Behavioral Ecology, 2025, **36**(5), araf095
https://doi.org/10.1093/beheco/araf095
Advance access publication 18 August 2025
Original Article

The influence of hunger and sex on the foraging decisions of frugivorous bats

Briana A. Sealey[1,2,*], Logan S. James[1,2], Michael J. Ryan[1,2], Rachel A. Page[1]

[1]Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Panamá
[2]Department of Integrative Biology, University of Texas, Austin, TX 78712, United States

*Corresponding author: Email: basealey@utexas.edu

An animal's internal state can shift its behavior. Animals that would typically avoid dangerous foraging conditions may choose to forego safety when food is restricted. Furthermore, physiological demands such as gravidness can drive sex differences in foraging behavior among individuals of the same species. In bats, moonlight can impose risk: some bat species decrease or completely avoid foraging on full moon nights when visually oriented predators are most active. In this study, we tested the hypothesis that hunger increases risky foraging behavior. Previous work with the Jamaican fruit bat, *Artibeus jamaicensis*, demonstrated that this species shifts its foraging behavior in moonlight by increasing latency to land. In this experiment, bats trained to feed from a food platform were then observed landing in conditions of satiation and food-restriction, with and without the presence of artificial full moonlight. As predicted, we found that bats forage significantly more quickly when food-restricted than when satiated. We found that bats showed a nonsignificant trend to avoid moonlight via increased latencies to land on the food platform. Males—but not females—were significantly slower to land in the presence of moonlight when satiated but not when food-restricted. Our results demonstrate that internal state influences foraging decisions, with individuals landing faster when hungry than when satiated, but that the increased foraging risks associated with moonlight affect male bats more than females.

Keywords: food-restriction; foraging; frugivores; lunar phobia; sex differences.

Introduction

Optimal foraging theory predicts the strategies organisms use to maximize energy intake while minimizing costs associated with obtaining food (Stephens and Krebs 1986). Foraging theory can predict various types of tradeoffs (eg, in tadpoles (Werner 1992; Anholt and Werner 1995), and birds (Lima 1985)) and can shed light on decision-making processes involved in acquiring resources (eg, in snakes (Lillywhite and Brischoux 2012), lizards (De Meester et al. 2018), and bats (Hemingway et al. 2017; Geipel et al. 2019)). One important prediction of optimal foraging theory is that foragers should adjust their behavior in response to predation risks associated with acquiring food, which has been demonstrated in various species and contexts (Elangovan and Marimuthu 2001; Welbergen 2006; Smith et al. 2017; Sealey et al. 2024). Risk assessment by prey can help determine optimal activity times to minimize vulnerability to predators (Tuttle and Ryan 1982; Vásquez 1994; Thapa et al. 2024). Optimal foraging theory often assumes animals are in their best physical state when assessing danger, however, predictions change when we consider variation in the internal state of foragers, such as when food-restricted.

In times of heightened hunger, individuals often become more risk-prone and may prioritize accessible food sources they can exploit quickly (Polis 1988; Pettersson and Brönmark 1993; Horat and Semlitsch 1994). Conversely, when satiated, foragers are more likely to exhibit selective feeding (Barnett et al. 2007), opting for higher-quality resources that may require more effort to obtain but offer greater energy rewards (Brodersen et al. 2008). Hunger state can modulate an animal's perception of the environment (Persons 1999), affecting its willingness to explore new areas (Balaban-Feld et al. 2019) and can facilitate tradeoffs between predatory risk and energy gain (Milinski and Heller 1978; Godin and Crossman 1994; Morton and Chan 1999; Whitham and Mathis 2000). The influence of hunger state on food decisions underscores the plasticity of foraging strategies, demonstrating how animals respond flexibly to changing metabolic needs and environmental conditions.

Fluctuations in the environment, such as the cycles of the moon, are known to affect foraging behavior in many nocturnal prey animals (Daly et al. 1992; Skutelsky 1996; Griffin et al. 2005; Kotler et al. 2010), presumably in response to visually oriented predators that increase foraging activity in waxing moonlight (Clarke 1983; Lillywhite and Brischoux 2012; Chen et al. 2024). Thus, an increase in moonlight is an indirect cue for prey animals regarding foraging risk. To account for waxing moonlight, prey animals can increase foraging during moonless nights or adjust their foraging behavior to be more cautious (Prugh and Golden 2014). Many studies have observed the interaction of prey and predator animals across moon cycles. None, however, have directly tested how the physiological state of prey may impact their assessments of indirect environmental contexts that suggest risky foraging conditions.

Bats are a model for testing for moonlight avoidance because most species forage exclusively at night and are consumed by diverse array of predators, including visually orienting birds

Received 18 March 2025; revised 13 July 2025; editorial decision 6 August 2025; accepted 17 August 2025.

(Ancillotto et al. 2013; Nyffeler and Knörnschild 2013; Mikula 2015; Szczygieł and Page 2020; Mikula et al. 2024). Evidence of moonlight avoidance is mixed, with species variation in avoidance behaviors (Lima and O'Keefe 2013). Jamaican fruit bats (*Artibeus jamaicensis*) have been shown to avoid full moonlight both when foraging over a 6-month period (Morrison 1978a) as well as during experimental trials in a flight cage (Sealey et al. 2024). Jamaican fruit bats are prey to many predators, including those that are visually oriented (Ortega and Castro-Arellano 2001) and may use the moonlight to hunt (Owings and Handa 1975; Clarke 1983).

In this study, we test the hypothesis that hunger increases risky foraging behavior in the Jamaican fruit bat. Previously, it was found that Jamaican fruit bats are slower to land on a food platform in artificial moonlight (Sealey et al. 2024) and exhibit "lunar phobia" (Morrison 1978a), or the avoidance of moonlight, possibly to evade nocturnal predators. Here we asked whether the aversion to light can be overcome when hungry. We predicted that bats would be more willing to forage in risky contexts when food-restricted than when satiated. Through this investigation, we aimed to determine how the animal's state of hunger influences its foraging decisions, and what implications these decisions might have in the natural world.

