



Early Morning Activity: New records of diurnal behavior in Mexican bats

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Resumen

Los murciélagos son animales predominantemente nocturnos, pero algunos estudios, principalmente de regiones templadas e islas, reportan murciélagos volando durante el día. Reportamos el forrajeo diurno de tres especies de murciélagos en México, una especie de la familia *Vespertilionidae*, y dos *Phyllostomidae* (*Anoura* y *Artibeus*). Además, documentamos el primer registro *in situ* del consumo de frutos en el suelo para *Artibeus*. El vuelo diurno en murciélagos es una conducta poco documentada en los trópicos. Además, sugerimos que el calor extremo y sequías pueden influenciar esta conducta, pues dos reportes ocurrieron durante periodos de sequías.

Palabras clave: Forrajeo diurno, *Phyllostomidae*, sequía, *Vespertilionidae*.

Abstract

Bats are predominantly nocturnal animals, but some studies, mainly from temperate regions and islands, report bats flying during the day. We report the diurnal foraging of three species of bats in Mexico, one species of the family *Vespertilionidae*, and two *Phyllostomidae* (*Anoura* and *Artibeus*). In addition, we document the first *in situ* record of fruit consumption on the ground for *Artibeus*. Diurnal flight in bats is a poorly documented behavior in the tropics. Furthermore, we suggest that extreme heat and drought may influence this behavior, as two reports occurred during periods of drought.

Key words: Diurnal foraging, drought, *Phyllostomidae*, *Vespertilionidae*.

Bats (Order Chiroptera) are mainly nocturnal mammals (Erkert 1982, Rydell & Speakman 1995), with most of the daily time spent at their roost sleeping (up to 80% of the day; see Harding *et al.*, 2022). Several reasons for this nocturnality have been proposed, including, 1) avoiding diurnal predators such as birds (Speakman *et al.*, 1991a; 1991b; 1994b; 1995; Rydell *et al.*, 1996; Mikula *et al.*, 2016; Chua & Aziz 2018); 2) reducing competition with diurnal birds (Miller 1962); 3) and minimize hyperthermia (Speakman & Racey 1991; *et al.*, 1994a), but several conditions determine bats' activity rhythms (see Erkert 1982). However, diurnal flying has been reported in arthropodivorous species from temperate regions, from the mainland (Speakman *et al.*, 2000; Russo *et al.*, 2011a; Frafjord 2021) and islands (Moore 1975; Speakman *et al.*, 1990; Russo *et al.* 2011b; Chua & Aziz 2019; Mc Arthur *et al.*, 2024). While diurnal flights are more likely to occur at higher latitudes (Speakman *et al.*, 1994a; Frafjord 2021) or during migration (see Lučan & Bartonička 2024), Paleotropical tree-roosting Pteropodidae are active diurnally (Welbergen 2008; Eitan *et al.*, 2022). Few reports of diurnal flying activity of bats come from the Neotropics (Vivas-Toro & Murillo-García 2020; Bôlla *et al.*, 2017; Bôlla *et al.* 2017, Sánchez *et al.*, 2023). Here, we report bat individuals of three species from Mexico engaging diurnal flight while foraging, contributing to our knowledge of this underexplored topic.

The first report comes from “Texolo” rainfalls (19°29'04"N, 96°59'40"W, 1080 m, Veracruz, Mexico), where, on November 26th 2016, the first author captured a male *Anoura peruana* (*sensu* Molinari *et al.*, 2023) in a mist net (Figure 1A) around 07h30 (sunrise at 05h50), in the secondary forest understory with elements of montane cloud forest (*Liquidambar* and *Platanus*). The bat carried pollen of a Tillandsioideae plant (Bromeliaceae). The ambient temperature was ca. 18° C and with a cloudy sky, relative humidity in the air was high (>70%). By studying bat visitation to different bat-pollinated plants in the area, we conclude that nectarivorous bats cease their visitation (and probably most of their activities) about 30 min before sunrise at the site.

