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Rapid foraging risk assessments in the Jamaican fruit bat, *Artibeus jamaicensis*

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Foraging increases predation risk. As such, prey frequently attend to potential predator cues when making decisions about foraging behaviour. Environmental cues, such as light levels, can impact predation risk, and populations from different environments may vary in how they respond to such cues. Here we experimentally manipulated foraging conditions for a frugivorous bat, the Jamaican fruit bat, to ask whether individuals rapidly alter their foraging behaviour based on potential predator cues and light levels. Specifically, we ran bats in multiple foraging trials across a night in which we varied the level of ambient light or predator cues (auditory or visual) and measured latencies to feed. We found that bats in a more urban population were most affected by simulated full moonlight, delaying their foraging behaviour. In contrast, bats from a rural population were sensitive to simulated urban light. Furthermore, rural bats were also more sensitive to potential predator cues and foraged more rapidly in the presence of novel objects and auditory predator cues. These results reveal variation across populations of the same species with respect to their response to potential predator cues, possibly indicating differences in their evaluations of foraging risks.

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Animals must remain vigilant of predators while foraging. Predation can cause shifts in prey foraging behaviour (Caldwell, 1986; Feener, 1988) and plays a pivotal role in shaping habitat use (Breviglieri et al., 2017; Metcalfe et al., 1987; Ripple & Beschta, 2003, 2004; Suraci et al., 2019). Predator cues can create a 'landscape of fear', altering prey behaviour to minimize their risk of predation (Jordan & Ryan, 2015), thereby indirectly influencing the distribution and abundance of prey species. Elements of the environment can be indicative of risky foraging areas, and prey can adjust their behaviour based on these cues (Skutelsky, 1996; Wirsing et al., 2021). Environmental conditions and light levels are crucial factors that can influence the saliency of these cues and affect the risks of predation.

Antipredator behaviour in foraging nocturnal prey animals can vary as a function of illumination from moonlight. In these cases, prey reduce foraging time during full moon phases of the month and maximize foraging time during new moon phases (Bowers, 1988; Price et al., 1984; Rode-Margono & Anne-Isola Nekaris, 2014; Wolfe & Tan Summerlin, 1989). Early studies in bats (Morrison, 1978c) and kangaroo rats (Lockard & Owings, 1974) observed a phenomenon called 'lunar phobia' and hypothesized that prey avoid moonlight because of increased exposure to visually orienting predators that hunt more effectively and successfully on moonlit nights (Chen et al., 2024; Clarke, 1983; Kotler et al., 1991; Lillywhite & Brischoux, 2012; Longland & Price, 1991). This hypothesis also predicts that prey that rely on auditory or olfactory cues (rather than visual cues) to forage are the main taxa that suppress foraging activity during waxing moon phases (Prugh & Golden, 2014).

The way in which animals integrate these environmental and predator cues can vary across populations. Recent work has demonstrated numerous anthropogenic effects on behaviour (Sanders et al., 2020). For instance, aversive responses to anthropogenic noise reduces foraging efficiency in bats (Luo et al., 2015) and artificial light at night affects foraging behaviour and predator avoidance in fish (Becker et al., 2013; Czarnecka et al., 2019; Perkin et al., 2011). Individuals from populations that span different levels of urbanization are shown to differ in how they integrate environmental (Audet et al., 2016) and novel cues (Sol et al., 2011) to make foraging decisions. The impacts of anthropogenic factors on foraging behaviours can vary widely depending on the species and the nature of the disturbance (Van Scoyoc et al., 2023), and this variation is why it is important to test for effects of urbanization in many species and across populations.

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Bats offer an excellent system to investigate behavioural and population level variation in response to predator threat. For example, the avoidance of moonlight has been widely documented in tropical frugivorous and nectivorous bats (Lima & O'Keefe, 2013; Saldaña-Vázquez & Munguía-Rosas, 2013). Studies of lunar phobia are mainly observational, such as one study that radiotracked the Jamaican fruit bat, a Neotropical frugivorous bat, for several weeks and documented that the bats were less active and interrupted feeding more often during full moon phases (Morrison, 1978c). Although there are observations of bats investigating distress calls (Russ et al., 1998) and mobbing predators (Knörnschild & Tschapka, 2012; Lučan & Šálek, 2013), overall, there is limited knowledge on nonlethal predator effects on bat foraging behaviour and the cues they use to locate predators (Lima & O'Keefe, 2013).

Here we experimentally manipulated the foraging conditions for Jamaican fruit bats to ask whether individuals rapidly alter their foraging behaviour based on potential predator cues and light levels. Specifically, bats were given brief opportunities to forage in conditions with varying light levels, a visual predator and novel cue or an auditory predator and novel cue. We hypothesized that increasing levels of light as well as predator-associated cues (but not novel stimuli) would increase the bats' latency to land on a feeding platform to forage. By determining how bats behave under these various foraging conditions in controlled experiments, we can pinpoint the cues they use when making risk assessments.