Ethical note

Procedures related to animal capture and handling were approved by the Panama Ministry of the Environment (permit numbers SE/AP-22-19 and ARG-278-2022) and approved with authorized protocols from the Animal Care and Use Committee of the Smithsonian Tropical Research Institute (ACUC-2020-0113-2023) and the University of Texas at Austin (AUP-2021-00063).

Materials and Methods

We captured bats in mist nets in Soberanía National Park near Gamboa, Panama between March and May in 2022. Each capture night, we used three to four 6 or 12 meter nets along a trail. We checked nets every 10–15 minutes to minimize time bats spent in the nets. All bats captured were immediately weighed, given unique haircuts (1 × 1 cm) for individual identification, and placed into soft cloth bags to minimize exposure to sound and light. After capture, bats were released into an outdoor flight cage (4.85 × 4.90 × 2.43 m) through a small, sealable hole (~0.15 m in diameter) and offered at least 6 hours to forage freely for ad libitum water and pieces of banana from a platform (41 × 2 × 29 cm) 40 cm off the ground. Bat mass at the time of capture, or "capture mass," was the baseline value we used to measure bat feeding habits. On feeding nights, all bats were palpated for satiation and weighed to ensure each individual was equal to or greater than its capture mass. The capture mass of bats used in the experiment ranged from 36 to 55 grams (mean ± SD = 45.9 ± 3.5 g) and did not significantly differ between male and female bats (t-test: $P = 0.586$; males: 46.3 ± 2.5 g; females: 45.3 ± 4.6 g). All experiments were completed between 18:00 and 01:00 h and recorded with Sony DCR-SR45 Handycam camcorders supplemented with CMVision IR130-850NM lights. To simulate artificial moonlight, we used a LED light with settings identical to previous studies that mimic the measured light level in the forest during a full moon (~0.089 lux; Cummings et al. 2008; Taylor et al. 2008; Cronin et al. 2019; Sealey et al. 2024).

Bats assigned to Order 1 (Fig. 1) were fed ad libitum on the second night after capture for at least 6 h in darkness, without moonlight. Bats in Order 1 were tested for artificial moonlight aversion on the third night, as follows: (1) the first trial was without artificial moonlight, in which bats were released into the flight cage and allowed to forage for pieces of banana on a platform ("control" trial); (2, 3) in the second and third trials, bats foraged for food under artificial moonlight; (4) in the fourth trial, bats foraged without artificial moonlight ("footprint" trial). Observations from this fourth, footprint trial address whether exposure to a risky environment cue can influence prey behavior even if the cue is removed. Thus, the control and footprint trial only differ in their order in that one precedes and the other follows the moonlit trials.

Each trial ended after bats landed on the platform for a piece of banana. After landing on the platform, bats were given 3 min to feed before being captured and held in a smaller holding cage (69 × 71 × 202 cm) while other bats were tested. If bats made no decision after 20 min, the trial was ended. A bat that made no decision for 3 consecutive trials was removed from further testing that night and fed until it reached capture mass. On the fourth night, bats were not tested and not fed. On the fifth night, bats were tested for light aversion following the same protocol as on the third night. After all testing was completed, bats foraged for banana for 1 h to regain capture mass and then were released at the point of capture.

To counter-balance order effects of hunger, Order 2 bats were not fed the second night. On the third night, bats were tested for light aversion following the same protocol as bats in Order 1. On the fourth night, bats were fed ad libitum with no testing. On the fifth night, bats were again tested for light aversion. As with Order 1, after all experiments were completed, bats foraged for banana for 1 h before release at the point of capture. For both groups of bats, the only time bats were below their capture mass was on the one night they were not fed, and on the night immediately following, until their first feeding trial. All bats were closely monitored for weight loss throughout the experiment and were released only after they had regained or surpassed their capture mass.

All statistical analyses were completed in R Program 4.3.1. We measured two parameters of antipredator behavior: whether the bats flew to the platform (binary variable: land = 1 or did not land = 0) and latency to land on the platform (in seconds). We cube-root transformed latency to improve normality. Our primary objective was to determine whether internal state ("satiated" or "food-restricted"), external stimulus ("full moon" or "control") and the interaction between internal state and stimulus impacted our dependent variables of bat behavior. Therefore, we ran general linear mix-effects models, where whether bats flew or not was a binary response variable with a binomial error family (library lme4) (Kuznetsova et al. 2017). The significance of effects in these models was determined using Type III Wald χ^2 tests (library car). We then ran full factorial mixed-effect models with latency to land (cube root transformed) as the dependent variable, internal state, external stimulus, and their interaction as independent variables, and bat ID as a random effect (library lme4) (Kuznetsova et al. 2017). The significance of effects in these models was determined using Type III analysis of variance (ANOVA) with Satterthwaite's method (library lmerTest). We additionally ran analyses of the raw latency to land values using generalized linear mixed-effects models with a Poisson error family. However, these models appeared to over-fit the data and overall provided outputs indicating much stronger effects. To ensure our conclusions are robust, we report outputs from the transformed data (but see uploaded data and code for all results), and we note that all our conclusions are supported by both sets of analyses.