The second report was documented in Chetumal (18°32'38.4"N, 88°15'50.4"W, 11 m, Quintana Roo, Mexico) by the second author, on June 6th, 2023. Two individuals of *Artibeus aff. lituratus* (by their external characteristics such as fur color, marked facial stripes, and relative size; Reid 2009) were found eating a fruit of *Brosimum alicastrum* (Moraceae) on the ground, about 14:23 h, at 33°C of ambient temperature. The main vegetation type was subcaducifolius rainforest, with an extreme drought during the previous weeks. One of the individuals flew away as we approached, but the other kept eating the fruit (Figure 1B, Video S1). Scarce fruits were observed on the trees. Some individuals were observed nearby, perching on the trees, but only that pair were eating on the ground. The third observation, by the third and fourth authors, was on January 29th, 2024 (20°09'39.69"N, 98°52'24.25"W, 2357 m, Hidalgo, Mexico). A Vespertilionidae bat was recorded flying over a natural pond at the bottom of the ravine (Figure 1C and D), at 12h38, with a clear sky and ca. 21 °C. The main vegetation type is xeric, predominantly *Schinus molle*, *Myrtillocactus geometrizans*, *Agave* spp. The area was experiencing a lengthy drought for several months. The individual was drinking water.

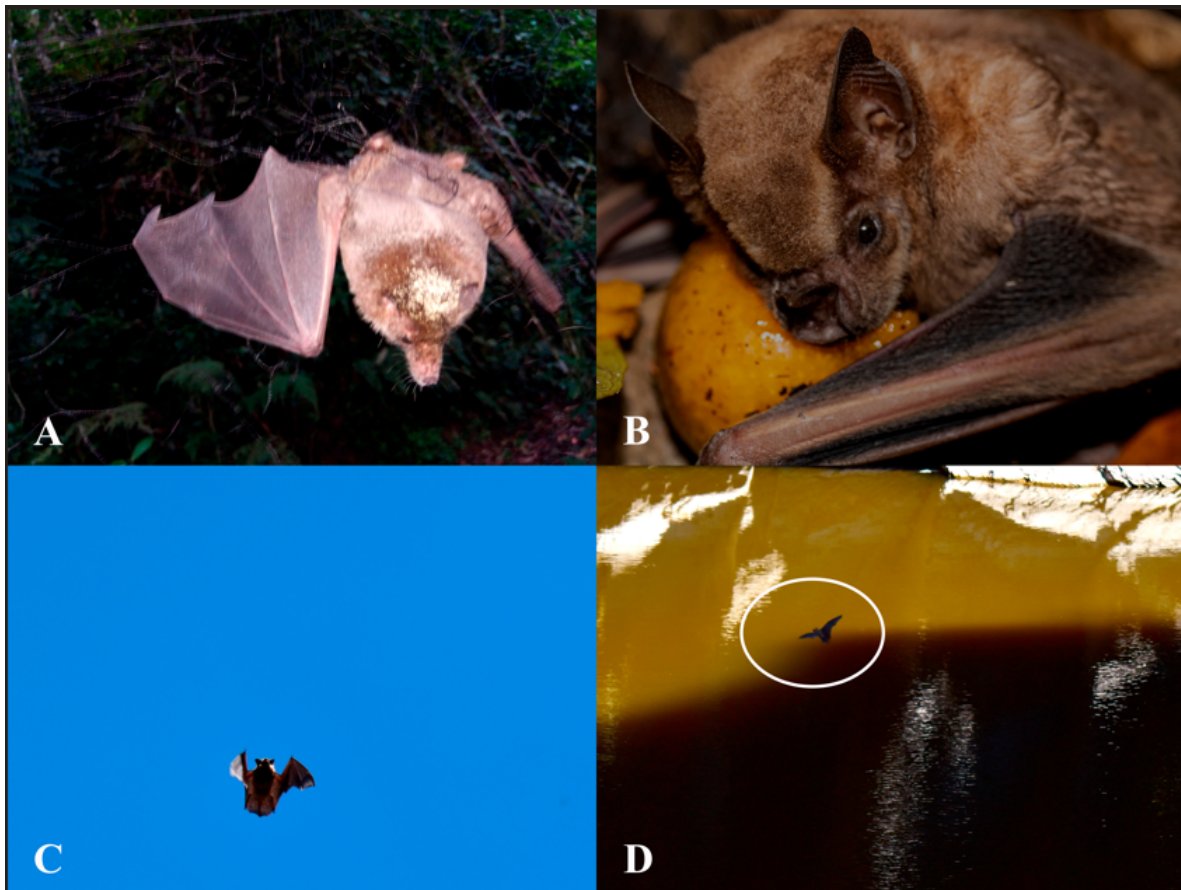


FIGURE 1. **A)** An *Anoura (geoffroyi) peruana* caught with pollen in Veracruz, Mexico. **B)** An *Artibeus* aff. *lituratus* eating a fruit of *Brosimum alicastrum* on the ground, in Quintana Roo, Mexico. **C)** and **D)** A *Vespertilionidae* bat flying (circle) over a natural pond in Hidalgo, Mexico. Photos by the authors.

Our report of *Anoura peruana* is the second species of a nectarivorous bat flying during the day (Bôlla *et al.*, 2017), and the first caught after its foraging bout, probably returning to its roosting site. Some bromeliads with nocturnal anthesis, unvisited during the night, can harbor nectar available to diurnal floral visitors (i.e., an unvisited individual of *P. grandis* produces ca. 4 mL of nectar per night; PAAR unpublished data). Nectarivorous bats have a high demand for nectar to supply their high metabolism (Voigt & Speakman 2007), and, when available, is possible that an individual could visit a flower with nectar on the way to its roosting site (see *Glossophaga soricina* visiting *Musa paradisiaca* before dawn; Pedrozo *et al.