NOTAS SOBRE
MAMÍFEROS SUDAMERICANOS

Sociedad Argentina para el Estudio de los Mamíferos

Notas sobre Mamíferos Sudamericanos 2024, vol. 6
DOI: https://doi.org/10.31687/SaremNMS24.01.6
Versión on-line ISSN 2618-4788

NOTAS SOBRE
MAMÍFEROS
SUDAMERICANOS

Activity patterns of short-tailed fruit bats *Carollia* Gray, 1838 in a premontane forest of central Peru

Jorge A. Rivero (1), Juan J. Pellón (1, 2), and Orlando J. Zegarra (2, 3)

(1) Laboratorio de Fisiología Animal y Biorremediación Luis Barrio Acosta, Universidad Nacional Agraria La Molina (UNALM), Lima, Peru. (2) Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (UNMSM), Lima, Peru. (3) División de Mastozoología, Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru. [Correspondence: jrivmon95@gmail.com]

Citación: Rivero, J. A., J. J. Pellón, & O. J. Zegarra. 2024. Activity patterns of short-tailed fruit bats *Carollia* Gray, 1838 in a premontane forest of central Peru. Notas sobre Mamíferos Sudamericanos 6:e24.01.6.

ABSTRACT
Time partitioning is an understudied mechanism for frugivorous bat species that coexist in competition. We describe activity patterns of *Carollia perspicillata* (Linnaeus, 1758), *Carollia brevicauda* (Schinz, 1821), and *Carollia benkeithi* Solari & Baker, 2006 using time of capture variation in a premontane forest of central Peru. For *C. perspicillata,* activity patterns of different sexes and seasons (rainy *vs.* dry) were also compared. We report temporal coincidence (Δ=0.91) among the three species being more active at the beginning of the night when resources are available. Neither sex nor season changed the activity pattern of *C. perspicillata*. Evidence suggests that these sympatric species do not reduce competition through time partitioning.

Keywords: competition, flying mammals, frugivores, nocturnal activity, temporal overlap

RESUMEN - Patrones de actividad de los murciélagos de cola corta *Carollia* en un bosque premontano del centro de Perú. La partición temporal es un mecanismo poco estudiado para especies de murciélagos frugívoros que coexisten en competencia. Describimos los patrones de actividad de *Carollia perspicillata* (Linnaeus, 1758), *Carollia brevicauda* (Schinz, 1821) y *Carollia benkeithi* Solari & Baker, 2006 basándonos en la variación temporal de las capturas en un bosque premontano del centro de Perú. Para *C. perspicillata,* también fueron comparados los patrones de actividad entre diferentes sexos y estaciones (húmeda *vs.* seca). Reportamos una superposición temporal (Δ=0,91) entre las tres especies, siendo más activas al principio de la noche cuando los recursos se encuentran más disponibles. Ni el sexo ni la estación cambiaron el patrón de actividad de *C. perspicillata*. La evidencia sugiere que estas especies simpátricas no reducen la competencia a través de la segregación temporal.

Palabras clave: actividad nocturna, competencia, frugívoros, mamíferos voladores, solapamiento temporal

---

Mammals have evolved physiological and behavioral adaptations that result in an hourly activity pattern related to abiotic and biotic conditions such as light, tempe-

Recibido el 19 de enero de 2023. Aceptado el 21 de noviembre de 2023. Editor asociado Mariano Sánchez.

rature, rainfall, wind, food supply, predation pressure, social factors and human disturbance (Erkert 1982; Halle & Stenseth 2000; Mistlberger & Antle 2011; Blake et al. 2012; Gaynor et al. 2018; Castillo-Figueroa et al. 2021). For bats, nocturnal patterns are greatly affected by the amount of energy available from their food items and their fluctuations in space and time, but also on species or individuals' specific energetic demands and requirements of digestion (Erkert 2000; Saldaña-Vázquez & Schondube 2013). Activity patterns can be affected by exploitative competition, especially for species with shared limited resources (Miller 1967). According to seminal studies of niche segregation (spatial, temporal, trophic, etc.) competition is an important process to explain species coexistence (MacArthur & Levins 1967; Cody & Diamond 1975), even in contemporary approaches (Chase & Leibold 2003; Donati & Borgognini-Tarli 2006; Violle et al. 2011). Therefore, sympatric species might exhibit different activity peaks and periods as a potential mechanism to reduce time overlap with competitors (Kronfeld-Schor & Dayan 2003).

Neotropical frugivorous phyllostomid bats are active throughout the night frequently exhibiting a unique peak (Brown 1968; La Val 1970; Davis & Dixon 1976; Marinho-Filho & Sazima 1989; Aguiar & Marinho-Filho 2004; Sampedro et al. 2007; Stuhler et al. 2019) and in some cases a second smaller peak (Verde et al. 2018). In many cases, timing of activity peaks varies across species and depends on population abundance and ecosystem sampled (Ortêncio-Filho et al. 2010; Arriaga-Flores et al. 2012; Mancina & Castro-Arellano 2013; Zeppelini et al. 2017). Weather conditions, photic cues and landscape features are extrinsic factors that potentially affect resource availability, competition, or predation risk in frugivorous bats (Thies et al. 2006; Castro-Arellano et al. 2009; Presley et al. 2009; Montaño-Centellas et al. 2015). Moreover, seasonal differences in activity patterns may reflect variation in fruit spatial distribution and availability, which can alter the time that bats spend on flying to different foraging patches and roosts (Fleming & Heithaus 1986; Fleming 1988). Conversely, intrinsic factors (i.e., sex, age, and reproductive condition) affect the individual´s energetic requirements and influence activity through foraging efficiency and social cues (Heithaus & Fleming 1978; Fleming & Heithaus 1986; Fleming 1988; Charles-Dominique 1991). Specifically, sex differences in activity patterns might be related to females´ higher daily energetic budget (Fleming 1988).