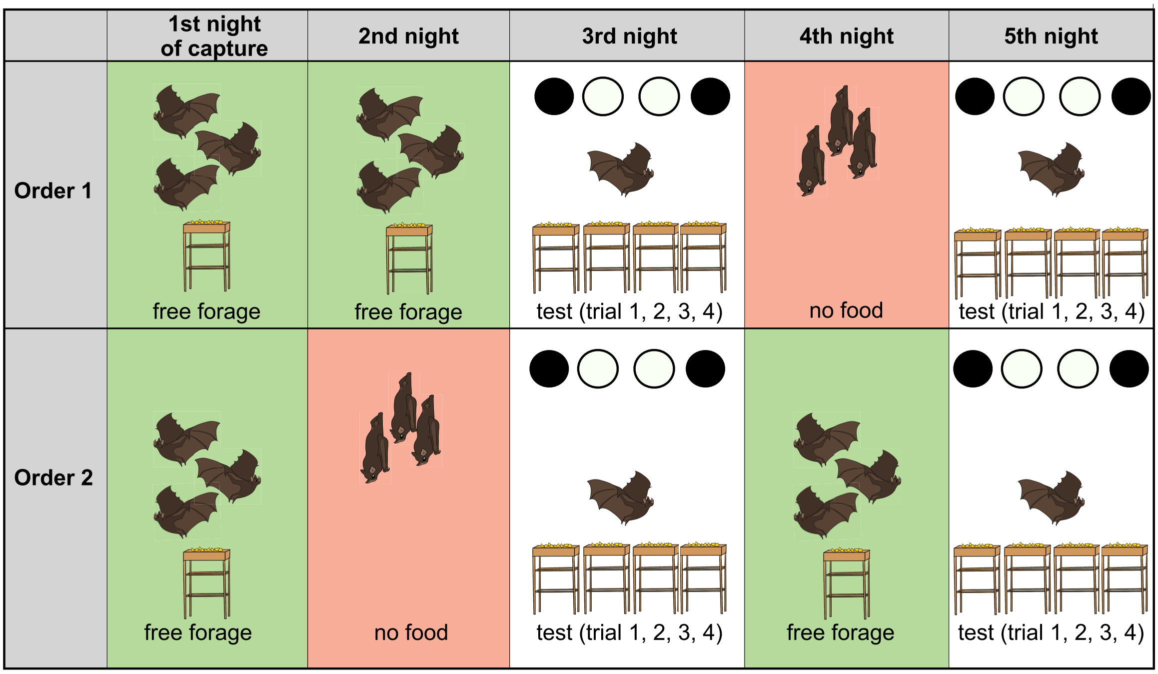

Fig. 1. Ordering schema to avoid the order effect of food-restriction. On "free forage" nights, bats fed ad libitum in their capture cohort and were not tested. On "test" nights, bats fed individually during four trials within a night: Trial 1: control (darkness, black circles); Trial 2: artificial moonlight (white circles); Trial 3: artificial moonlight; Trial 4: control. Afterwards, bats fed until they were at their capture mass. On "no food" nights, bats were kept in the holding cage with ad libitum water and not fed.

Finally, while not directly related to our primary hypotheses, we also conducted follow-up analyses to ask whether sex or capture mass influenced behavioral responses. For these, we included sex or mass as the sole independent variable or as an additional independent variable in full-factorial models with our main effects (internal state and external stimulus). For our generalized linear mixed model testing for an effect of sex on whether the bats landed, our model failed due to unbalanced data (female bats always landed), thus we employed the BOBYQA optimizer to ensure convergence. We note that, while we carefully monitored the mass of bats at the end of each night to ensure the bats' health, we did not weigh the bats prior to each test to avoid potential stress and its influence on behavior. Therefore, we were only able to test for the effect of capture mass on behavior.

Results

Of the 20 bats that were captured for this experiment, 8 bats were tested in Order 1 (3 females and 5 males) and 10 bats in Order 2 (4 females and 6 males). Two bats were removed from analyses because they did not land in experimental trials (both females). Each bat was tested in 8 trials (4 trials per night over 2 nights of testing) for a total of 144 trials in our dataset. Satiated bats landed on the platform in 89% of trials, with an average latency to land of 383 ± 402 s (mean ± SD). We observed considerable variation in latency to land for satiated bats, with 5 s as the shortest latency, and 19 min as the longest. When food-restricted, bats landed on the platform in 99% of trials, and the average latency to land was 87 ± 178 s, with the fastest bat landing within 1 s and the slowest at ~600 s.

Our primary objective was to test whether the external stimulus (artificial moonlight) and internal state (food-restriction) independently or interactively affect bats' decision-making regarding foraging. The model to test for an interaction effect of internal state and stimulus on whether bats landed in the experiment was inaccurate because most bats landed in most trials, leading to missing values in the variance-covariance matrix (interaction effect: $\chi^2_1 = 0.0$, $P = 1.0$). Therefore, we removed the interaction term from the model and found a significant main effect of internal state, with food-restricted bats significantly more likely to land than satiated bats ($\chi^2_1 = 6.0$, $P = 0.0140$). There was no significant effect of stimulus on the decision to land ($\chi^2_1 = 2.0$, $P = 0.1549$). In follow-up analyses, we found no significant effect of sex on the decision to land ($\chi^2_1 = 0.0$, $P = 0.9528$; female bats always landed, and only 4 male bats did not land across 9 trials), nor a significant effect of capture mass on the decision to land ($\chi^2_1 = 0.0$, $P = 0.8825$).

We then tested whether stimulus, internal state, and/or their interaction influenced bats' latency to land on the platform. We found that latency to land for food-restricted bats was significantly lower for satiated bats ($F_{1,123} = 82.8$, $P < 0.0001$). We found a non-significant trend for an effect of stimulus ($F_{1,123} = 3.0$, $P = 0.0838$), where bats took longer to land on the platform in moonlight treatments, and we found no interaction effect ($F_{1,123} = 0.70$, $P = 0.4049$). In a model comparing the control condition (satiated, no moonlight) to other possible conditions, we found that both food-restricted conditions were significantly different from control ($P < 0.0001$ for both) and we found a nonsignificant trend for satiated bats in moonlight to take more time to land than control ($P = 0.0706$) (Fig. 2).