*, 2018). The species *Anoura peruana* in Mexico also eats Lepidoptera insects (Caballero-Martínez *et al.* 2009; referred to as *Anoura geoffroyi*), so we cannot rule out that this individual was foraging on flying insects during the morning, as proposed for diurnal flights in insect-eating bat species (Lučan & Bartonička 2024; Mc Arthur *et al.*, 2024).

One of the most cited reasons for diurnal flight in bats is to cope with hyperthermia (Speakman *et al.*, 1994a; Voigt & Lewanzik 2011). Ravines and canyons, especially ponds, might be a suitable habitat for a bat during droughts (cooler environments with water availability, i.e., Bôlla *et al.*, 2017), a possible explanation for the sighting of the vespertilionid bat. Another possible explanation is the presence of a high abundance of

insects in water ponds. For example, *Myotis horsfieldii* are active during diurnal hours flying over streams and rivers and foraging on insects (Mc Arthur *et al.*, 2024). The flight pattern (with continuous and rapid turns and change of direction), suggests that the vesper bat observed in this report might be foraging insects and drinking water.

This is the second report of *Artibeus* aff. *lituratus* feeding on the ground (Gastal & Bizerril 1999), and the first time with direct observation of this behavior. In Brazil, *A. lituratus* fed on the fruits of *Sacoglottis guianensis*, mostly feeding on their tree-roosts, but 11 individuals, in addition to an individual of *Platyrrhinus lineatus*, were captured on ground traps baited with *S. guianensis* fruits nearby their tree-roosts, which suggested that both species can forage on the ground and the importance of this fruit on the diet of both bat species. However, the study of Gastal and Bizerril (1999) suggested that it was a nocturnal activity, unlike this report, probably reflecting a more common but poorly documented behavior. This species also has a high visual acuity (Antonio *et al.*, 2010) for detecting food items in high-light conditions.