The drivers of coexistence among three or more species of the genus *Carollia* have been little explored (Fleming 1991; York & Papes 2007). Available information of activity patterns for *Carollia* is mainly limited to localities where only one or two species are present (Bernard 2002; Bonaccorso et al. 2007; Castro-Arellano et al. 2009; Montaño-Centellas et al. 2015; Vásquez-Parra et al. 2017; Verde et al. 2018; but see La Val 1970; Presley et al. 2009). In this context, our study site is a suitable area to compare activity patterns because three species coexist and are relatively abundant: *Carollia benkeithi* Solari & Baker 2006, *Carollia brevicauda* (Schinz, 1821), and *Carollia perspicillata* (Linneus, 1758) (Zegarra 2019) Moreover, there is evidence that these bat species share fruit resources of at least nine different plant species (Pellón et al. 2021). Our aim was to compare activity patterns of these three sympatric species of the genus *Carollia* within the first seven hours after dusk and, for *C. perspicillata*, describe activity patterns of each sex and season in a premontane forest of central Peru.

The study site is located in the province of Satipo, department of Junín, Peru (latitude -11.16583; longitude -74.65722). According to Holdridge (1967) classification, the area belongs to the "very humid tropical Premontane Forest (bmh-PMT)" life zone. Forest has a secondary succession plant composition, covers 113 ha and has rolling and steep topography, with moderate slopes and hills (Marcelo-Peña & Reynel 2014). Based on data from the Satipo meteorological station of SENAMHI (Servicio Nacional de Meteorología e Hidrología del Perú 2019), annual temperature and rainfall fluctuate between 24–26°C and 1500–2000 mm, respectively. The climate in this region is characterized by two main seasons: (1) dry season, from April to September, defined by temperatures from 25-26*°C* and monthly precipitations ranging approximately from 55 to 120 mm; (2) wet season, from October to March, defined by temperatures from 24-25°C and monthly precipitations ranging approximately from 150 to 270 mm (Rivero-Monteagudo et al. 2021).

Time of capture data was obtained from two bat surveys conducted from 2013 to 2016 (Zegarra 2019; Pellón et al. 2021; Rivero-Monteagudo et al. 2021). In both surveys, different numbers of mist nets were deployed at 3-4 m above the ground (12 m length, 2.5 m height), in small forest gaps, water flows and near potential roosting sites or feeding patches with vegetation dominated by species of *Piper*, *Solanum*, and *Cecropia*. Data of the first survey were taken from Zegarra (2019), which was conducted in two dry seasons (August 2013 and July 2014, Sampling effort: 3168 and 4608 meters per hour, respectively) and one rainy season (January to March 2015, Sampling effort: 7776 meters per hour). Data of the second survey were taken from Rivero-Monteagudo et al. (2021), which was conducted every month from October 2015 to September 2016 (12 nets per month, Sampling effort: 10368 meters per hour), including an additional sampling in May 2015 (12 nets, Sampling effort: 864 meters per hour) taken from Pellón et al. (2021). Total sampling effort was 26784 meters of net per hour (see Zegarra 2019; Pellón et al. 2021; Rivero-Monteagudo et al. 2021, for details in sampling design). Mist nets were opened between 17:30-18:30 h, closed between 00:00-01:00 h and checked every 30 minutes. To account for variation in night length throughout the year, we subtracted the sunset time from the time of capture and expressed our units in hours after sunset. Time of sunset was obtained using the *Suncalc* package (Thieurmel & Elmarharaoui 2019) in R software and varied from 17:43 h in May (dry season) to 18:29 h in January and February (wet season). Individuals captured during the seasonal survey (Zegarra 2019) were marked by fur trimming (Presley et al. 2009) and those captured during the annual survey (Pellón et al. 2021; Rivero-Monteagudo et al. 2021) by nail polish (Stawski 2012; Kemenesi et al. 2015; Dekeukeleire et al. 2016) to prevent double counting. Sex was determined based on external characteristics of reproductive organs (Kunz et al. 1996; Racey 2009) and species identification was made using taxonomic keys (Pacheco & Solari 1997; Gardner 2008; Díaz et al. 2011).

Bats were handled following the recommendations of the Animal Care and Use Committee of the American Society of Mammalogists (Sikes et al. 2016).

Each bat captured per night was considered an independent event for activity analysis. We had a total of 419 independent records of three *Carollia* species: 196 for *C. perspicillata* (46.78 %), 126 for *C. benkeithi* (30.07 %) and 97 for *C. brevicauda* (23.15 %). We pooled data into a total of seven 1-hour intervals and calculated hourly occurrence frequencies per each species, which were the number of individuals per hour divided by the total number of individuals. In addition, we calculated hourly occurrence frequencies per sex and season, considering the total number of males or females or the total records during rainy or dry months respectively. For *C. perspicillata*, we captured a total of 108 females and 86 males (two individuals had no sex data), and a total of 88 individuals for the driest period and 108 individuals for the wettest period. We did not perform this analysis for *C. benkeithi* or *C. brevicauda* due to low capture rates for each sex and season separately.