Finally, we evaluated whether sex influenced bats' foraging decisions. In a full factorial model with sex, internal state, and stimulus as independent factors, we observed significant interactions between sex and both internal state ($F_{1,120} = 4.7$, $P = 0.0313$) and stimulus ($F_{1,120} = 4.5$, $P = 0.0359$) (Fig. 3), and a trend of a main effect of sex on the latency to land ($F_{1,16} = 4.1$, $P = 0.0592$) where male bats were slower to land on the platform than females. Regarding treatment, post hoc Tukey's tests revealed male bats landed on the platform significantly slower in full moonlight than control treatments ($P = 0.0369$), and that male bats exhibited a nonsignificant trend for landing slower than female bats in full moonlight trials ($P = 0.0584$). For internal state, post hoc Tukey's tests confirmed our earlier main effects, with all satiated bats landing more slowly than food-restricted bats ($P < 0.0002$ for all). However, we also found a nonsignificant trend for a sex difference within satiated bats ($P = 0.0558$), with satiated female bats landing quicker than satiated male bats. We found little evidence that capture mass predicted bats' latencies to land (full-factorial model, $P > 0.09$ for all main effects and their interactions).

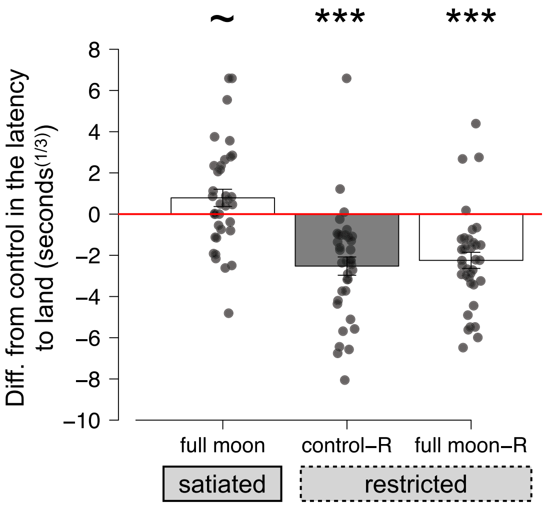

Fig. 2. Latency to land across treatments and internal state. Dots depict individual data points: we calculated the average landing time in the control condition (satiated, no moonlight; "control mean" for each bat), then subtracted each bat's response to a specific treatment from the bat's control mean. Satiated full moon treatment is to the left and food-restricted treatments to the right, as indicated by the labels below the x-axis. The red line depicts the mean of all control treatments; the error bars depict standard error. Asterisks (***) and tildes (~) are differences from the control treatment where $P < 0.0001$ and $P < 0.08$, respectively, as calculated from linear mixed-effects models.

Discussion

Optimal foraging theory can predict how animals behave under various foraging conditions (Pyke 2019). We know that environmental context, such as predator stimuli (Shogren et al. 2023) or interfering light (Barré et al. 2023), can influence foraging behavior and duration. Animals may also adjust their foraging strategies under specific conditions of physiological stress, such as gravidness (in snakes: Kojima and Mori 2015; seals: Shero et al. 2018) or food-restriction (fish: Wilson et al. 2019; deer: Oates et al. 2019). Tests for how these variables may influence foraging choices can help us understand how animals make decisions under conflicting environmental and internal conditions.

We investigated how perceived predation risk interacts with hunger state to affect foraging decisions in the frugivorous bat, *A. jamaicensis*. While several studies show the importance of considering physiological state when explaining why animals make certain food choices (Anholt and Werner 1995; Balaban-Feld et al. 2019), counter to expectation, we did not find a strong interaction between internal state and external stimulus on foraging decisions. Overall, the nonsignificant effect of moonlight on the latency to land on the platform (Fig. 2) was smaller than we expected given that previous work did find there to be an effect for both sexes in this population of bats (Sealey et al. 2024). Interestingly, the current effect of moonlight on behavior was stronger in male bats (Fig. 3a). Sex differences in latency to land are consistent with formerly observed sex-specific differences in foraging strategies within this species (Morrison 1978), as well as in other bats (Bonaccorso and Gush 1987; Krull et al. 1991; Wilkinson and Barclay 1997; Suutari et al. 2024) and other animals (scorpions: Carlson et al. 2014, guppies: Laland 1999, and whales:

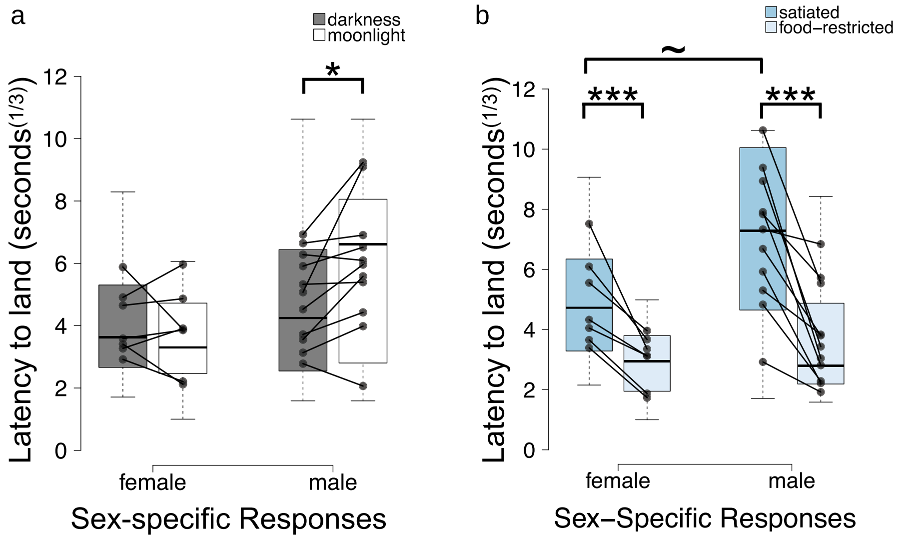

Fig. 3. Effect of (a) treatment and (b) internal state on latencies to land on the food platform with respect to sex. In (a) dark gray and white boxes represent when bats were tested in darkness and simulated full moonlight, respectively. In (b) blue (satiated) and light blue (food-restricted) boxes represent responses of female and male bats with different internal states. For all panels, boxplots depict the distribution of all responses from all bats. Black dots depict individual means, with lines connecting the mean responses from the same individual. The asterisk denotes a significant difference, $P < 0.05$ (*) and $P < 0.002$ (***), while the tilde indicates a nonsignificant trend, $P < 0.06$ (~), as calculated from post hoc Tukey's tests.