Why both *Artibeus* individuals were feeding on the ground? A possible explanation is that diurnal foraging might be promoted by insufficient food intake during the previous night (Speakman 1990), or dehydration. Body temperature in *Artibeus lituratus* is about 36.8-35.8 °C (Morrison & McNab 1967), so, an upper ambient temperature might impose thermogenic stress (even if being considered a good thermoregulator in Morrison & McNab 1967) and encourage seeking sugary and watery food sources, such as *B. alicastrum* fruit, the only fruiting tree in the vicinity of the observed roost. Moreso, hyperthermia will constrain diurnal activities in larger bat species than in smaller ones (Speakman *et al.*, 1994a), being *A. lituratus* one of the biggest bat species in the region (>70 g; Reid 2009). At over 35°C, tree-roosting species (as *A. lituratus*), might reduce sleeping time and engage in cooling behaviors (see Downs *et al.*, 2015 for an example in *Epomophorus wahlbergi*, which weights 87-123 g [Rollinson *et al.*, 2013]), one of which could seek fallen fruits (see Sánchez *et al.*, 2023) and lay while eating them (bats lose water when flying; Carpenter 1969), even at the risk of predators. How extended ground-foraging is in Phyllostomid bats needs further research, since members of Stenodermatinae subfamily are not known to be well-adapted to quadrupedal locomotion, and hence, the common idea is that they would be less likely to forage on ground (Schutt & Simmons 2006).

The reports of diurnal flights in bats offer an interesting insight into the ecology and behavior of different species and allow us to suggest if it represents a mechanism to cope with various environmental conditions, such as light, insect availability, predators, or even high environmental temperatures (the latter an important consideration in the light of anthropogenic climate change). Diurnal behavior in bats seems very common and extended among sites and species, but still poorly studied, and in need of a systematic revision.

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REFERENCES

- Antonio EA, Sá FB, Santos P KR, Lima Junior NB, Silva FR, Aguilar Júnior FCA, Vieira JRC. 2020. Comparative retinal histomorphometry and visual acuity of three bat species of the genus *Artibeus* (Phyllostomidae: Stenodermatinae). *Pesquisa Veterinária Brasileira* 40: 933-945. <https://doi.org/10.1590/1678-5150-pvb-6701>
- Bôlla D, Carvalho F, Zocche JJ, Bianco A, Bittencourt Vitto JA, Santos R. 2017. Phyllostomid bats flying in daylight: a case from the Neotropics. *Journal Of Natural History* 51: 2947-2953. <https://doi.org/10.1080/00222933.2017.1397227>
- Bôlla D, Morim Novaes RL, Carvalho F. 2023. Bats got a place in the sun: new findings of daytime flight in Brazil. *Therya Notes*, 4: 129-134. https://doi.org/10.12933/therya_notes-23-119
- Caballero-Martínez LA, Rivas-Manzano IV, Aguilera-Gómez LI. 2009. Feeding habits of *Anoura geoffroyi* (Chiroptera: Phyllostomidae) in Ixtapan del Oro, Mexico State. *Acta Zoológica Mexicana* (n.s.) 5: 161-175. <https://doi.org/10.21829/azm.2009.251609>
- Carpenter RE. 1969. Structure and Function of the Kidney and the Water Balance of Desert Bats. *Physiological Zoology* 42: 288-302. <https://doi.org/10.1086/physzool.42.3.30155492>
- Chua MAH, Aziz SA. 2018. Into the light: atypical diurnal foraging activity of Blyth's horseshoe bat, *Rhinolophus lepidus* (Chiroptera: Rhinolophidae) on Tioman Island, Malaysia. *Mammalia* 83: 78-83. <https://doi.org/10.1515/mammalia-2017-0128>
- Connel K, Munro U, R Torpy F. 2006. Daytime behaviour of the grey-headed flying fox *Pteropus poliocephalus* Temminck (Pteropodidae: Megachiroptera) at an autumn/winter roost. *Australian Mammalogy* 7-14. <https://doi.org/10.1071/am06002>
- Downs CT, Awauh A, Jordaan M, Magagula L, Mkhize T, Susan Paine C, Raymond-Bourret E, Hart L. 2015. Too Hot to Sleep? Sleep behaviour and surface body temperature of Wahlberg's Epauletted fruit bat. *PloS ONE* e0119419. <https://doi.org/10.1371/journal.pone.0119419>
- Eitan O, Weinberg M, Danilovich S, Barkai Y, Assa R, Yovel Y. 2022. Functional daylight echolocation in highly visual bats. *Current Biology* 32: 309-310. <https://doi.org/10.1016/j.cub.2022.02.075>
- Erkert, H.G. 1982. Ecological aspects of bat activity rhythms. In: Kunz TH, editor. *The ecology of bats*. New York, USA: Plenum Press. p. 201-242.
- Frafjord K. 2021. The influence of night length: Activity of the northern bat *Eptesicus nilssonii* under conditions of continuous light in midnight sun compared to a southern population. *BMC Zoology* 6. <https://doi.org/10.1186/s40850-021-00099-1>
- Gastal ML, Bizerril MXA. 1999. Ground foraging and seed dispersal of a gallery forest tree by the fruit-eating bat *Artibeus lituratus*. *Mammalia* 63: 108-112.
- Gutiérrez E de A, Pessoa VF, Aguilar LMS, Pessoa DMA. 2014. Effect of light intensity on food detection in captive great fruit-eating bats, *Artibeus lituratus* (Chiroptera: Phyllostomidae). *Behavioural Processes* 109: 64-69. <https://doi.org/10.1016/j.beproc.2014.08.003>
- Harding CD, Yovel Y, Peirson SN, Hackett TD, Vyazovskiy VV. 2022. Re-examining extreme sleep duration in bats: implications for sleep phylogeny, ecology, and function. *Sleep* 45. <https://doi.org/10.1093/sleep/zsac064>
- Lučan RK, Bartonička T. 2024. Diurnal activity in an insectivorous bat during migration period. *Journal of Mammalogy* 105: 643-651. <https://doi.org/10.1093/jmammal/gyae006>
- Mc Arthur E, Huang JCC, López-Baucells A, Rocha R, Khan FAA. 2024. Diurnal Activity of a trawling insectivorous bat species, *Myotis horsfieldii*, in Gunung Mulu National Park, Malaysian Borneo. *Journal of Natural History* 58: 1559-1573. <https://doi.org/10.1080/00222933.2024.2393464>