METHODS

Study Species

The Jamaican fruit-eating bat is found throughout Middle America and northern South America. Its primary diet consists of figs, supplemented with flowers, nectar, pollen and insects (Kunz & Diaz, 1995; Rodríguez-Durán & Vázquez, 2001; Teixeira et al., 2009). This species is an ideal subject for this study because it is widely abundant and readily consumes fruit in captivity. We captured bats at two different sites: one site was situated in the forests adjacent to human populations surrounding the Smithsonian Tropical Research Institute's Gamboa field station in Panama, and bats were captured during October 2021 – November 2021 and November 2022; the other site was situated in an area more isolated from anthropogenic influences on Barro Colorado Island (BCI), and bats were captured during June 2023.

During mist netting, two to four nets (6–12 m in length) were placed within 500 m of each other and checked every 10–15 min to minimize the time bats spent in the nets. Once an individual bat was found in a net, all bats in the nets were removed within 0.5–20 min. Nontarget species and juvenile, pregnant or lactating female bats and bats that appeared stressed were released upon capture. Target species were immediately placed in soft cloth bat bags until release into the flight cages. We minimized handling time to avoid unnecessary stress. Before release into the flight cage, bats were given small, unique haircuts (~1 × 1 cm), as a noninvasive method for identifying individuals for short periods.

To capture bats at known roosts during the day, we gently placed a butterfly net over the roost entrance until several bats (6–15 bats) flew into the net (10–20 s). We then closed the net, opening it just enough to remove all individuals quickly and gently until each bat was placed into a soft cloth bat bag (5–10 min).

Upon capture, bats were released into an outdoor flight cage (4.85 × 4.90 × 2.43 m; Fig. 1a) to forage freely for 6 h. Food (small pieces of banana) was placed on a platform (41 × 2 × 29 cm) 40 cm off the ground, and bats learned to forage there for two nights before experiments began. As the bats learned to obtain food from the platform, we videorecorded the bats from a separate room. Between nights, after bats had become accustomed to readily retrieving fruit from the platform, they were placed in a smaller holding cage (69 × 71 × 202 cm) with ad libitum water. By the sixth hour of the second night, if bats had not learned to obtain food from the platform and if their palpated stomachs felt empty, bats were hand-fed banana and permitted a third night to learn. Bats that did not eat bananas during hand feeding or after four nights in the flight cage were released at their point of capture. We followed the same protocol on BCI, although the dimensions of the flight cage and the holding cage were different: flight cage dimensions were 4.85 × 5.3 × 2.5 m, and we used a pop-up tent (75 × 106 × 68 cm) as the holding cage.

Ethical Note

All animal-related procedures were approved by the Panama Ministry of the Environment (permit numbers SE/AP-22-19 and ARG-278-2022) and were conducted in accordance with approved 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).

Behavioural Trials

This study aimed to determine how (1) environmental light contexts, (2) predator visual cues and (3) predator auditory cues affect bat foraging behaviour (Fig. 1a). We used artificial lights to simulate three environmental contexts: full moon and half-moon phases and urban light pollution (i.e. from a streetlight). For both artificial moonlight stimuli, we used the same LED model (Maxxima Mini Green Always Night Lights) as in previous studies (i.e. Taylor et al., 2019), which emits a light spectrum similar to that measured at night in the forest. Our full moonlight treatment was 0.089 lx, and our half-moon treatment was 0.044 lx. We used white night lights (MagicPro Plug-in LED) to simulate urban light pollution (1.21 lx). All lux levels were measured with a Dr. Meter 1330B-V luxmeter. To test bats' responses to a visual predatory stimulus, we used an owl model constructed to match the dimensions (41 × 23 cm) of a spectacled owl, *Pulsatrix perspicillata*, a common species observed consuming *Artibeus* bat species (Restrepo-Cardona et al., 2018). We also conducted trials with a cardboard box that was roughly the same height and width as the owl model (30 × 20 × 44 cm) to serve as a novel object. Finally, to test for responses to auditory stimuli, we used spectacled owl calls and a novel sound stimulus (iPhone 'Opening' ringtone; Fig. 1b). Owl calls consisted of playbacks of a recording of natural calls of the spectacled owl that were 3–4 s in duration with 5–9 s of silence between calls. Ambient forest sounds were included in the owl call playback. The novel sound stimulus (ringtone) was looped continuously without silent intervals for the duration of the trial. Both auditory stimuli were broadcast at 75 dB SPL re. 20 μPa at 0.5 m, as measured with a RadioShack Digital Sound Level Meter 33-2055 and both were broadcast continuously for the duration of the trial. The sound pressure level of the acoustic playbacks was calibrated each night before testing. Lights, sound and physical sources were 1.63 m, 1.85 m and 1.28 m above the platform, respectively. Experiments were recorded using one Sony DCR-SR45 Handycam camcorders, with a lateral view 2.27 m from the platform, and two CMvision IR lights, placed 2.44 m and 3.23 m from the platform.