For each pair of species, sexes, or seasons, we also reported measures of temporal overlap using the Pianka index “α” (Pianka 1973), which approaches zero for species with non-overlapping activity patterns and equals 1 if activity patterns are identical. This index has been used previously on studies of bats activity patterns (Presley et al. 2009; Castro-Arellano et al. 2010). We tested if the three *Carollia* species showed a significant temporal coincidence (more overlap than expected by chance) using ROSARIO Algorithm with 10000 iterations in the TimeOverlap Software (Castro-Arellano et al. 2010).

All species had at least one record in each hour of the night and exhibited a peak of activity early in the night followed by a decreasing trend towards midnight (Fig. 1). Each species showed a peak of activity at a different hour: two (~19:00-20:30 h), three (~20:00-21:30 h), and four (~21:00-22:30 h) hours after sunset for *C. perspicillata*, *C. brevicauda* and *C. benkeithi* respectively (Fig. 1). We reported an average temporal overlap of 0.91 among the three species of *Carollia* ($\alpha_{C.\ brevicauda\ -\ C.\ benkeithi} = 0.92$, $\alpha_{C.\ perspicillata\ -\ C.\ benkeithi} = 0.89$, $\alpha_{C.\ perspicillata\ -\ C.\ brevicauda} = 0.93$). Temporal coincidence was statistically significant ($p = 0.04$).

Analysis per sex and season of *C. perspicillata* showed similar trends between frequencies of males and females, and between frequencies of rainy and dry season (Fig. 2), with very high temporal overlap values ($\alpha_{Sex} = 0.91$, $\alpha_{Season} = 0.93$). Both sexes displayed activity at every sampling hour, although there were slight differences: more than 25% of females were captured two hours after sunset, while only between 9 and 15% were captured each hour for the rest of the sampled night period (Fig. 2a). Most males were captured between two, and three hours after sunset (~22.7% each interval), and then between four (~18.2%) and five (~15.9%) hours after sunset (Fig. 2b). During both seasons, *C. perspicillata* displayed higher activity two hours after sunset. Nevertheless, during the dry season captures were slightly more evenly distributed in the first five hours of the night (between 13.6% and 17% each hour, with a small peak of 20.5% two hours after sunset) and then decreased (Fig. 2c), whereas during the rainy season the peak at two hours after sunset was more pronounced and followed by a progressive decline toward midnight (Fig. 2d).

An exhaustive revision of studies on other Neotropical localities (Heithaus & Fleming 1978; Fleming 1988; Aguiar & Marinho-Filho 2004; Thies et al. 2006; Ortêncio-Filho et al. 2010; Zeppelini et al. 2017) shows that the main foraging period of species of the genus *Carollia* is from dusk to midnight. In our study, there is a considerable high degree of overlap (0.91) among the activity of the three *Carollia* species. The general trend of their activity patterns is consistent with most studies of short-tailed fruit bats, which typically display the activity peak during the first hours of the night followed by a subsequent decrease towards midnight (Bernard 2002; Moratelli & Perachi 2007; Castro-Arellano et al. 2009; Presley et al. 2009; Mello et al. 2013; Verde et al. 2018; but see Pedrozo 2014; Vásquez-Parra et al. 2017; Pereira et al. 2018). The decreasing foraging activity of *Carollia* is possibly associated with a reduction in ripe fruit availability during the night (Marinho-Filho & Sazima 1989; Thies et al. 2006). *Piper* fruits are regarded as high nutritional and caloric fruit resources (Herbst 1986; Bohlender et al. 2018; Borray-Escalante et al. 2022); however, ripening of a few fruits per night per plant is typical in *Piper*, which limits the night availability of mature fruits (Fleming 1985; Thies & Kalko 2004). Some bats might consume enough *Piper* fruit to fulfill their daily energetic needs during the high availability period and return to their daily roosts after the first three hours of the night (Thies et al. 2006). As availability decreases, other individuals who were unable to consume enough calories might continue foraging for fruit from less preferred plant species (i. e., *C. sciadophylla*) that are more available throughout the night (Bonaccorso et al. 2007).

Peaks of activity among *Carollia* species differ only by one hour (Fig. 1). La Val (1970) reports similar results in a tropical wet forest of Costa Rica during the rainy season: the hourly catch of *C. perspicillata* and *C. sowelli* (cited as *C. brevicauda*) was higher between 0 and 1 hours after sunset, while activity of *C. castanea* peaked between 2 and 3 hours after dusk. Nevertheless, the activity of *C. castanea* peaked early during the night in tropical forests of Panamá, coinciding with maximum availability of ripe fruits from understory pepper plants (Thies et al. 2006). Moreover, in Ecuador, *C. castanea* has shown earlier roost emergence, shorter commuting flights, and shorter foraging periods (limited by *Piper* fruits depletion) than *C. perspicillata*, suggesting that these species coexist through exploitative competition (Bonaccorso et al. 2007).