- Mikula P, Morelli F, Lučan RK, Jones DN, Tryjanowski P. 2016. Bats as prey of diurnal birds: a global perspective. *Mammal Rev* 46: 160-174. <https://doi.org/10.1111/mam.12060>
- Miller DH. 1962. Daytime Attack on a Bat by Blackbirds. *Journal Of Mammalogy*. 43: 546. <https://doi.org/10.2307/1376923>
- Molinari J, Gutiérrez EE, Lim BK. 2023. Systematics and Biogeography of *Anura cultrate* (Mammalia, Chiroptera, Phyllostomidae): a morphometric, niche, modeling, and genetic perspective, with a taxonomic reappraisal of the genus. *Zootaxa* 5297: 151-188. <https://doi.org/10.11646/zootaxa.5297.2.1>
- Moore NW. 1975. The diurnal flight of the Azorean bat (*Nyctalus azoreum*) and the avifauna of the Azores. *Journal Of Zoology* 177: 483-486. <https://doi.org/10.1111/j.1469-7998.1975.tb02248.x>
- Morrison P, McNab BK. 1967. Temperature regulation in some Brazilian phyllostomid bats. *Comparative Biochemistry and Physiology* 207-221. [https://doi.org/10.1016/0010-406x\(67\)90130-2](https://doi.org/10.1016/0010-406x(67)90130-2)
- Pedrozo AR, Costa Gomes LA, Uieda W. 2018. Feeding behavior and activity period of three Neotropical bat species (Chiroptera: Phyllostomidae) on *Musa paradisiaca* inflorescences (Zingiberales: Musaceae). *Série Zoologia* 108. <https://doi.org/10.1590/1678-4766e2018022>
- Reid, FA. 2009. A field guide of the mammals of Central American and Southeast Mexico. Nueva York, USA: Oxford University Press.
- Rollinson DP, Coleman JC, Downs CT. 2013. Seasonal differences in foraging dynamics, habitat use and home range size of Wahlberg's epauletted fruit bat in an urban environment. *African Zoology* 48: 340-350. <https://doi.org/10.1080/15627020.2013.11407601>
- Russo D, Cistrone L, Garonna AP, Jones G. 2011a. The early bat catches the fly: Daylight foraging in soprano pipistrelles. *Mammalian Biology* 76: 87-89. <https://doi.org/10.1016/j.mambio.2009.08.002>
- Russo D, Maglio G, Rainho A, Meyer CFJ, M Palmeirim J. 2011b. Out of the dark: Diurnal activity in the bat *Hipposideros ruber* on São Tomé Island (West Africa). *Mammalian Biology* 76: 701-708. <https://doi.org/10.1016/j.mambio.2010.11.007>
- Rydell J, Entwistle A, Racey PA. 1996. Timing of Foraging Flights of Three Species of Bats in Relation to Insect Activity and Predation Risk. *Oikos* 243. <https://doi.org/10.2307/3546196>
- Rydell J, Speakman JR. 1995. Evolution of nocturnality in bats: Potential competitors and predators during their early history. *Biological Journal of The Linnean Society* 54: 183-191. <https://doi.org/10.1111/j.1095-8312.1995.tb01031.x>
- Sánchez Z, Guevara N, Montenegro K, Correa M. 2023. Consumo diurno de fruto por *Artibeus lituratus* en Coclé, República de Panamá. *Revista Mexicana de Mastozoología* 13: 44-48. <https://doi.org/10.22201/ie.20074484e.2023.13.2.394>
- Schutt WA, Simmons NB. 2006. Quadrupedal bats: form, function, and evolution. In: Zubaid A, McCracken GF, Kunz TH, editors. *Functional and Evolutionary Ecology of Bats*. New York, USA: Oxford Academic Press. p. 145-159.
- Speakman J R. 1991a. The impact of predation by birds on bat populations in the British Isles. *Mammal Review* 21: 123-142. <https://doi.org/10.1111/j.1365-2907.1991.tb00114.x>
- Speakman J R. 1991b. Why do insectivorous bats in Britain not fly in daylight more frequently? *Functional Ecology* 5: 518-524. <https://doi.org/10.2307/2389634>
- Speakman J, Rydell J, Weeb PI, Hayes JP, Hays GC, Hulbert IA, Mcdevitt Speakman RM, Hays JP, Hulbert GC, R And IA. 2000. Activity patterns of insectivorous bats and birds in northern Scandinavia

