31" W), in the Atlantic Forest, where we recorded 3 sights (Table 1), during monthly field campaigns to monitoring a *Myotis nigricans* (family Vespertilionidae) colony in a house roof. Some individuals of a colony are estimated to have from 596 to 1,050 individuals (more details in Mottin *et al.* 2018). According to the heat index (Table 1), it was an atypical hot day when some individuals started flying outside the roost near 13:00 hr (35 °C, the greatest value for the heat index of all records here described). It was impossible to count exactly how many individuals were flying. However, we managed to register that more than 10 individuals were flying simultaneously. After 30 minutes, about 20 individuals flying outside the colony were lying on the ground dead.

The fourth record in Atlantic Forest was made on May 15 (during the dry season) 2014, at the Fiocruz Atlantic Forest Biological Station settled in the Pedra Branca Massif, Rio de Janeiro (22° 56' 29" S, 46° 24' 36" W). A male of *Myotis riparius* (family Vespertilionidae) was captured with the help of an improvised entomological net made with a cotton fabric at 14:15 hr after being observed for more than 15 minutes foraging in an Ombrophilous Dense Forest clearing near a river. The sky was cloudy, and the forest interior seemed to the authors to have low luminosity, even though it was not measured directly.

Table 1. Bat species, sites and meteorological data in day and time of the diurnal records. All data were extracted from the nearest automatic or regular meteorological stations of the record sites, provided by the National Institute of Meteorology (INMET) and accessed online in November 19, 2020. Temp. = Temperature; °C = degrees Celsius; KJ = Kilojoule; m² = square meter; m = meter; s = second and % = per cent.

Site	Taxa	Time	Temp.	Heat index	Humidity	Radiation	Wind velocity	Nebulosity
			(°C)	(°C)	(%)	(KJ/m ²)	(m/s)	(%)
Serra da Jitirana	<i>Neoplatymops mattogrossensis</i>	15:30	33.4	34	36	2099.00	2.7	10
Rio Piauí	<i>Noctilio albiventris</i>	14:50	35.1	34	28	2619.18	3.4	65
Pedras Grandes	<i>Myotis nigricans</i>	13:00	32.9	35	44	3023.51	0.5	-
Maciço da Pedra Branca	<i>Myotis riparius</i>	14:15	26.7	27	47	2471.30	0.9	-
Chapada do Araripe	<i>Glossophaga soricina</i>	11:54	29.0	28	33	3408.00	3	0
Urban site	Undetermined Molossidae	11:40	23.5	23	55	2114.44	2.4	-

The fifth record was made in Chapada do Araripe, Crato, Ceará (07° 19' 55" S, 39° 24' 46" W) at 11:54 hr on October 23 (during the dry season) 2017. About 7 individuals of *Glossophaga soricina* (family Phyllostomidae) were flying around a cave entrance localized in a humid Tropical Subperennial Forest. These bats kept flying for more than 10 minutes and were already flying when one of the researchers approached the cave to take photographs from them (Figure 1). The bats kept flying after the photos were taken, but the total flying time could not be recorded.

Finally, the sixth record was made in an urban site of Criciúma, Santa Catarina (28° 41' 36" S, 49° 27' 42" W) at 11:40 hr on October 12 (during the spring) 2020. One individual of the Molossidae family was observed, using binoculars, flying in circles and drinking water over a small artificial lake (Figure 1) with the aquatic macrophytes (*Eleocharis* sp. and *Schoenioplectus californicus*) amidst eucalyptus stands and a remnant of Dense Submontane Rainforest. The observation was about 2-3 min long.

Bats recorded in the present study were flying at the daytime in the hot climate of Brazil located in Caatinga scrublands and in the subtropical region located in the Ombrophilous Atlantic Forest, from 7 to 28° S of latitude. Modeling the overheating in bats flying in daytime, [Speakman et al. \(1994\)](#) wrote that "... as one moves away from the equator, and temporally away from the noon, the problem of heat stress for bats flying in daylight becomes less severe". Even though this is a predictable assumption for many small nocturnal animals, heat stress during daytime in bats may not avoid their diurnal flight near the equator, and these bats may try to keep homeostasis in different ways, depending on physiological and morphological traits, like reproductive status and body mass (see [Speakman 1995](#)).