Bats were tested individually between 1800 and 0300 hours. Experiments began and ended with trials in darkness and in the absence of predator or novel stimuli (control) to assess each bat's baseline responses to the captive foraging conditions. Between the controls, bats were tested in seven randomly ordered stimuli:

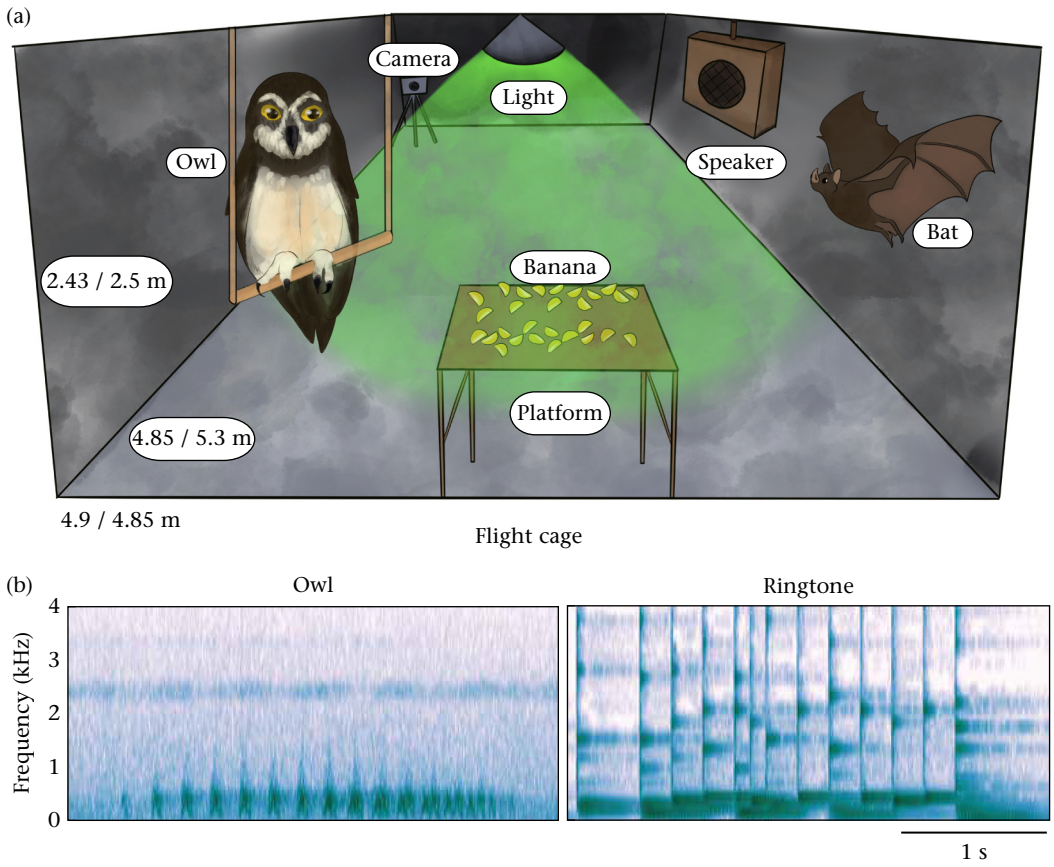

Figure 1. Experimental set-up. (a) Flight cage set-up. Each bat experienced seven experimental treatments in random order: either light, sound, or object trials. The light source emitted full moon, half-moon or white light; the speaker broadcast the owl calls and ringtone; and the perch was where the owl model and box were positioned for object treatments. Measurements of flight cage in Gamboa/BCI are labelled accordingly in meters. (b) Spectrograms of the acoustic stimuli used: owl call (left) and ringtone (right).

simulated full moonlight, simulated half-moon light, simulated urban light, owl model, cardboard box, spectacled owl call and phone ringtone. During preliminary runs of this experiment, we found that a single adult bat can eat half a banana within 6 h (roughly 50 g) and one whole banana over the course of an entire night (~100 g). To control for satiation, once a bat landed on the platform, it was allowed to feed on ~1–2 g of banana for 3 min or until it began to fly over the platform again. Bats were not tested again until all other individuals in their cohort completed their respective trial. Although wait times were not the same for each bat, by testing bats in cohorts, we maintained their social wellbeing while housed in the flight cages (see Ratcliffe et al., 2003) and maximized our ability to test as many individuals as possible over short periods of fieldwork. If a group of bats did not complete all seven stimuli within a night, we stopped testing at 0300 hours to allow bats to rest and finished testing the next night. Bats were tested for a maximum of two nights. Each bat was tested once in each of the seven stimuli and twice per night in the control condition.