Differences in hourly activity by frugivorous bats were suggested to be related with a differential fruit consumption (Pedro & Taddei 2002). In the study area, *C. benkeithi* focus on a small group of plants different to the main resources in the broad diets of *C. perspicillata* and *C. brevicauda* (Pellón et al. 2021). This suggests that diet is a determinant of their coexistence, but some degree of temporal segregation could be an additional mechanism that reduces the competition within congeners (La Val 1970). Although, this mechanism has been neglected since fruits are not renewable and typically do not ripen at different hours of the night (Marinho-Filho & Sazima 1989), frugivorous bats might still reduce competition by direct interference (Heithaus et al. 1975).

Seasonal changes in fruit distribution and availability are common in Neotropical environments (Heithaus et al. 1975; Dinerstein 1986; Fleming & Heithaus 1986; Thies & Kalko 2004; Mello et al. 2004) and might affect the temporal activity patterns for *C. perspicillata*. In the study area, the activity pattern of this species did not show any notable seasonal differences. Studies from other environments also indicate that seasonality had no effect on the activity pattern of *C. perspicillata* from sunset to midnight (Fleming 1988; Presley et al. 2009). Fruit scarcity and dispersion during the lowest fruit availability period could force individuals to search for more feeding patches at greater distances from their roosts (Fleming & Heithaus 1986). Nevertheless, seasonal differences in flying distance do not necessarily indicate differences in the number of flights or flight time (Charles-Dominique 1991).

The fact that the peak of activity was more pronounced in the rainy season, could be related to a higher occurrence of pregnant and lactating females (Rivero-Monteagudo et al. 2021). Reproductive females reduce flight time due to a higher energetic demands, resulting in a more pronounced peak of activity at early hours (Charles-Dominique 1991). This also would explain why captures were more evenly distributed in the dry season, the non-reproductive period of *C. perspicillata*. From a subset of our female dataset during the rainy season (N = 47), we estimated a proportion of 40% in a reproductive stage (N = 19). The activity patterns of non-reproductive and reproductive females had a high overlap (87%) and both peaked two hours after sunset at different proportions (Reproductive: 25%, Non-reproductive: 15%). Nevertheless, this analysis should be conducted with a larger dataset. Additional factors to consider could be year to year variation in resource availability and seasonal differences in foraging movements (Fleming & Heithaus 1986).

Our results show that the activity pattern of *C. perspicillata* is similar for males and females ($\alpha_{Sex} = 0.91$). Other reports stated that there are no differences in foraging time spend between males and females (Heithaus & Fleming 1978; Charles-Dominique 1991). The fact that females' peak of activity is more pronounced two hours after sunset might represent short intense feeding episodes, followed by prolonged stays in day roosts (Thies et al. 2006). Sex-differences in fruit consumption patterns have been reported for *Carollia* over seasons, which could be related to different foraging strategies (Alviz & Pérez-Torres 2020). Earlier foraging times could be available to females, but unavailable for most bachelor males due to inaccessibility into harem males' territories. Fleming & Heithaus (1986) suggested intraspecific differences in resource accessibility and foraging behavior may be due to social status of males. Further studies that address variation in foraging timing between sexes should disaggregate the activity patterns of males and females from different social status and reproductive condition respectively. In this regard, body size is related to energetic demands and could be an explanatory factor to account for differences in sex and reproductive condition (Castillo-Figueroa 2022).

This study provides the first comparison of activity per hour among three bat species of the genus *Carollia* for premontane forests in central Peru, which is necessary to propose further detailed studies about the temporal activity of the studied *Carollia* species. For example, employing pit-tag systems (Thomson 2020; Rivera-Villanueva

2021) and simultaneously evaluating fruit availability through the night (Bonaccorso 2007) could provide new insights about the potential drivers of their activity such as reproductive condition, social status or environmental factors. Evidence from this study supports temporal coincidence among *Carollia* species, being more active at early night and decreasing their activity towards midnight.

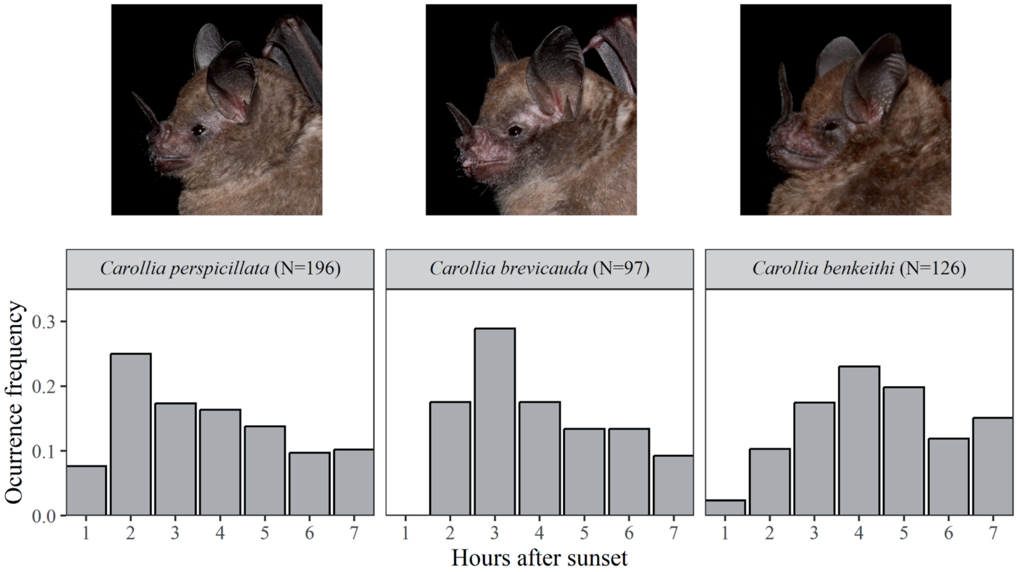

Figure 1. Activity of *Carollia* species within seven hours after sunset. Photos provided by Oscar Quispe Hure.

