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Volume 3, 2025 Journal of North American Bat Research No. 9

Journal of North American Bat Research

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Foraging Patterns of Orange Nectar Bats at a Panama Hummingbird Feeder

Mark Stanback[1,*], Julia Barnfield[1,2], and Eleanor Diamant[3,4]

Abstract - We observed foraging *Lonchophylla robusta* (Orange Nectar Bats) at a hummingbird feeder in Panama for at least 1 night per week for over a year. Our goal was to understand better the factors that influence the foraging behavior of nectar bats in the Neotropics. We addressed effects of season, time of night, and phase of the moon on bat foraging behavior. Time of night had a significant effect, with more feeding visits during the morning. Although season had a minor effect, we found no effect of moon phase on the number of bat visits to the feeder. Finally, we found that bats decreased their foraging behavior when a *Didelphis marsupialis* (Common Opossum) was near the feeder.

Resumen - Observamos a *Lonchophylla robusta* (Murciélagos Nectarívoros Anaranjados) forrajeando en un bebedero de colibríes en Panamá por al menos una noche semanalmente durante un año. Nuestro objetivo fue mejorar el entendimiento de los factores que influyen el comportamiento de forrajeo de estos murciélagos nectarívoros en el Neotrópico. Investigamos los efectos de temporada (lluviosa/seca), hora (noche/madrugada), y la fase lunar en el comportamiento de forrajeo de estos mamíferos. Hallamos un efecto significativo entre la hora de forrajeo y la tasa de visitas, con un mayor número de visitas al bebedero durante las horas de la madrugada. Aunque la temporada tuvo un efecto menor en el forrajeo de estos murciélagos, no hubo diferencias en el número de visitas al bebedero dependiendo de la fase lunar. Finalmente, observamos que la actividad de forrajeo de los murciélagos disminuyó basado a la presencia de *Didelphis marsupialis* (Zarigüeya Común) cerca del bebedero.

Introduction

Bats constitute approximately half of all Neotropical mammals (Emmons and Feer 1990, Simmons 2005, Simmons and Cirranello 2024) and fill various ecological niches. Despite their importance for Neotropical biodiversity and ecological function, basic biological information is lacking for most species. Because bats are small, nocturnal, and extremely mobile, they can be challenging to study. Biologists' implementation of innovative technology (e.g. miniature sensors) has advanced our understanding of bat biology (Reher and Dausman 2021, Toledo et al. 2020), but these technologies are expensive and require substantial expertise to operate. Therefore, development of more affordable techniques for bat research is useful for increasing our understanding of bat biology.

Supplemental feeders offer such a pathway for improving our understanding of bat biology. Among ornithologists, monitoring of bird feeders is an increasingly popular technique for drawing inferences on bird biology because of their ubiquity, low cost, and ease of use (Bonter and Greig 2021). Studies of bird behavior at feeders have revealed insights on topics as diverse as physiology (Wilcoxen et al. 2015), community ecology

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Associate Editor: J. Angel Soto-Centeno, Rutgers University.

(Plummer et al. 2019), and neophobia (Stanback and Burke 2020). Feeders used by bats, particularly nectarivorous species, which make frequent use of hummingbird feeders (Fleming et al. 2021, Fleming 2023), offer similar insights for chiropterologists. Maguina and Muchhala (2017) found that the presence of hummingbird feeders did not affect the pollen loads of nectarivorous bats, nor the flower visitation rates and breeding success of a bat-pollinated plant (though bat abundance was greater near feeders).

The distribution, abundance, and activity of bat species is influenced by various factors, including the state of vegetation and the availability of roost sites (Bernard and Fenton 2002). For many Neotropical bats, the timing of activity presumably reflects not only the availability of their food resources (Rothenwohrer et al. 2011), but also the activity of their predators (Baker 1962, Lima and O'Keefe 2013) and of competing bats (Delaval et al. 2005). Monitoring of hummingbird feeders visited by nectarivorous bats may elucidate the role of these factors in shaping bat activity.