At the beginning of each trial, the bat was released into the flight cage through a small entrance that was then sealed. During acoustic trials, we ceased playbacks once the bat landed on the platform. If a bat did not land on the platform after 20 min, we ended the trial, removed the bat from the flight room and tested the next bat. If a bat failed to forage three consecutive times, we placed it back into the holding room and allowed it to feed on bananas ad libitum until all other bats in its cohort had finished with experiments, and we removed it from the analysis.

Follow-up Experiment: Multiple Stimuli

Preliminary results of our main experiment in Gamboa suggested that the full moonlight and ringtone stimuli had the largest effects on foraging behaviour. Furthermore, these stimuli had opposite effects, with the moonlight stimulus increasing latencies and the ringtone stimulus decreasing latencies. To test how bats integrate multiple stimuli, we tested a group of bats ($N = 12$; October 2022) on a combination trial presenting both full moonlight and the auditory ringtone stimuli simultaneously. Before and after this trial, the bats were tested in silence and darkness as baseline controls. Given the preliminary results from bats tested in Gamboa, on BCI we removed the half-moon stimulus and replaced it with a combination of full moonlight + owl model stimulus to ascertain whether the combined effect of light and a visual predator cue would influence behaviour.

Statistical Analysis

We completed all statistical analyses using R Program 4.1.1 and used the packages 'dplyr' (Wickham et al., 2022) and 'stringr' (Wickham, 2022) to organize data and the package 'lme4' (Bates et al., 2015) for (general) linear mixed-effects models. We used the package 'lmerTest' (Kuznetsova et al., 2017) to calculate *P* values for linear mixed-effects models (type III analysis of variance table with Satterthwaite's method), the package 'car' (Fox & Weisberg, 2019) for generalized linear mixed-effects models (type II Wald

chi-square tests) and the package 'emmeans' to generate Tukey's post hoc analyses (Lenth, 2023).

While bats may modulate their behaviour in many ways, we focused on two behavioural measures: whether bats chose to forage and their latency to fly. First, we asked whether the motivation to forage at all differed across stimuli. Because trials were ended after 20 min, we coded a binary forage variable (0 = did not land on the platform, 1 = did land on the platform). This was used as the dependent variable in a generalized linear mixed-effects model (function 'glmer') with bat identity (ID) as a random effect and a binomial error family. Because bats were tested on multiple nights and multiple trials per night, we first checked whether this affected response rates by including night or trial as the fixed effect. We also ran the model with sex and mass as fixed effects to determine whether these variables affected response rates. None of these were significant predictors of foraging (see Results); thus, we ran our main model with stimulus as the sole fixed effect.

We next asked whether the stimulus affected the time it took bats to land on the platform (latency to fly, in seconds). We cube root-transformed these values to improve normality. Following a similar paradigm as above, we first asked whether the night, the trial within the night, sex or mass affected the time to land. We found that trial within the night was strongly correlated with the time to land. Therefore, our main mixed-effects model (function 'lmer') included both trial and stimulus as fixed effects, time to land as the dependent factor and bat ID and night as random effects. For our main analysis, we coded all bats that failed to land at a ceiling of 1200 s. However, we also ran the same analyses with these bats excluded.

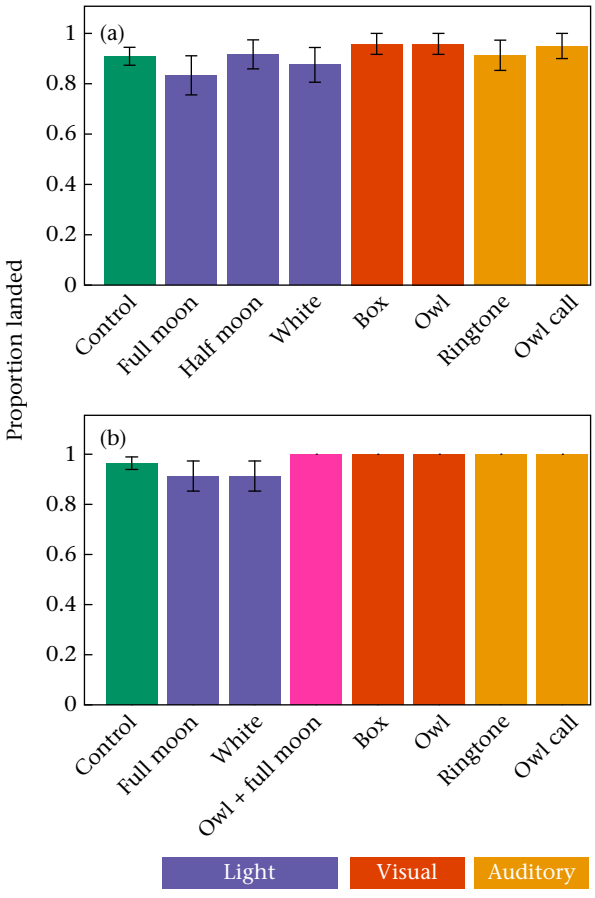

Figure 2. Proportion of trials in which (a) Gamboa and (b) Barro Colorado Island (BCI) bats landed on the platform. Bars represent the means ± SE. Note that in (b) there are no error bars for stimuli owl + full moon, box, owl, ringtone and owl call because bats landed in all trials for those treatments.