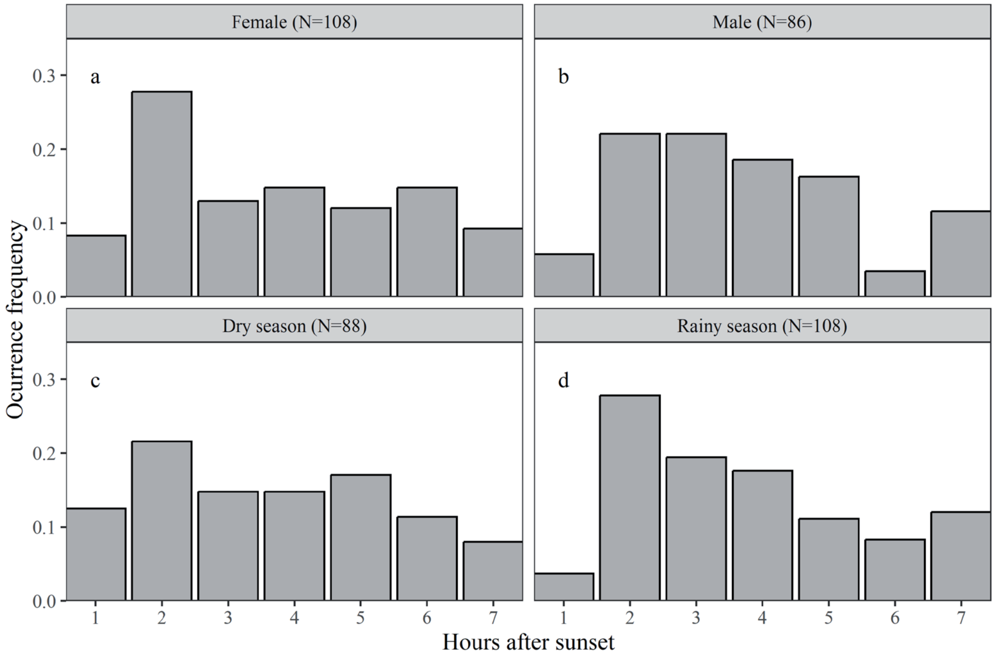

Figure 2. Activity of *Carollia perspicillata* within seven hours after sunset between sexes (a, b) and seasons (c, d).

ACKNOWLEDGEMENTS

We are grateful to all the people who participated in the fieldwork, especially to M. Quispe. We thank Daniel Ibañez IV for reviewing English in previous versions of this manuscript. We thank M. Williams for her important support in the development of this work. This research was partially funded by the Research Office of Universidad Nacional Agraria La Molina. We also thank R. Blas, C.M. Huamancha and R. Espinoza for the support with accommodations and authorizations to work in Fundo Santa Teresa.

We would like to thank the entire field team who gave us support, anonymous reviewers and editors who helped us improve the text.

LITERATURE CITED

Aguiar, L. M., & J. Marinho-Filho. 2004. Activity patterns of nine Phyllostomid bat species in a fragment of the Atlantic Forest in southeastern Brazil. Revista Brasileira de Zoologia 21:385–390. https://doi.org/10.1590/S0101-81752004000200037

Alviz, A., & J. Pérez-Torres. 2020. A difference between sexes: temporal variation in the diet of *Carollia perspicillata* (Chiroptera, Phyllostomidae) at the Macaregua cave, Santander (Colombia). Animal Biodiversity and Conservation 43:27–35. https://doi.org/10.32800/abc.2020.43.0027

Arriaga-Flores, J. C., I. Castro-Arellano, A. Moreno-Valdez, & A. Correa-Sandoval. 2012. Temporal niche overlap of a riparian forest bat assemblage in subtropical Mexico. Revista Mexicana de Mastozoología (Nueva Época) 2:3–17. https://doi.org/10.22201/ie.20074484e.2012.2.1.18

Bernard, E. 2002. Diet, activity and reproduction of bat species (Mammalia, Chiroptera) in Central Amazonia, Brazil. Revista Brasileira de Zoologia 19:173–188. https://doi.org/10.1590/S0101-81752002000100016

Blake, J. G., D. Mosquera, B. A. Loiselle, K. Swing, J. Guerra, & D. Romo. 2012. Temporal activity patterns of terrestrial mammals in lowland rainforest of eastern Ecuador. Ecotropica 137:137–146.