Tennessen et al. 2023). However, we did observe strong overall effects of internal state, with latency decreasing when bats were food-restricted with no food provided the night before testing. Our results support the hypothesis that if animals are nutritionally deprived, they are quicker to approach food sources (Pettersson and Brönmark 1993; Horat and Semlitsch 1994; Morton and Chan 1999; Tigreros et al. 2018). Furthermore, sex differences were observed in satiated bats but were weaker in food-restricted bats, which is consistent with previous observations in pied flycatchers where sex-specific foraging strategies were reduced under harsh environmental conditions (Mand et al. 2013).

With respect to environmental context, female bats were observed to be consistent in their foraging strategies in darkness and full moonlight. However, our sample set only had 11 male bats and 7 female bats, and we may not have had a large enough sample size to detect differences in female bats. Alternatively, captured female bats were assessed to be neither pregnant nor lactating between March and May (peak reproductive season); however, females may have been pregnant but not detectibly so (Ortega et al. 2021). Studies in other animals demonstrated that female animals shift their foraging (Clark 1980; Barclay 1989; Kurta et al. 1989; Henry et al. 2002; Thometz et al. 2014) and antipredator behavior (Brodie III 1989; Lecomte et al. 1993; Carlson et al. 2014; Freinschlag and Schausberger 2016) when gravid and this could also explain why female bats observed in our study behaved differently than male bats.

We evaluated just two antipredator behaviors of bats: whether the bats flew to the platform and latency to land on the platform. We did not observe alarm calling or mobbing, perhaps because bats were tested alone which renders these behaviors less useful. We know bats have a suite of other antipredator behaviors (eg, changes in flight path (Barré et al. 2023) and physiological state (Lewanzik et al. 2012)). Future studies would benefit in considering these parameters to test foraging responses. Furthermore, we observed a nonsignificant effect of full moonlight, which we expect is largely due to our limited sample size. Nonetheless, despite the presence of artificial moonlight, the latency to land was lower when bats were food-restricted, suggesting metabolic needs to replenish energy lost outweighed the avoidance of potential predators.

Previous work has shown that predation risk influences prey foraging behavior (bats: Baxter et al. 2006; fish: Metcalfe et al. 1987), but this can be influenced by internal states such as hunger level (Milinski and Heller 1978; Godin and Crossman 1994). Understanding the physiological state provides insights into the immediate nutritional demands of an organism and how internal state can affect foraging decisions, food preferences, and the strategies employed to maximize energy intake (Lind and Cresswell 2005). Whether an animal is in a state of hunger can impact the allocation of time and energy between reproductive investment and competition (Dixon et al. 1993) and predator avoidance (Anholt and Werner 1995; Bridges 2002). Considering physiological conditions improves our understanding of how organisms adapt their foraging behaviors to optimize survival and reproduction in response to internal states and external cues.

The need to balance nutritional requirements with the risk of predation often leads prey to make foraging decisions that contribute to their survival in dangerous environments. Our study tested two extremes: satiation, where bats fed for an entire foraging night and food-restriction, where bats did not eat for an entire night. Future work could test for antipredator behavior at different gradients of hunger or test for food preferences in risky conditions. Testing different gradients of hunger (eg ½ night food-restricted, ½ night satiated, etc.) could reveal at which gradient the switch from predator avoidance is overcome by the metabolic needs of hunger. Our results here show that bats fly to food platforms in almost all trials and previous work showed bats will fly to food platforms even in trials with model predators (owls in Sealey et al. 2024). It may be that because bats have such high metabolisms (Austad and Fischer 1991), they are tasked with feeding under any kind of condition, even those deemed dangerous. Future work could explore whether bats shift their target food resource based on perceived predation risk.

Here we directly tested for how the physiological state of an animal can influence their assessments of indirect environmental contexts indicative of risky foraging conditions. Although long-term moonlight avoidance has been observed in *A. jamaicensis* (Morrison 1978a) and may be difficult to test for in bats because they would need to be tracked individually for long periods of time, it would be valuable to observe the effect of seasonal food-restriction (ie dry season) and moonlight avoidance in lunar phobic species of bats. Long-term studies evaluating the seasonal effect of moonlight on lagomorphs demonstrates how predation risk can fluctuate regarding both harsh conditions and moonlight exposure (Griffin et al. 2005). In other predator–prey systems where the behavioral response to an indirect environmental context is strong (ie nocturnal rodents (Kotler et al. 2010)), future studies could reveal links between seasonal variation, physiological demands, and mortality.

Author contributions

Briana Sealey (Conceptualization [lead], Data curation [lead], Formal analysis [equal], Funding acquisition [lead], Investigation [lead], Methodology [lead], Project administration [equal], Resources [equal], Software [equal], Validation [equal], Visualization [lead], Writing—original draft [lead], Writing—review & editing [lead]), Logan James (Formal analysis [equal], Methodology [supporting], Software [supporting], Validation [equal], Writing—review & editing [equal]), Michael Ryan (Conceptualization [equal], Formal analysis [supporting], Funding acquisition [lead], Project administration [supporting], Supervision [lead], Writing—original draft [supporting], Writing—review & editing [supporting]), and Rachel Page (Conceptualization [equal], Funding acquisition [lead], Project administration [equal], Supervision [lead], Writing—original draft [supporting], Writing—review & editing [supporting])

Funding

This work was supported by grant funding from the University of Texas at Austin's Ecology, Evolution and Behavior Program, the National Science Foundation's Graduate Research Fellowship Program, and research funds from the Smithsonian Tropical Research Institute.

Conflicts of interest

None declared.

Data availability

Analyses reported in this article can be reproduced using the data provided by Sealey et al. (2025).

References

Ancillotto L, Serangeli MT, Russo D. 2013. Curiosity killed the bat: domestic cats as bat predators. Mamm Biol. 78:369–373. https://doi.org/10.1016/j.mambio.2013.01.003.