- (69 N), during continuous midsummer daylight. *Oikos* 88: 75-86. <https://doi.org/10.1034/j.1600-0706.2000.880109.x>
- Speakman J. 1995. Chiropteran nocturnality. *Symposia of the Zoological Society of London* 67: 188-201. <https://doi.org/10.1093/oso/9780198549451.003.0012>
- Speakman JR, Hays GC, Webb PI. 1994a. Is hyperthermia a constraint on the diurnal activity of bats? *Journal of Theoretical Biology* 171: 325-339. <https://doi.org/10.1006/jtbi.1994.1235>
- Speakman JR, Lumsden LF, Hays GC. 1994b. Predation rates on bats released to fly during daylight in south-eastern Australia. *Journal of Zoology* 233: 318-321. <https://doi.org/10.1111/j.1469-7998.1994.tb08593.x>
- Speakman JR, Racey PA. 1991. No cost of echolocation for bats in flight. *Nature* 350: 421-423. <https://doi.org/10.1038/350421a0>
- Vivas-Toro I, Murillo-García OE. 2020. Diurnal Flying Activity of a Neotropical Bat (*Saccopteryx leptura*): Effect of Light Intensity, Temperature, and Canopy Cover. *Acta Chiropterologica* 22: 87. <https://doi.org/10.3161/15081109acc2020.22.1.008>
- Voigt CC, Lewanzik D. 2011. Trapped in the darkness of the night: thermal and energetic constraints of daylight flight in bats. *Royal Society* 2311-2317. <https://doi.org/10.1098/rspb.2010.2290>
- Voigt CC, Speakman JR. 2007. Nectar-feeding bats fuel their high metabolism directly with exogenous carbohydrates. *Functional Ecology* 21: 913-921. <https://doi.org/10.1111/j.1365-2435.2007.01321.x>
- Welbergen A. 2008. Variation in twilight predicts the duration on the evening emergence of fruit bats from a mixed species roost. *Animal Behaviour* 75: 1543-1550. <https://doi.org/10.1016/j.anbehav.2007.10.007>

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