We observed visits by *Lonchophylla robusta* Miller (Orange Nectar Bats) to a hummingbird feeder in central Panama. After determining whether a 10-min watch was sufficient to capture meaningful variation in feeding visits, we considered 4 factors that potentially affect the rate of observed feeding visits by this species: time of year, time of night, phase of the moon, and the presence of a potential predator. Although these factors were not mutually exclusive, we did predict that the observed feeding rate would be lower when the moon was brighter and when a potential predator was present.

Field-site description

We made our observations through a webcam operated by the Cornell Lab of Ornithology and located at the Canopy Lodge, near El Valle de Anton, in Cocle Province, Panama (8°31'31.4034"N, -80°2'20.58"W; https://www.allaboutbirds.org/cams/panama-fruit-feeders/). El Valle de Anton is a village with <8,000 residents. The lodge was located in the Cerro Gaital at an elevation of approximately 730 m. A camera, platform, and feeder were located 13 m from the main lodge building, with the next closest buildings 1600 m north and south of the lodge. Although the main lodge had electric lights, the platform which the camera faces was not lit at night. The platform (1 m x 0.5 m), on which fruit is provided for birds, was 1.5 m off the ground and located in an area of vegetation (Fig. 1). Although 5 different nectar-feeding bats live in Central America, the only bat that has been observed at the hummingbird feeder was *Lonchophylla robusta* (J. Slifkin, Canopy Lodge, El Valle de Anton, Panama, pers. comm.). In fact, *Carollia perspicillata* (Linnaeus) (Seba's Short-tailed Bat) has only been observed visiting the web cam platform once (to eat fruit).

Methods

A glass hummingbird feeder (Big Gulp, More Birds, Lancaster, PA) with 7 ports hung 0.5 m above the platform. This feeder was refilled regularly and was never completely drained in a single night. Although the bottle somewhat obscured our view of bats feeding from the ports on the far side of the feeder, such visits were nevertheless easily tallied because of the hovering of feeding bats. We defined a feeding visit as a bat hovering over a feeding port for a long enough period of time to feed (about 1 sec). We did not count as feeding visits cases during which bats simply flew close to the feeder. From 6 December 2020 through 16 February 2022, we counted the number of feeding visits made by Orange Nectar Bats at the feeder. Specifically, on observation nights (at least 1 night per week), we tallied feeding visits for 10 min at the top of each hour. To determine whether a 10-min watch was sufficient to capture meaningful variation in feeding visits, we first compared 2 consecutive 5-min periods. We hypothesized that if the number of feeding visits did not differ significantly between 2 adjacent 5-min sample periods, we could assume that the entire 10-min sample period was adequate to capture meaningful behavioral activity.

Because the webcam allows viewers to scroll back for 12 h, we could make our observations without having to view the webcam live. On nights when we made our observations, we watched for a total of 100 min. Generally, we watched from 20:00 to 20:10, then 21:00 to 21:10, then 22:00 to 22:10, etc. Our last observation session ran from 05:00 to 05:10. Although bats were observed at the feeder by 19:00 during months with long nights, we chose not to include those data because, during months with short nights, it was not necessarily fully dark at 19:00. Because it was difficult to assess the degree to which it was raining during an observation period, we did not try to quantify rainfall, and similarly, we ignored the effects of wind.

We assessed the influence of 4 factors on bat feeding activity: time of year, time of night, phase of the moon, and the presence of a potential predator. The Neotropics are characterized by alternating wet and dry seasons that influence vegetation phenology and, therefore, resource availability for nectarivorous bats. In Panama, the period between 16 April and 15 December is considered the "wet" season, while the "dry" season runs from 16 December through 15 April. Note the differing lengths of seasons.

To address whether bat foraging differed across the time of night, we divided each night in half. We designated the period from 20:00 to 00:10 as "evening" and the period running from 01:00 to 05:10 as "morning". We did not account for seasonal changes in sunrise/sunset.