Anholt BR, Werner EE. 1995. Interaction between food availability and predation mortality mediated by adaptive behavior. Ecology. 76:2230–2234. https://doi.org/10.2307/1941696.

Austad SN, Fischer KE. 1991. Mammalian aging, metabolism, and ecology: evidence from the bats and marsupials. J Gerontol. 46: B47–B53. https://doi.org/10.1093/geronj/46.2.B47.

Balaban-Feld J et al. 2019. State-dependent foraging among social fish in a risky environment. Oecologia. 190:37–45. https://doi.org/10.1007/s00442-019-04395-z.

Barclay RMR. 1989. The effect of reproductive condition on the foraging behavior of female hoary bats, *Lasiurus cinereus*. Behav Ecol Sociobiol. 24:31–37. https://doi.org/10.1007/BF00300115.

Barnett C, Bateson M, Rowe C. 2007. State-dependent decision making: educated predators strategically trade off the costs and benefits of consuming aposematic prey. Behav Ecol. 18:645–651. https://doi.org/10.1093/beheco/arm027.

Barré K, Thomas I, Le Viol I, Spoelstra K, Kerbiriou C. 2023. Manipulating spectra of artificial light affects movement patterns of bats along ecological corridors. Anim Conserv. 26: 865–875. https://doi.org/10.1111/acv.12875.

Baxter DJM, Psyllakis JM, Gillingham MP, O'Brien EL. 2006. Behavioural response of bats to perceived predation risk while foraging. Ethology. 112(10):977–983. https://doi.org/10.1111/j.1439-0310.2006.01249.x.

Bonaccorso FJ, Gush TJ. 1987. Feeding behaviour and foraging strategies of captive phyllostomid fruit bats: an experimental study. J Anim Ecol. 56:907–920. https://doi.org/10.2307/4956.

Bridges CM. 2002. Tadpoles balance foraging and predator avoidance: effects of predation, pond drying, and hunger. J Herpetol. 36:627–634. https://doi.org/10.1670/0022-1511(2002)036[0627:TBFAPA]2.0.CO;2.

Brodersen J, Nilsson PA, Hansson L-A, Skov C, Brönmark C. 2008. Condition-dependent individual decision-making determines cyprinid partial migration. Ecology. 89:1195–1200. https://doi.org/10.1890/07-1318.1.

Brodie ED III. 1989. Behavioral modification as a means of reducing the cost of reproduction. Am Nat. 134:225–238. https://doi.org/10.1086/284977.

Carlson BE, McGinley S, Rowe MP. 2014. Meek males and fighting females: sexually-dimorphic antipredator behavior and locomotor performance is explained by morphology in bark scorpions (*Centruroides vittatus*). PLoS One. 9:e97648. https://doi.org/10.1371/journal.pone.0097648.

Chen FSE, Dawson SJ, Fleming PA. 2024. Housework or vigilance? Bilbies alter their burrowing activity under threat of predation by feral cats. Behav Ecol. 35:arad073. https://doi.org/10.1093/beheco/arad073.

Clark DA. 1980. Age- and sex-dependent foraging strategies of a small mammalian omnivore. J Anim Ecol. 49:549–563. https://doi.org/10.2307/4263.

Clarke JA. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deermice (*Peromyscus maniculatus*). Behav Ecol Sociobiol. 13:205–209. https://doi.org/10.1007/BF00299924.

Cronin AD, Ryan MJ, Page RA, Hunter KL, Taylor RC. 2019. Environmental heterogeneity alters mate choice behavior for multimodal signals. Behav Ecol Sociobiol. 73:1–10. https://doi.org/10.1007/s00265-019-2654-3.

Cummings ME, Bernal XE, Reynaga R, Rand AS, Ryan MJ. 2008. Visual sensitivity to a conspicuous male cue varies by reproductive state in *Physalaemus pustulosus* females. J Exp Biol. 211:1203–1210. https://doi.org/10.1242/jeb.012963.

Daly M, Behrends PR, Wilson MI, Jacobs LF. 1992. Behavioural modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. Anim Behav. 44:1–9. https://doi.org/10.1016/S0003-3472(05)80748-1.

De Meester G et al. 2018. Hunt or hide: how insularity and urbanization affect foraging decisions in lizards. Ethology. 124:227–235. https://doi.org/10.1111/eth.12722.

Dixon AFG, Wellings PW, Carter C, Nichols JFA. 1993. The role of food quality and competition in shaping the seasonal cycle in the reproductive activity of the sycamore aphid. Oecologia. 95:89–92. https://doi.org/10.1007/BF00649511.

Elangovan V, Marimuthu G. 2001. Effect of moonlight on the foraging behaviour of a megachiropteran bat *Cynopterus sphinx*. J Zool. 253: 347–350. https://doi.org/10.1017/S0952836901000310.

Freinschlag J, Schausberger P. 2016. Predation risk-mediated maternal effects in the two-spotted spider mite, *Tetranychus urticae*. Exp Appl Acarol. 69:35–47. https://doi.org/10.1007/s10493-016-0014-9.

Geipel I, Smeekes MJ, Halfwerk W, Page RA. 2019. Noise as an informational cue for decision-making: the sound of rain delays bat emergence. J Exp Biol. 222(Pt 3):jeb192005. https://doi.org/10.1242/jeb.192005.

Godin J-GJ, Crossman SL. 1994. Hunger-dependent predator inspection and foraging behaviours in the threespine stickleback (*Gasterosteus aculeatus*) under predation risk. Behav Ecol Sociobiol. 34:359–366. https://doi.org/10.1007/BF00197006.

Griffin PC, Griffin SC, Waroquiers C, Mills LS. 2005. Mortality by moonlight: predation risk and the snowshoe hare. Behav Ecol. 16:938–944. https://doi.org/10.1093/beheco/ari074.

Hemingway CT, Ryan MJ, Page RA. 2017. Rationality in decision-making in the fringe-lipped bat, *Trachops cirrhosus*. Behav Ecol Sociobiol. 71:94. https://doi.org/10.1007/s00265-017-2321-5.