Bohlender, E. E., J. Pérez-Torres, N. A. Borray-Escalante, & R. D. Stevens. 2018. Dietary variation during reproduction in Seba's short-tailed fruit bat. Journal of Mammalogy 99:440–449. https://doi.org/10.1093/jmammal/gyx189

Bonaccorso, F. J., et al. 2007. Evidence for exploitative competition: comparative foraging behavior and roosting ecology of short-tailed fruit bats (Phyllostomidae). Biotropica 39:249–256. https://doi.org/10.1111/j.1744-7429.2006.00251.x

Borray-Escalante, N. A., J. Pérez-Torres, & M. E. Castro-Benitez. 2022. Nutritional ecology of *Carollia perspicillata* (Chiroptera: Phyllostomidae): relationship between the preference and the nutritional content of fruits. Acta Chiropterologica 24:177–185. https://doi.org/10.3161/15081109ACC2022.24.1.014

Brown, J. H. 1968. Activity patterns of some Neotropical bats. Journal of Mammalogy 49:754–757. https://doi.org/10.2307/1378737

Castillo-Figueroa, D. 2022. Does Bergmann's rule apply in bats? Evidence from two neotropical species. Neotropical Biodiversity 8:200–221. https://doi.org/10.1080/23766808.2022.2075530

Castillo-Figueroa, D., D. Martínez-Medina, & M. E. Rodríguez-Posada. 2021. Activity patterns of medium and large mammals in two savanna ecosystems in the Colombian Llanos. Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales 45:1071–1083. https://doi.org/10.18257/raccefyn.1461

Castro-Arellano, I., S. J. Presley, M. R. Willig, J. M. Wunderle, & L. N. Saldanha. 2009. Reduced-impact logging and temporal activity of understorey bats in lowland Amazonia. Biological Conservation 142:2131–2139. https://doi.org/10.1016/j.biocon.2009.04.013

Castro-Arellano, I., T. E. Lacher Jr., M. R. Willig, & T. F. Rangel. 2010. Assessment of assemblage-wide temporal niche segregation using null models. Methods in Ecology and Evolution 1:311–318. https://doi.org/10.1111/j.2041-210X.2010.00031.x

Charles-Dominique, P. 1991. Feeding strategy and activity budget of the frugivorous bat *Carollia perspicillata* (Chiroptera: Phyllostomidae) in French Guiana. Journal of Tropical Ecology 7:243–256. https://doi.org/10.1017/S026646740000540X

Chase, J. M., & M. A. Leibold (eds.). 2003. Ecological Niches: Linking Classical and Contemporary Approaches. University of Chicago Press, Chicago.

Cody, M. L., & J. W. Diamond (eds.). 1975. Ecology and evolution of communities. Belknap, Harvard University Press, Massachusetts.

Davis, W. B., & J. R. Dixon. 1976. Activity of bats in a small village clearing near Iquitos, Peru. Journal of Mammalogy 57:747–749. https://doi.org/10.2307/1379444

Dekeukeleire, D., R. Janssen, A. J. Haarsma, T. Bosch, & J. Van Schaik. 2016. Swarming behaviour, catchment area and seasonal movement patterns of the Bechstein's bats: implications for conservation. Acta Chiropterologica 18:349–358. https://doi.org/10.3161/15081109ACC2016.18.2.004

Díaz, M. M., L. F. Aguirre, & R. M. Barquez. 2011. Clave de identificación de los murciélagos del cono sur de Sudamérica. Centro de estudios de Biología Teórica y Aplicada, Cochabamba.

Dinerstein, E. 1986. Reproductive ecology of fruit bats and the seasonality of fruit production in a Costa Rican cloud forest. Biotropica 18:307–318. https://doi.org/10.2307/2388574

Donati, G., & S. M. Borgognini-Tarli. 2006. From darkness to daylight: cathemeral activity in primates. Journal of Anthropological Sciences 84:7–32.

Erkert, H.G.1982. Ecological aspects of bat activity rhythms. Ecology of bats (T.H. Kunz, ed.). Springer, Massachusetts.

Erkert, H.G. 2000. Bats, flying nocturnal mammals. Activity patterns in small mammals (S. Halle & N. C. Stenseth, eds.). Springer Berlin, Heidelberg.

Fleming, T. H. 1985. Coexistence of five sympatric *Piper* (Piperaceae) species in a tropical dry forest. Ecology 66:688-700. https://doi.org/10.2307/1940530

Fleming, T. H. (ed.). 1988. The short-tailed fruit bat: a study in plant-animal interactions. University of Chicago Press, Chicago.

Fleming, T. H. 1991. The relationship between body size, diet, and habitat use in frugivorous bats, genus *Carollia* (Phyllostomidae). Journal of Mammalogy 72:493–501. https://doi.org/10.2307/1382132

Fleming, T. H., & E. R. Heithaus. 1986. Seasonal foraging behavior of the frugivorous bat *Carollia perspicillata*. Journal of Mammalogy 67:660-671. https://doi.org/10.2307/1381127

Gardner, A. L. (ed.). 2008. Mammals of South America, volume 1: marsupials, xenarthrans, shrews, and bats. University of Chicago Press, Chicago.

Gaynor, K. M., C. E. Hojnowski, N. H. Carter, & J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. Science. 360:1232–1235. https://doi.org/10.1126/science.aar712

Halle, S., & N. C. Stenseth. (Eds.). 2000. Activity Patterns in Small Mammals: An Ecological Approach. Springer Science & Business Media, Berlin.

Heithaus, E. R., & T. H. Fleming. 1978. Foraging movements of a frugivorous bat, *Carollia perspicillata* (Phyllostomatidae). Ecological Monographs 48:127–143. https://doi.org/10.2307/2937296

Heithaus, E. R., T. H. Fleming, & P. A. Opler. 1975. Foraging patterns and resource utilization in seven species of bats in a seasonal tropical forest. Ecology 56:841–854. https://doi.org/10.2307/1936295

Herbst, L. H. 1986. The role of nitrogen from fruit pulp in the nutrition of the frugivorous bat *Carollia perspicillata*. Biotropica 18:39–44. https://doi.org/10.2307/2388360

Holdridge, L. R. 1967. Life Zone Ecology. Tropical Science Center, San José.