RESULTS

Gamboa Bats

Of the 47 bats captured in Gamboa, 35 were tested across all stimuli and 12 were tested only in the follow-up experiment. Of the 35 bats (17 females, 7 males) tested across all stimuli, five bats never learned to approach the platform for food and six bats failed to forage while testing and were removed from further experiments ($N = 24$ for analyses). Of the 12 bats (4 females, 8 males) tested in the follow-up experiment, one bat (male) never learned to approach the platform ($N = 11$ for analyses).

In the main experiment, bats readily foraged for the fruit presented. Of the 229 total trials presented to bats in the main experiment, bats landed on the platform in all but 20 trials (91%). We observed substantial variation in the time it took bats to forage (mean ± SD = 426 ± 346 s; range 5–1126 s).

We first assessed the probability of bats landing on the platform across the night and across the trial (within the night) and did not find a significant effect of either ($\chi^2_1 = 0.03$, $P = 0.8560$; trial: $\chi^2_1 = 1.4$, $P = 0.2318$). There was also no significant effect of sex ($\chi^2_1 = 2.3$, $P = 0.133$) or mass ($\chi^2_1 = 1.6$, $P = 0.2063$) and no significant effect of stimulus ($\chi^2_7 = 4.0$, $P = 0.7743$) on the probability of bats landing on the platform (Fig. 2a).

Next, we assessed the latency of bats to land on the platform (s, cube root). We found that night of testing, sex and mass did not significantly influence the latency to land (night: $F_{1,222} = 1.7$, $P = 0.1917$; sex: $F_{1,22} = 0.99$, $P = 0.3298$; mass: $F_{1,21} = 0.44$, $P = 0.5149$); however, we observed a strong effect of trial within night ($F_{1,209} = 15$, $P < 0.0001$), with latencies decreasing across the night (Fig. 3a). When stimulus and trial were included in the model, we continued to find a significant effect of trial ($F_{1,202} = 14$, $P < 0.0002$) and found that full moon treatments were significantly different than control (i.e. darkness) treatments ($P = 0.0304$; Fig. 3b). Post hoc Tukey's tests revealed that the full moon treatment was marginally different than the ringtone treatment ($P < 0.09$). To standardize the data for visualization, we calculated the average landing time in the control treatments (control mean for each bat), then subtracted each bat's response to a treatment from the bat's control mean.

We conducted these same analyses with trials where bats did not land on the platform excluded. We continued to observe a significant effect of trial on latency to land ($F_{1,189} = 12$, $P < 0.0005$). In the model with both trial and stimulus as fixed effects, we observed a significant effect of trial ($F_{1,181} = 9.4$, $P < 0.003$) and marginal effects of full moonlight ($P = 0.0898$) and ringtone ($P = 0.0992$) treatments. Post hoc Tukey's tests revealed no significant differences between treatments.

Because the full moonlight treatment had the strongest impact on behaviour and the ringtone treatment showed the largest effect in the opposite direction, we conducted a follow-up study designed to determine how bats integrate these two stimuli. We found that bats responded similarly to this combined stimulus treatment and to the control conditions ($F_{1,21} = 2.1$, $P = 0.158$), suggesting that they may additively integrate these stimuli.

Barro Colorado Island (BCI) Bats

Of the 24 bats captured on BCI (12 females, 11 males), one bat (male) failed to forage while testing and was removed from further experiments ($N = 23$ for analyses). Of the 216 total trials presented to bats in the main experiment, bats landed on the platform in all but six trials (97%). We observed substantial variation in the time it took bats to forage (mean ± SD = 189 ± 285 s; range 3–1174 s).