Henry M, Thomas DW, Vaudry R, Carrier M. 2002. Foraging distances and home range of pregnant and lactating Little Brown Bats (*Myotis lucifugus*). J Mammal. 83:767–774. https://academic.oup.com/jmammal/article-abstract/83/3/767/2373247?redirectedFrom=fulltext.

Horat P, Semlitsch RD. 1994. Effects of predation risk and hunger on the behaviour of two species of tadpoles. Behav Ecol Sociobiol. 34: 393–401. https://doi.org/10.1007/BF00167330.

Sealey BA, James LS, Ryan MJ, Page RA. 2025. Data from: The influence of hunger and sex on the foraging decisions of frugivorous bats [data set]. Texas Data Repository. https://doi.org/10.18738/T8/XIQT50.

Kojima Y, Mori A. 2015. Active foraging for toxic prey during gestation in a snake with maternal provisioning of sequestered chemical defences. Proc Biol Sci. 282:20142137. https://doi.org/10.1098/rspb.2014.2137.

Kotler BP, Brown J, Mukherjee S, Berger-Tal O, Bouskila A. 2010. Moonlight avoidance in gerbils reveals a sophisticated interplay among time allocation, vigilance and state-dependent foraging. Proc Biol Sci. 277:1469–1474. https://doi.org/10.1098/rspb.2009.2036.

Krull D, Schumm A, Metzner W, Neuweiler G. 1991. Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). Behav Ecol Sociobiol. 28:247–253. https://doi.org/10.1007/BF00175097.

Kurta A, Bell GP, Nagy KA, Kunz TH. 1989. Energetics of pregnancy and lactation in free-ranging Little Brown Bats (*Myotis lucifugus*). Physiol Zool. 62:804–818. https://doi.org/10.1086/physzool.62.3.30157928.

Kuznetsova A, Brockhoff PB, Christensen RHB. 2017. lmerTest: tests in linear mixed effects models. J Stat Softw. 82:1–26. https://doi.org/10.18637/jss.v082.i13.

Laland KN. 1999. Foraging innovation is inversely related to competitive ability in male but not in female guppies. Behav Ecol. 10: 270–274. https://doi.org/10.1093/beheco/10.3.270.

Lecomte J, Clobert J, Massot M. 1993. Shift in behaviour related to pregnancy in *Lacerta vivipara*. Revue d'Écologie. 48:99–107. https://doi.org/10.3406/revec.1993.2088.

Lewanzik D, Kelm DH, Greiner S, Dehnhard M, Voigt CC. 2012. Ecological correlates of cortisol levels in two bat species with contrasting feeding habits. Gen Comp Endocrinol. 177:104–112. https://doi.org/10.1016/j.ygcen.2012.02.021.

Lillywhite HB, Brischoux F. 2012. Is it better in the moonlight? Nocturnal activity of insular cottonmouth snakes increases with lunar light levels. J Zool. 286:194–199. https://doi.org/10.1111/j.1469-7998.2011.00866.x.

Lima SL. 1985. Maximizing feeding efficiency and minimizing time exposed to predators: a trade-off in the black-capped chickadee. Oecologia. 66:60–67. https://doi.org/10.1007/BF00378552.

Lima SL, O'Keefe JM. 2013. Do predators influence the behaviour of bats? Biol Rev Camb Philos Soc. 88:626–644. https://doi.org/10.1111/brv.12021.

Lind J, Cresswell W. 2005. Determining the fitness consequences of antipredation behavior. Behav Ecol. 16:945–956. https://doi.org/10.1093/beheco/ari075.

Mand R, Rasmann E, Magi M. 2013. When a male changes his ways: sex differences in feeding behavior in the pied flycatcher. Behav Ecol. 24:853–858. https://doi.org/10.1093/beheco/art025.

Metcalfe NB, Huntingford FA, Thorpe JE. 1987. The influence of predation risk on the feeding motivation and foraging strategy of juvenile Atlantic salmon. Animal Behaviour. 35(3):901–911. https://doi.org/10.1016/S0003-3472(87)80125-2.

Mikula P. 2015. Fish and amphibians as bat predators. Eur J Ecol. 1: 71–80. https://doi.org/10.1515/eje-2015-0010.

Mikula P, Lučan RK, Pellón JJ, Valdez JW, Fenton B. 2024. Bats as prey. In: Russo D, Fenton B, editors. A natural history of bat foraging: evolution, physiology, ecology, behavior and conservation. Elsevier. p. 157–171. https://doi.org/10.1016/B978-0-323-91820-6.00003-6.

Milinski M, Heller R. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L. Nature. 275:642–644. https://doi.org/10.1038/275642a0.

Morrison DW. 1978a. Lunar phobia in neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Anim Behav. 26: 852–855. https://doi.org/10.1016/0003-3472(78)90151-3.

Morrison DW. 1978b. Foraging ecology and energetics of the frugivorous bat *Artibeus jamaicensis*. Ecology. 59:716–723. https://doi.org/10.2307/1938775.

Morton B, Chan K. 1999. Hunger rapidly overrides the risk of predation in the subtidal scavenger *Nassarius siquijorensis* (Gastropoda: Nassariidae): an energy budget and a comparison with the intertidal *Nassarius festivus* in Hong Kong. J Exp Mar Biol Ecol. 240: 213–228. https://doi.org/10.1016/S0022-0981(99)00060-X.

Nyffeler M, Knörnschild M. 2013. Bat predation by spiders. PLoS One. 8:e58120. https://doi.org/10.1371/journal.pone.0058120.

Oates BA et al. 2019. Antipredator response diminishes during periods of resource deficit for a large herbivore. Ecology. 100: e02618. https://doi.org/10.1002/ecy.2618.