Kemenesi, G., et al. 2015. Genetic characterization of a novel picornavirus detected in *Miniopterus schreibersii* bats. Journal of General Virology 96:815–821. https://doi.org/10.1099/jgv.0.000028

Kronfeld-Schor, N., & T. Dayan. 2003. Partitioning of time as an ecological resource. Annual Review of Ecology, Evolution, and Systematics 34:153–181. https://doi.org/10.1146/annurev.ecolsys.34.011802.132435

Kunz, T.H., C. Wemmer, & V. Hayssen. 1996. Sex, age and reproductive condition. Measuring and monitoring biological diversity: standard methods for mammals (D. E. Wilson, F. R. Cole, J. D. Nichols, R. Rudran & M. S. Foster, eds.). Smithsonian Institution Press, Washington D.C.

La Val, R. K. 1970. Banding returns and activity periods of some Costa Rican bats. The Southwestern Naturalist 15:1–10. https://doi.org/10.2307/3670196

Macarthur, R., & R. Levins. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101:377–385. http://dx.doi.org/10.1086/282505

Mancina, C. A., & I. Castro-Arellano. 2013. Unusual temporal niche overlap in a phytophagous bat ensemble of western Cuba. Journal of Tropical Ecology 29:511–521. https://www.jstor.org/stable/43831681

Marcelo-Peña, J. L., & C. Reynel. 2014. Patrones de diversidad y composición florística de parcelas de evaluación permanente en la selva central de Perú. Rodriguésia 65:35–47. https://doi.org/10.1590/S2175-78602014000100003

Marinho-Filho, J. S., & I. Sazima. 1989. Activity patterns of six Phyllostomid bat species in southeastern Brazil. Revista Brasileira de Biologia 49:777–782.

Mello, M. A., E. K. Kalko, & W. R. Silva. 2013. Effects of moonlight on the capturability of frugivorous phyllostomid bats (Chiroptera: Phyllostomidae) at different time scales. Zoologia (Curitiba) 30:397–402. https://doi.org/10.1590/S1984-46702013000400005

Mello, M. A., G. M. Schittini, P. Selig, & H. G. Bergallo. 2004. A test of the effects of climate and fruiting of *Piper* species (piperaceae) on reproductive patterns of the bat *Carollia perspicillata* (Phyllostomidae). Acta Chiropterologica 6:309–318. https://doi.org/10.3161/001.006.0209

Miller, R. S. 1967. Pattern and process in competition. Advances in Ecological Research 4:1–74. https://doi.org/10.1016/S0065-2504(08)60319-0

Mistlberger, R. E., & M. C. Antle. 2011. Entrainment of circadian clocks in mammals by arousaland food. Essays in Biochemistry 49:119–136. https://doi.org/10.1042/bse0490119

Montaño-Centellas, F., et al. 2015. Community and species–level responses of phyllostomid bats to a disturbance gradient in the tropical Andes. Acta Oecologica 62:10–17. https://doi.org/10.1016/j.actao.2014.11.002

Moratelli, R., & A.L. Peracchi. 2007. Morcegos (Mammalia, Chiroptera) do Parque Nacional da Serra dos Órgãos. Ciência e Conservação na Serra dos Órgãos (C. Cronemberger & E. B. Viveiros de Castro, eds.). Instituto Chico Mendes para la Conservación de la Biodiversidad, Brasilia.

Ortêncio-Filho, H., N. R. Reis, & C. V. Minte-Vera. 2010. Time and seasonal patterns of activity of phyllostomid in fragments of a stational semidecidual forest from the Upper Paraná River, Southern Brazil. Brazilian Journal of Biology 70:937–945. https://doi.org/10.1590/S1519-69842010000500004

Pacheco, V., & S. Solari. 1997. Manual de los murciélagos peruanos con énfasis en las especies hematófagas. Organización Panamericana de la salud, Lima.

Pedro, W. A., & V. A. Taddei. 2002. Temporal distribution of five bat species (Chiroptera, Phyllostomidae) from Panga Reserve, south-eastern Brazil. Revista Brasileira de Zoologia 19:951–954. https://doi.org/10.1590/S0101-81752002000300033

Pedrozo, A. 2014. Os morcegos frugívoros *Carollia perspicillata* e *Sturnira lilium* apresentam distribuição de atividade similar durante a noite? Uma análise local e regional. Dissertação de Mestrado, Universidade Federal Rural do Rio de Janeiro. Rio de Janeiro, Brazil.

Pellón, J. J., J. Rivero, M. Williams, & M. Flores. 2021. Trophic relationships within the genus *Carollia* (Chiroptera, Phyllostomidae) in a premontane forest of central Peru. Journal of Mammalogy 102:195–203. https://doi.org/10.1093/jmammal/gyaa141

Pereira, E. M., L. F. Junior, A. C. Menezes, & D. M. C. Santos. 2018. Horário de atividades de três espécies de morcegos da RPPN Fazenda Bom Retiro, Casimiro de Abreu, RJ. Revista Ciência Atual 11:2–15.