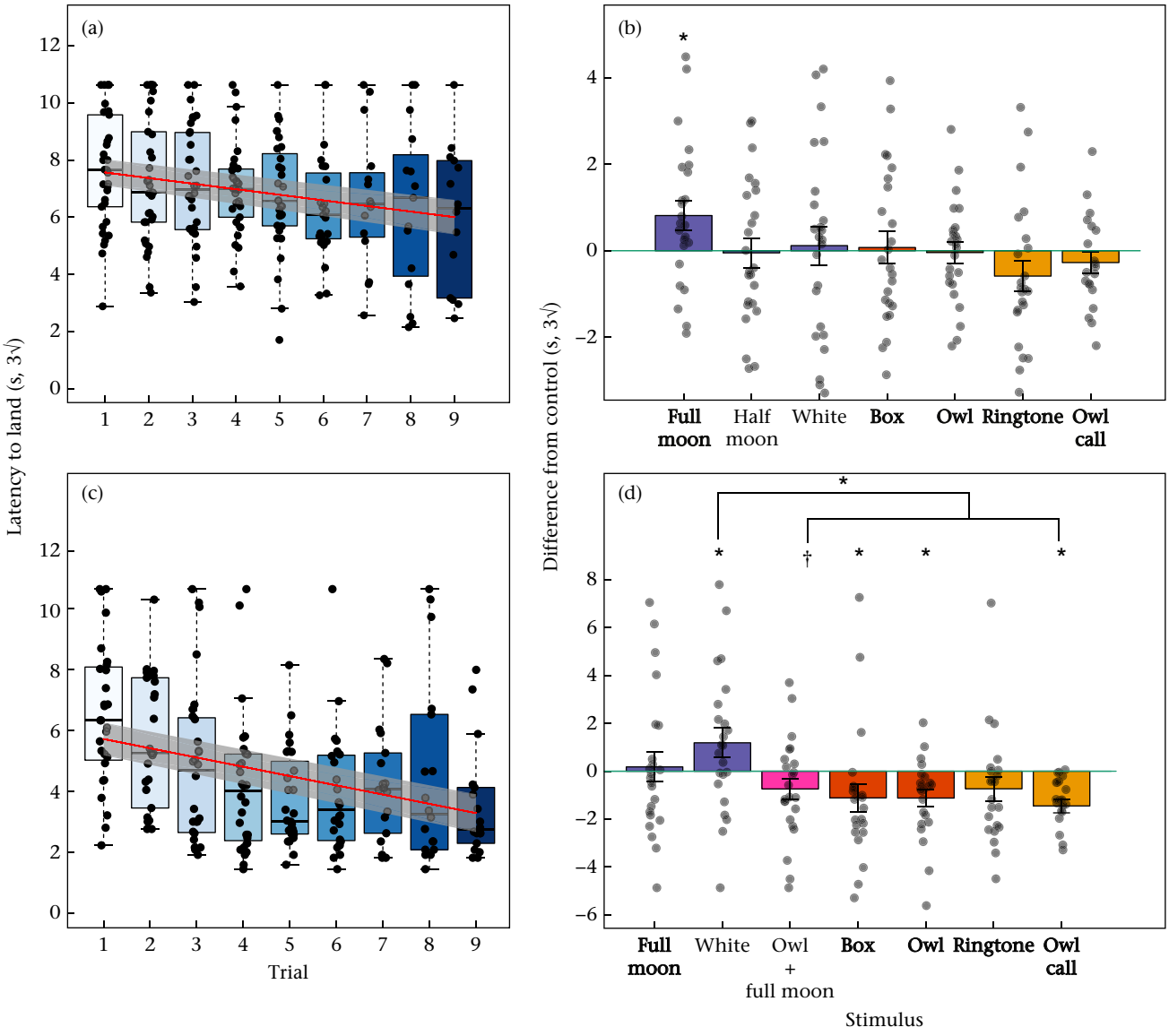

Figure 3. Effects of trial number within a night and stimulus on the latency of (a) Gamboa and (c) Barro Colorado Island (BCI) bats to land on the feeding platform; the red line depicts the output and confidence range from a simple linear regression. Differences in the latency of (b) Gamboa and (d) BCI bats to land on the feeding platform by stimulus; the horizontal green line depicts the mean of all control treatments and error bars are standard errors. Dots depict individual data points. In (b, d), differences from the control treatment, calculated from linear mixed-effects models: †$P < 0.08$; *$P < 0.05$; stimuli in bold on the *X* axis indicate significant differences between Gamboa and BCI bats' time to land on the platform ($P < 0.04$).

Like the Gamboa results, we found that night of testing, sex and mass did not significantly influence the bats' latency to land on the platform (night: $F_{1,201} = 0.65$, $P = 0.4215$; sex: $F_{1,21} = 0.41$, $P = 0.5311$; mass: $F_{1,20} = 0.34$, $P = 0.5688$). However, we observed a strong effect of trial within night ($F_{1,200} = 27$, $P < 0.0001$), with latencies decreasing across the night (Fig. 3c). When we included stimulus and trial in the model as fixed effects, we continued to find a significant effect of trial ($F_{1,191} = 27$, $P < 0.0001$) and a strong effect of stimulus ($F_{7,185} = 4.6$, $P < 0.0001$). White light, box, owl and owl call treatments differed significantly from the control (i.e. darkness) treatment ($P < 0.04$; Fig. 3d), and the owl + full moon treatment differed marginally from the control treatment ($P = 0.0683$). Post hoc Tukey's tests revealed that the white light treatment differed significantly from the other treatments ($P < 0.04$) except for the full moon treatment, and that the full moonlight treatment differed marginally from the owl call treatment ($P = 0.0777$).