Another potential bias in the foraging activities of bats is "lunar phobia", or moonlight avoidance. Lunar-phobic bats tend to be more active under dark nighttime conditions compared to brighter conditions (Lang et al. 2005). Lunar phobia is often described as a type of anti-predation behavior in which individuals minimize their exposure to predators during periods of greater susceptibility. Because it is difficult to quantify the brightness of the moon

Figure 1. Screenshot from the live feed we used for data collection, showing the platform, feeder, and an Orange Nectar Bat (circled in red). Note the large piece of wood on the platform.

through the webcam alone, we used the phases of the moon to indicate lunar brightness at any given time. To estimate the brightness and phase of the moon at the top of each hour, we used the website timeanddate.com. Values for moon phase ranged from 0 (no moon) to 1 (full moon). Although we were unable to control for clouds, precipitation, or vegetation when assessing the importance of moonlight, we believe that the phase of the moon is an adequate proxy for the purposes of our study. We do know, based on footage from the live feed taken during the day, that the site is somewhat, though not totally, shaded by vegetation.

To test the effects of seasonality, time of night, and moon phase on foraging, we first conducted a preliminary regression tree analysis with the package *rpart* (Therneau et al. 2013) in R v.4.3.1 (R Core Team 2023). We included season, time of night, and moon phase as independent variables. This regression tree suggested that the effects of moon phase and season interact such that moon intensity is relevant only during the dry season. Next, we fit a generalized linear model (GLM). Our dependent variable was the number of visits, and our fixed effects were moon phase, season, and the interaction between moon phase and season. Count data were gamma distributed, and thus, the model included a gamma distribution link function. Likelihood-ratio χ^2 statistics were calculated with the package *car* (Fox and Weisberg 2019).

Finally, we addressed the threat of predation more directly by assessing whether Orange Nectar Bats reduce their visitation when a potential predator—*Didelphis marsupialis* Linnaeus (Common Opossum)—is on the platform under the hummingbird feeder. The Common Opossum and *Philander opossum* (Linnaeus) (Gray Four-eyed Opossum), both native to Central and South America, have been observed feeding on bats, though in both cases the bats were caught in nets or other types of live traps (Fleming 1972). Nevertheless, these accounts support the idea that bats should view mid-sized mammals as potential predators and, therefore, reduce their foraging when these perceived threats are present.

Because the platform was supplied with fruit, Common Opossums often visited during the night. When an opossum appeared on the platform during one of our 10-min observation periods, we shifted our standard data collection to the 10 min immediately prior to the appearance of the opossum. To quantify the effect of a visiting opossum on nectar bat foraging, we first counted the number of bat visits to the feeder during the period that the opossum was present on the platform. If the opossum was present for <1 min, we omitted the data and did not perform a control watch prior to the appearance of the opossum. If the opossum was present for >10 min, we ended our data collection after 10 min and conducted a control observation (lasting exactly 10 min) immediately prior to the arrival of the opossum. For opossum visits lasting between 1 and 10 min, we performed a control watch of equal length immediately prior to the arrival of the opossum. We omitted incidents during which no bat visited during the opossum visit or the control period for the visit. We then used a paired *t*-test to determine whether the presence of an opossum on the platform affected the number of feeding visits of nectar bats (comparing the number of feeding visits during the control period and the period during which an opossum was present). We restricted our analyses to cases in which at least 1 feeding visit by a bat occurred during either the opossum visit or the control interval. All means are reported ± *SD*.

Results

The number of feeding visits during our 10-min observation periods ranged from 0 to 200. There was no difference in number of visits between the first and second 5-min interval within each 10-min observation period (mean difference = -0.2 ± 12.6, n = 1450 pairs, paired t_{1449} = -0.62, P = 0.54). This suggests that a 5-min interval provides no less information than a 10-min period, and that our 10-min intervals were sufficiently long.