[Speakman \(1990\)](#) reinforced the idea that size matters in overheating: small bats would support and dissipate greater amounts of heat than larger bats due to the rela-

tion between the areas of the body and wing and/or tail membranes. In Neotropical bats, heat stress in roosts may be reduced through flight. In this case, most heat is dissipated from the wing and tail membranes ([Speakman et al. 1994](#)), which may force bats to leave roosts for a while, even in sunlight. Then, in general, large bats dissipate less endogenous heat than small bats but dissipate it better on wings by radiation and less per unit area by convection ([Speakman et al. 1994](#); [Webb et al. 1995](#)).

Considering bats lose ample proportions of water by evapotranspiration when flying ([Carpenter 1969](#)), it is likely that, when bats are forced to leave roosts because of overheating, they have already lost so much water (in the roost and during flight) that it is necessary replenishing it before coming back to roosts ([Webb et al. 1995](#)). Therefore, if small bats (like neotropical *Myotis* and *Neoplaticymops*) would better avoid overheating faster than bigger ones (like *Noctilio*), by folding flight membranes away, flying near the roost and away enough from other bats in the colony, bigger bats should spend more time flying to solve the excessive heat and, this way, ingesting water becomes necessary to replenish the deficit caused by evapotranspiration (e.g., [Carpenter 1969](#); [Speakman and Racey 1988](#); [Webb et al. 1995](#)).

The bats we recorded are small to medium-sized. [Speakman and collaborators' models \(1994\)](#) suggested that the probability of a small bat with 9 g of body mass (as *M. nigricans*, *M. riparius*, *N. mattogrossensis*, and *G. soricina*) flying at 14:30 hr at latitude 10 (near Piauí latitude) would be constrained and, at latitude 20 (near Rio de Janeiro latitude), this flight will be less probable than 10 % to occur. Also, the probability of large-sized bats with 90 g of body mass (more than a half bigger than *N. albiventris*) would be less than 5 % to have its diurnal flight constrained at latitude 10. [Speakman et al. \(1994\)](#) models proposed that larger bats are less likely to perform diurnal flights than small bats. However, the medium-sized bat *Macronycteris commersoni* (mean body mass: females = 46.3 g; males = 79.6 g) was



Figure 1. Bats in daytime flight from Brazil: A) individuals of *Glossophaga soricina* flying in the entrance of a cave in daylight in Chapada do Araripe, Crato, Ceará, Brazil; B) Molossid bat flying in the border of an urban remnant in Criciúma, Santa Catarina, Brazil.

recorded doing torpor and microtorpor under high temperature conditions in Madagascar (Reher and Dausmann 2021). Also, these physiological responses are newly discovered to be associated with hyperthermia, and not only hypothermia, shedding light on how tropical bats cope with the increasing hot weather (Reher and Dausmann 2021). We still lack information on how bats respond when the air temperature exceed their torpor threshold ability, how many tropical bats can undergo these responses, and if the species reported here, whether big or small, were or will be able to adapt to hyperthermia.

Even though we did not record large species, Bòlla *et al.* (2017) described the behavior of larger bats (*Phyllostomus* sp.) leaving their roosts to forage and drink water during the daytime. In the present study, we observed individuals of the medium-sized *N. albiventris* (body mass < 40 g; Hood and Pitocchelli 1983) drinking water during the daytime. Studier (1970) recorded vespertilionid bats losing 15-16 % of body mass, attributed to water loss when roosting for about 12 hr in natural roosts. It reinforces the idea that the bigger the bat gets, the harder it gets to control overheating only by flying, making water ingestion necessary. We now believe that dehydration may be one of the most important issues large bats face since water ingested to keep body temperature may avoid overheating in tropical regions, as recorded here. Another factor constraining bat diurnal flights is the abundance of predators in the Neotropical region, which is not true for the former records made in Europe (Speakman 1990, 1991, 1995; Speakman *et al.* 1994, 2000), an island of Africa (Russo *et al.* 2011) and a desert in Oceania (Bondarenco *et al.* 2014). Mobbing by predators is an important factor for bats, especially for species that commonly roost in open habitats and have small body sizes (Mikula *et al.* 2016).