We conducted these same analyses excluding trials where bats did not land on the platform (1 = did land on the platform). We continued to observe a significant effect of trial on the bats' latency to land ($F_{1,193} = 29$, $P < 0.0001$). In the model with both trial and stimulus as fixed effects, we observed a significant effect of trial ($F_{1,185} = 28$, $P < 0.0001$) and stimulus ($F_{7,179} = 3.5$, $P < 0.002$). When compared to control, bats responded more slowly in the white light treatments ($P = 0.0329$), faster in the owl call treatments ($P = 0.0083$) and marginally faster in the box and owl treatments ($P < 0.07$). Post hoc Tukey's tests revealed that the white light treatment differed significantly from all other treatments ($P < 0.04$) except the ringtone treatment ($P = 0.0957$).

To determine whether bats in Gamboa responded differently than bats on BCI, we compared control, full moon, white light, box, owl, ringtone and owl call treatment responses across both sites. We conducted unpaired two-sample *t* tests for treatments that were normally distributed and nonparametric two-sample

Wilcoxon tests for treatments that were not normally distributed. Overall, bats on BCI responded faster than bats in Gamboa in the control ($W = 950$, $N = 122$, $P < 0.0001$), full moon ($W = 142$, $N = 47$, $P = 0.0043$), box ($W = 61$, $N = 47$, $P < 0.0001$), owl ($t_{45} = -5.8$, $P < 0.0001$), ringtone ($t_{45} = 130$, $P < 0.004$) and owl call ($t_{41} = -6.2$, $P < 0.0001$) treatments. There was no significant difference for white light treatments ($t_{45} = -1.1$, $P = 0.295$).

DISCUSSION

Prey adjust their foraging behaviour in response to predation pressure (Brown, 1999; Suraci et al., 2019). For instance, correlational studies in many species of bat have documented the phenomenon of 'lunar phobia', describing the hypothesis that bats adjust their foraging behaviour in response to the moon's phase to decrease predation risk from visually orienting predators, such as birds (Clarke, 1983; Kotler et al., 1991). Here, we utilized experimental manipulations to ask whether Jamaican fruit bats would rapidly alter their foraging behaviour in response to changing environmental conditions (light levels) and predator cues (physical or auditory) and whether their behaviour would differ depending on their proximity to urbanization.

We found evidence that bats from our more urban population (Gamboa) were slower to initiate their foraging in simulated full moonlight, providing additional support for the phenomenon of lunar phobia in this species (Morrison, 1978c). Furthermore, we found marginal evidence that a novel auditory stimulus can cause bats to initiate foraging faster. Indeed, playback of this novel auditory stimulus appeared to abolish the effect of moonlight. Contrary to our expectations, we did not see any behavioural response to our white light treatment (1.21 lx), despite a previous study finding an aversion to artificial white light (4.5 lx) in the frugivorous bat *Carollia sowelli* (Lewanzik & Voigt, 2014). It may be that for Gamboa bats, white light at night is perceived as a constant environmental characteristic that has no relation to changes in how the bat's predators behave; the streetlights around the town of Gamboa are consistently on at night. We also note that, while testing the experimental set-up prior to data collection, Jamaican fruit bats (individuals different than those in this study) completely forewent foraging while a brighter (4 lx) white light was on for over an hour.

Bats in Gamboa did not change their foraging behaviour in response to visual cues (owl model or cardboard box). Mobbing behaviour has been observed across various bat species (Knörnschild & Tschapka, 2012; Lučan & Šálek, 2013), and we expected some form of investigation, alarm calling or mobbing of the owl model, but most bats ignored the model. Gamboa bats also did not respond to auditory cues, although we did observe a marginal effect of the ringtone treatment. Although some bats do not alter their behaviour in response to predators' acoustic cues while foraging in the wild (e.g. Neotropical aerial insectivorous bats: *Pteronotus alitonus*, *Pteronotus rubiginosus*, *Centronycteris maximiliani*, *Cormura brevirostris*, *Saccopteryx bilineata*, *Saccopteryx leptura* and *Peropteryx kappleri*: Appel et al., 2023; frugivorous species: *Artibeus lituratus* and *Artibeus planirostris*: Breviglieri et al., 2013), other bats rely extensively on acoustic cues while foraging, such as *Trachops cirrhosus* (Page et al., 2014; Tuttle & Ryan, 1981) and *Lophostoma silvicolum* (formerly *Tonatia sylvicola*) (Falk et al., 2015; Tuttle et al., 1985). Other investigations show reduced bat foraging behaviour in the presence of acoustic stimuli, including owl and woodpecker calls (Baxter et al., 2006). In the context of roost emergence, the gleaning bat, *Micronycteris microtis*, delays leaving the roost in response to rain noise (Geipel, Smeekes, et al., 2019), although roost emergence is not delayed by traffic noise (Geipel, Amin, et al., 2019). Future studies could test how broadcasting novel auditory cues outside the roosting or feeding sites of Jamaican fruit bats may affect emergence times or feeding behaviours.