The best-supported GLM considered season, time of night, moon phase, and the interaction between season and moon phase (Table 1). Orange Nectar Bats visited the feeder significantly more often during the dry season (mean = 24.7 ± 24.2 feeding visits per 10-min, n = 1180) than during the wet season (mean = 17.1 ± 26.8 visits per 10-min, n = 630; χ_1^2 = 34.3, P < 0.0001). Additionally, we found a significant effect of time of night on foraging activity (χ_1^2 = 7.03, P = 0.008). There were more feeding visits during the morning sessions (mean = 23.9 ± 25.4, n = 905) than evening sessions (mean = 20.3 ± 25.2, n = 905).

If Orange Nectar Bats timed their foraging bouts to avoid unnecessary exposure to moonlight, fewer visits to the feeder should have occurred when moonlight was especially bright (i.e., when the moon was close to full). While initial model results showed a significant effect of moon intensity on foraging rate (Table 1), this variable did not have a significant likelihood ratio χ^2 (n = 1742, χ_1^2 = 1.34, P = 0.25). However, there was a significant interaction between moon phase and season (χ_1^2 = 56.50, P < 0.0001). Specifically, there was no effect of moon brightness on foraging during the dry season; during the wet season, higher moon brightness was associated with more foraging.

Visiting opossums generally spent their time extracting citrus from rinds on the platform or eating from bananas hung above the platform (about 0.5 m from the hummingbird feeder). We never observed an opossum attempting to capture a bat. We observed a total of 261 opossum visits in which we could compare bat feeding visits in the presence and absence of an opossum. Because opossum visits tended to last <10 min, for a bat to avoid the hummingbird feeder entirely during the presence of an opossum does not require that the bat avoid the feeder for long periods of time.

Bats reduced their feeding rate significantly in the presence of opossums (paired t_{260} = 8.19, P < 0.0001). With an opossum present, mean number of feeding visits per minute was 0.27 ± 0.35 (n = 261). The rate in the absence of an opossum was 0.43 ± 0.46 (n = 261) feedings per minute.

Table 1. Output of generalized linear mixed model, including parameter estimates, null and residual deviance, and associated degrees of freedom. Likelihood ratios of each variable are presented in the text.

Response variable: Number of feeding visits per interval

Predictors	*Estimates*	*95% CI*	*P*
(Intercept)	1.04	1.03 – 1.04	< 0.001
Season	1.04	1.03 – 1.05	< 0.001
Moon phase	1.01	1.00 – 1.02	0.015
Time	1.01	1.00 – 1.01	0.008
Season x moon phase	0.94	0.93 – 0.96	< 0.001
Number of observations	1810		
Null deviance	19392 on 1809 *df*		
Residual deviance	19240 on 1805 *df*		
AIC	3163.4		

Discussion

Orange Nectar Bats used the feeder at all times of the year, but with slightly more frequency during the wet season. We found the greater use of the feeder during the wet season somewhat unexpected because rainfall reduces bat activity in nearby Costa Rica (LaVal and Lawton 2021) and because floral resources are generally more available during the wet seasons (Cascante-Marin et al. 2017). Because Orange Nectar Bats presumably reproduce during the dry season (Tschapka 2019), it is unclear how the observed pattern of activity reflects the energetic burdens of pregnancy and lactation.

We recorded a greater number of feeding visits during the morning (between 0100 and 0510) than during the evening (between 2000 and 0010). Unfortunately, we cannot say how the greater number of visits in the morning was related to the availability of natural foods (Deleval et al. 2005, Marinho-Filho and Sazima 1989). Because nectarivorous bats often supplement their diet with insects (Gardner 1977, Herrera et al. 2001), pinpointing the exact cause of any deviation from uniformity of visitation at a hummingbird feeder is difficult.