Until now, most of the diurnal events were recorded in the Northern Hemisphere, where bat species are predominantly insectivores (Speakman 1990, 1991, 1995; Speakman *et al.* 1994, 2000) and where phytophagous bats are rare or do not occur. However, other insectivorous bats were recorded during daytime incursions in Africa and Oceania, and an omnivorous bat was recorded feeding on termites in Brazil (Russo *et al.* 2011; Bondarenco *et al.* 2014; Bòlla *et al.* 2017). The species here recorded in southeastern and northeastern Brazil were predominantly insectivores. However, the sample includes a primary nectarivore, *G. soricina*, which consumes insects in its diet (Clare *et al.* 2014). Insectivores are the most documented bats flying during daytime, probably because they do not acquire as much water from the diet as frugivores and can suffer more severely from dehydration.

Diurnal incursions are expected to be more tolerable on cloudy days (Speakman *et al.* 1994). A hypothetical small bat (6 g of body mass) flying in the daytime with 60 % nebulosity can tolerate up to 37.8 °C, at 10 % to 33.8 °C and 34.8 °C when clouds are absent. Since large bats may hardly deal with high temperatures compared to small ones, individu-

als of *N. albiventris* we recorded would be near lethal risk since it was recorded flying at 35.1 °C (maximum non-lethal temperature: 37.8 °C). *Neoplatymops mattogrossensis* were recorded flying at 33.4 °C, only 0.45 °C below the maximum non-lethal temperature for a bat with a similar body mass. Another small bat (7-12 g of body mass), *G. soricina* was recorded when the air temperature was 5.85 °C below the maximum non-lethal for no cloud days.

Myotis nigricans, the only species with known records (third record here described) of a possible lethal overheating in Neotropics, is a very small bat (3-4 g) recorded while flying close to noon at very high air temperatures and solar radiation. According to the Speakman *et al.* (1994) models, a bat of 9 g would die at the air temperature of 33.85 °C, and many bats of this colony died at only 32.9 °C. It is possible that, as roosting on a house roof, the colony was facing higher temperatures than those recorded by the meteorological station from which we obtained the related information because of the roof characteristics as well as the high number of individuals roosting together, which may have reached the temperature of < 33.85 °C modeled by Speakman *et al.* (1994).

Air temperature, humidity, and airflow could be the most important environmental factors influencing bats in selecting diurnal roosts (Tuttle and Stevenson 1982; Hill and Smith 1984). Three of the 5 records we made were obtained from bats roosting in rocky environments: sandstone outcrops and caves. Webb *et al.* (1996) proposed that, in ambient humidity lower than 50 %, as in the sites here recorded, low temperatures' roosts may aid bats to lose less water for evapotranspiration, but savings are still marginal (average evaporative water loss in resting *Plecotus auritus* = 1,0075 ul.min⁻¹). However, humidity seems to play a small role in roost selection in Neotropical areas compared to air temperature (Avila-Flores and Medellín 2004), since the authors could not find any pattern relating temperature and roost selection in México. The availability of rocky-type roosts in very hot areas as those in Brazil, may work in favor of bats, mainly the large species, since roosts as caves are thermally insulated systems (Badino 2004). Despite this, the stable temperature in rocky environments does not seem to avoid bat overheating and daytime incursions, as we recorded.

Bats flying during daytime is poorly documented in the Neotropics, with very dubious and old records related to Rabies virus infections in the Brazilian Amazon and Atlantic Forest (Carini 1911; Silva 1967). Since bats were not tested for Rabies; and more recent records involving 3 bat genera also in Amazon Forest (Bòlla *et al.* 2017) and *Saccopteryx leptura* in a rainforest of Colombia (Vivas-Toro and Murillo-García 2020), we believe that this kind of event is more common than documented in scientific literature, but its causes remain unknown.

Unfortunately, studies on thermoregulatory mechanisms in bats, evidencing data on the natural history of bat species as we provided here are very scarce near the equator even it may be essential to model the how differ-

ent aspects of species (including physiological and distributional aspects) will be influenced by climate change in the future (Jones and Rabelo 2013). Deforestation, land conversion into large agricultural fields and urban development can increase global warming (Letcher 2021) forcing different species to adapt their behaviors and physiology to new climatic conditions and resources or they can be led to extinction (see Festa et al. 2022). We recommend more studies to be carried out in hot regions that assess how bats would deal mainly with higher temperatures, including monitoring it in roost sites and contemplating physiological questions on tropical and subtropical bat species.

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