Ortega J, Castro-Arellano I. 2001. *Artibeus jamaicensis*. Mamm Species. 662:1–9. https://doi.org/10.2307/0.662.1

Ortega J, Gutiérrez EG, Moreno-Santillán DD, MacSwiney G MC. 2021. Seasonal reproductive synchrony in colonies of the Jamaican fruit–eating bat (*Artibeus jamaicensis*) in southeast Mexico. Mamm Res. 66:627–634. https://doi.org/10.1007/s13364-021-00582-7.

Owings DH, Handa E. 1975. Shadows and detection of movement by a burrowing owl (*Speotyto cunicularia*). Condor. 77:501–502. https://doi.org/10.2307/1366105.

Persons MH. 1999. Hunger effects on foraging responses to perceptual cues in immature and adult wolf spiders (Lycosidae). Anim Behav. 57:81–88. https://doi.org/10.1006/anbe.1998.0948.

Pettersson LB, Brönmark C. 1993. Trading off safety against food: state dependent habitat choice and foraging in crucian carp. Oecologia. 95:353–357. https://doi.org/10.1007/BF00320988.

Polis GA. 1988. Foraging and evolutionary responses of desert scorpions to harsh environmental periods of food stress. J Arid Environ. 14: 123–134. https://doi.org/10.1016/S0140-1963(18)31082-6.

Prugh LR, Golden CD. 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. J Anim Ecol. 83:504–514. https://doi.org/10.1111/1365-2656.12148.

Pyke GH. 2019. Optimal foraging theory: an introduction. In: Choe JC, editor. Encyclopedia of animal behavior. 2nd ed. Elsevier. p. 111–117. https://doi.org/10.1016/B978-0-12-809633-8.01156-0.

Sealey BA, James LS, Cohen G, Ryan MJ, Page RA. 2024. Rapid foraging risk assessments in the Jamaican fruit bat, *Artibeus jamaicensis*. Anim Behav. 216:45–53. https://doi.org/10.1016/j.anbehav.2024.07.015.

Shero MR, Goetz KT, Costa DP, Burns JM. 2018. Temporal changes in Weddell seal dive behavior over winter: are females increasing foraging effort to support gestation? Ecol Evol. 8:11857–11874. https://doi.org/10.1002/ece3.4643.

Shogren FG, Hebets EA, DeLong JP. 2023. Functionally redundant multimodal predator cues elicit changes in prey foraging behavior. Behav Ecol. 34:334–339. https://doi.org/10.1093/beheco/arac130.

Skutelsky O. 1996. Predation risk and state-dependent foraging in scorpions: effects of moonlight on foraging in the scorpion *Buthus occitanus*. Anim Behav. 52:49–57. https://doi.org/10.1006/anbe.1996.0151.

Smith JA et al. 2017. Fear of the human 'super predator' reduces feeding time in large carnivores. Proc Biol Sci. 284:20170433. https://doi.org/10.1098/rspb.2017.0433.

Stephens DW, Krebs JR. 1986. Foraging theory. Princeton University Press (Monographs in behavior and ecology).

Suutari MS, Lehikoinen A, Lehto HJ, Lilley TM. 2024. Antipredator responses of bats during short boreal nights with variable climatic conditions. J Mammal. 106:385–393. https://doi.org/10.1093/jmammal/gyae124.

Szczygieł HA, Page RA. 2020. When the hunter becomes the hunted: foraging bat attacked by pit viper at frog chorus. Ecology. 101: e03111. https://doi.org/10.1002/ecy.3111.

Taylor RC, Klein BA, Stein J, Ryan MJ. 2008. Faux frogs: multimodal signalling and the value of robotics in animal behavior. Anim Behav. 76:1089–1097. https://doi.org/10.1016/j.anbehav.2008.01.031.

Tennessen JB et al. 2023. Divergent foraging strategies between populations of sympatric matrilineal killer whales. Behav Ecol. 34: 373–386. https://doi.org/10.1093/beheco/arad002.

Thapa H et al. 2024. Predator metamorphosis and its consequence for prey risk assessment. Behav Ecol. 35:arae014. https://doi.org/10.1093/beheco/arae014.

Thometz NM, Tinker MT, Staedler MM, Mayer KA, Williams TM. 2014. Energetic demands of immature sea otters from birth to weaning: implications for maternal costs, reproductive behavior and population-level trends. J Exp Biol. 217:2053–2061. https://doi.org/10.1242/jeb.099739.

Tigreros N, Wang EH, Thaler JS. 2018. Prey nutritional state drives divergent behavioural and physiological responses to predation risk. Funct Ecol. 32:982–989. https://doi.org/10.1111/1365-2435.13046.

Tuttle MD, Ryan MJ. 1982. The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. Behav Ecol Sociobiol. 11:125–131. https://doi.org/10.1007/BF00300101.

Vásquez RA. 1994. Assessment of predation risk via illumination level: facultative central place foraging in the cricetid rodent *Phyllotis darwini*. Behav Ecol Sociobiol. 34:375–381. https://doi.org/10.1007/BF00197008.

Welbergen JA. 2006. Timing of the evening emergence from day roosts of the grey-headed flying fox, *Pteropus poliocephalus*: the effects of predation risk, foraging needs, and social context. Behav Ecol Sociobiol. 60:311–322. https://doi.org/10.1007/s00265-006-0167-3.

Werner EE. 1992. Individual behavior and higher-order species interactions. Am Nat. 140:S5–S32. https://doi.org/10.1086/285395.

Whitham J, Mathis A. 2000. Effects of hunger and predation risk on foraging behavior of graybelly salamanders, *Eurycea multiplicata*. J Chem Ecol. 26:1659–1665. https://doi.org/10.1023/A:1005590913680.

Wilkinson LC, Barclay RMR. 1997. Differences in the foraging behaviour of male and female big brown bats (*Eptesicus fuscus*) during the reproductive period. Écoscience. 4:279–285. https://doi.org/10.1080/11956860.1997.11682406.

Wilson ADM et al. 2019. Conformity in the collective: differences in hunger affect individual and group behavior in a shoaling fish. Behav Ecol. 30:968–974. https://doi.org/10.1093/beheco/arz036.