Avoiding predation is presumably paramount for long-lived species, such as Orange Nectar Bats. Because of their ability to fly, typical nocturnal habits, and choice of safe places to roost and hibernate, bats generally face low rates of extrinsic mortality, resulting in unusually long lifespans compared to similar-sized mammals (Moore 1975, Wilkinson and South 2002). If Orange Nectar Bats avoid unnecessary activity during periods when moonlight makes them more conspicuous (lunar phobia) (Lang et al. 2005), we would expect more visits to the feeder during periods with less moonlight. The fact that we did not observe this suggests a lack of lunar phobia, and that visits to the feeder represented overall activity patterns. Of course, bats vary in the degree to which they are affected by moonlight (Prugh and Golden 2014, Vasquez et al. 2020). Some bats, particularly swarming European species, do not to exhibit lunar phobia (Apoznanski et al. 2024). It is unclear how a nectarivorous diet or tropical habitat influence the observed activity patterns of Orange Nectar Bats. Similarly, it is unclear what role small body size (and thus lower predation frequency) plays for Orange Nectar Bats (but see Hopkins and Hopkins 1982).

Our most direct consideration of predation results from our observations of bat foraging in the presence of a potential mammalian predator. We observed fewer visits of Orange Nectar Bats when a Common Opossum was on the platform below the feeder. While data on nocturnal predation of bats by mammals are limited, there have been reports of *Procyon lotor* Linnaeus (Raccoons) and *Felis cattus* Linnaeus (Domestic Cats) grabbing bats out of the air (Lima and O'Keefe 2013). The fact that foraging activity was curtailed when a potential predator was present was, therefore, not particularly surprising. As mentioned above, avoiding predation is important for long-lived animals, such as bats. Indeed, nectarivorous bats tend to make short, repeated trips to feed instead of remaining at a single foraging site for an extended period of time to reduce vulnerability to predators (Hopkins and Hopkins 1982).

Unfortunately, the literature on predator perception and behavioral responses by bats is limited. A study on *Eptesicus fuscus* (Palisot de Beauvois) (Big Brown Bats) showed that these animals do not alter their behavior in response to the chemical cues of two known predators, *Pantherophis obsoletus* (Say) (Black Rat Snakes) and Raccoons (Boyles and Storm 2007). Research also shows that some species of bats, including the Big Brown Bat, do not alter foraging activity when presented with owl calls (Janos and Root, 2014). A similar study was conducted which tested how frugivorous phyllostomid bats altered their foraging behaviors in response to various predator stimuli, including auditory and visual cues (Breviglieri et al. 2013). While recordings of the calls of *Tyto alba* (Scopoli) (Barn Owl), a known predator of bats, had no significant impact on bat behavior, the presence of a stuffed model predator did decrease the foraging frequency of these frugivorous bats (Breviglieri et al. 2013). These studies and others suggest that the physical presence of predators is a substantial deterrent for bats during foraging (Petrželková and Zukal 2003).

Although our results demonstrate that Orange Nectar Bats reduce their foraging around a potential mammalian predator, we did not test the bats with other objects (either living or non-living). Consequently, our ability to generalize is limited. While the mechanisms of predator perception and avoidance in bats is still not fully understood, our study builds on the existing evidence that bats alter their behavior and will reduce foraging in response to the presence of a perceived predator.

Our study of bat foraging is obviously limited by our focus on a single hummingbird feeder. However, because we made observations throughout the night for over a year, we feel that we were able to draw several conclusions about the activity and foraging patterns of free-living Orange Nectar Bats. As expected, we found that there are multiple variables involved in the feeding patterns of these creatures.

Acknowledgments

We thank Raul Arias de Para and Jonathan Slifkin of Canopy Lodge for facilitating our study. Matina Kalcounis-Reuppell and Jesse Alston provided needed expertise on bats. The Cornell Laboratory of Ornithology maintains the webcam at Canopy Lodge. We also thank Sydney Kellgren for assistance with the Spanish translation. The following Davidson College students assisted in data collection: Tiffany Haydt, Faith Kipnis, Tifani Panek, Max Rollfinke. Earlier versions of the manuscript were improved by Jesse Alston, an anonymous reviewer, and the editor of this journal.

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