Pianka, E. R. 1973. The structure of lizard communities. Annual Review of Ecology and Systematics 4:53–74. https://www.jstor.org/stable/2096804

Presley, S. J., M. R. Willig, I. Castro-Arellano, & S. C. Weaver. 2009. Effects of habitat conversion on temporal activity patterns of phyllostomid bats in lowland Amazonian rain forest. Journal of Mammalogy 90:210–221. https://doi.org/10.1644/08-MAMM-A-089.1

Racey, P.A. 2009. Reproductive assessment of bats. Ecological and behavioural methods in the study of bats (T. H. Kunz & S. Parsons, eds.). The Johns Hopkins University Press, Baltimore.

Rivera-Villanueva, A. N. 2021. Patrones de actividad de *Leptonycteris yerbabuenae* en relación a factores intrínsecos y extrínsecos. Tesis de Maestría. Centro Interdisciplinario de Investigación para el

Desarrollo Integral Regional Unidad Durango. Durango, México.

Rivero-Monteagudo, J. A., J. J. Pellón, & M. Williams. 2021. Environmental seasonality explains reproductive timing of short-tailed fruit bats in a premontane forest of central Peru. Acta Chiropterologica 23:59–69. https://doi.org/10.3161/15081109ACC2021.23.1.005

Saldaña-Vázquez, R. A., & J.E. Schondube. 2013. Food intake changes in relation to food quality in the Neotropical frugivorous bat *Sturnira ludovici*. Acta Chiropterologica 15: 69–75. https://doi.org/10.3161/150811013X667867

Sampedro, A. C., et al. 2007. Nuevos registros de especies de murciélagos para el departamento de Sucre y algunos datos sobre su ecología en esta región colombiana. Caldasia 29:355–362.

Servicio Nacional de Meteorología e Hidrología del Perú (SENAMHI). 2019. Estación Satipo, Tipo Convencional-Meteorológica (2013–2018). Dirección de Redes de Observación y Datos. <https://www.senamhi.gob.pe/mapas/mapa-estaciones/_dat_esta_tipo.php? estaciones=000571>.

Sikes, R. S., W. L. Gannon, & the animal care and use committee of the American Society of Mammalogists. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 97:663–688. https://doi.org/10.1093/jmammal/gyw078

Stawski, C. 2012. Capture and care of northern long-eared bats (*Nyctophilus bifax*) and seasonal changes in insect abundance. Australian Mammalogy 34:245–250. https://doi.org/10.1071/AM11043

Stuhler, J.D., A.N. Kildow, & R.D. Stevens. 2019. Ecology of *Platyrrhinus lineatus* in Atlantic Forest of Paraguay: reproductive patterns, activity, seasonality, and morphometric variability. From field to laboratory: A memorial volume in honor of Robert J. Baker (R.D. Bradley, H. H. Genoways, D. J. Schmidly & L. C. Bradley, eds.). Special Publications of the Museum of Texas Tech University, Texas.

Thies, W., & E. K. Kalko. 2004. Phenology of Neotropical pepper plants (Piperaceae) and their association with their main dispersers, two short-tailed fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). Oikos 104:362–376. https://doi.org/10.1111/j.0030-1299.2004.12747.x

Thies, W., E. K. Kalko, & H. U. Schnitzler. 2006. Influence of environment and resource availability on activity patterns of *Carollia castanea* (Phyllostomidae) in Panama. Journal of Mammalogy 87:331–338. https://doi.org/10.1644/05-MAMM-A-161R1.1

Thieurmel, B., & A. Elmarharaoui. 2019. Suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. R package version 0.5.0. <https://github.com/datastorm-open/suncalc>.

Thomson, B. G. 2020. Social interactions, roost usage and notes on the breeding system of the chocolate wattled bat (*Chalinolobus morio*) in south-east Queensland, Australia. Australian Journal of Zoology 67:290–300. https://doi.org/10.1071/ZO20049

Vásquez-Parra, O. Y., F. J. García, & M. Machado. 2017. Actividad nocturna y uso del espacio vertical en algunas especies de murciélagos frugívoros (Chiroptera: Phyllostomidae) en Venezuela. Revista Biodiversidad Neotropical 7:258–268. https://doi.org/10.18636/bioneotropical.v7i4.689

Verde, R. S., R. C. Silva, & A. M. Calouro. 2018. Activity patterns of frugivorous Phyllostomid bats in an urban fragment in southwest Amazonia, Brazil. Série Zoologia 108:e2018016. https://doi.org/10.1590/1678-4766e2018016

Violle, C., D. R. Nemergut, Z. Pu, & L. Jiang. 2011. Phylogenetic limiting similarity and competitive exclusion. Ecology Letters 14:782–787. https://doi.org/10.1111/j.1461-0248.2011.01644.x

York, H. A., & M. Papes. 2007. Limiting similarity and species assemblages in the short-tailed fruit bats. Journal of Zoology 273:249–256. https://doi.org/10.1111/j.1469-7998.2007.00321.x

Zegarra, O. 2019. Diversidad y distribución estacional de los ensambles de quirópteros en el bosque secundario del Fundo Santa Teresa en Satipo, Perú. Tesis de Grado. Universidad Nacional Agraria La Molina. Lima, Perú.

Zeppelini, C. G., I. Jerônimo, K. M. C. Rego, M. P. A. Fracasso, & L. C. S. Lopez. 2017. Description of whole-night activity patterns for Neotropical bat species. Acta Chiropterologica 19:155–160. https://doi.org/10.3161/15081109ACC2017.19.1.012