The bats from our more rural population (BCI) behaved differently than the bats in Gamboa. The BCI bats responded faster to ringtones and owl calls and their latencies to respond to these stimuli differed significantly from the latencies for the Gamboa bats. Although audiograms suggest that the low frequencies of owl calls may be particularly difficult for Jamaican fruit bats to detect (Heffner et al., 2003), our results show that BCI bats were sensitive to these sounds. There can be discrepancies between different methods used to measure auditory sensitivity (as shown in frogs; Taylor et al., 2019), and we also acknowledge that changes in bats' behaviour to the owl call stimuli may include their responses to the forest noise included in the stimuli. Further work is needed to understand the exact acoustic features that elicit variation in responses. Hearing in bats is crucial for navigation, and previous work has shown that noise pollution can negatively impact bat foraging behaviour (Bunkley & Barber, 2015; Domer et al., 2021; Luo et al., 2015; Schaub et al., 2009; Siemers & Schaub, 2011; Wang et al., 2022). If populations of bats differ in their levels of sensitivity after prolonged exposure to urbanization, shifts in bat audiograms would be a worthwhile area of future study.

We also observed sensitivity to white light in the BCI bats, behaviour we did not observe in the bats of Gamboa. We expected bats to respond more slowly in white light treatments, as bats have previously been shown to be aversive to foraging in artificial white light (Barré et al., 2023; Lewanzik & Voigt, 2014). The responses of the BCI bat population are consistent with previous work showing that bats spend overall less time outside of their roost and beeline towards fig trees rather than assess multiple food sources when foraging conditions are expected to be more dangerous (Morrison, 1978c). However, full moonlight had no significant effect on the bats' foraging behaviour, which is surprising because this is the same location where Morrison radiotracked Jamaican fruit bats and observed lunar phobia in this species. Other studies have also observed decreased foraging behaviour in response to lunar cycles in various bat species (Breviglieri et al., 2017; Elangovan & Marimuthu, 2001; Riek et al., 2010) and other nocturnal animals (Bowers, 1988; Watanuki, 1986; Wolfe & Tan Summerlin, 1989), although behaviours may be related to prey activity (Lang et al., 2006). A loss of moonlight avoidance may suggest a change in predation pressure, as was suggested for a population of Jamaican fruit bats in Puerto Rico that also showed no signs of lunar phobia (Rodríguez-Durán & Vázquez, 2001), or that the design of our experiment (rapid changes compared to long-term observation) captured a different set of behavioural responses. Furthermore, lunar phobia cannot be generalized across all species of bats, as it is not supported in many frugivorous (Gannon & Willig, 1997) and insectivorous (Hecker & Brigham, 1999; Musila et al., 2019; Negraeff & Brigham, 1995) species, and overall responses to lunar cycles are disparate in nocturnal mammals (Erkert, 1974; Prugh & Golden, 2014). As shown for Jamaican fruit bats, antipredator responses can vary not only between species within a taxon but also across populations of species.

Overall, BCI bats responded faster than Gamboa bats in most treatments (control, box and owl model). The distribution of food sources and safe refuges can also affect antipredator behaviour observed in our experiment. Variation in food availability can modulate predation risk and thus may depend on seasonality or refuge distance to food sources (Gable et al., 2023) or can be affected by anthropogenic effects (Van Scoyoc et al., 2023). For example, bats do not have to return to day roosts or find safe feeding roosts in the forest when fruiting fig trees are near human structures (e.g. B. A. Sealey, personal observations in Gamboa).

Experience with human infrastructure may explain the lower impact of experimental manipulations on Gamboa bat behaviour compared to the BCI bats. Both populations are exposed to predation from spectacled owls and other nocturnal predators, but we conjecture that Jamaican fruit bats on the mainland are protected from predation by their proximity to anthropogenic activity whereas Jamaican fruit bats on the island are not, as anthropogenic activity is much lower. Behavioural divergence can occur within a species because of many external and internal factors, and other populations of Jamaican fruit bats may respond differently. However, our results suggest that anthropogenically induced variation in environmental factors explain the differences in antipredator behaviour in two populations of this species.

Stimuli tested within the same individual were not independent of each other and there was wide variation in individual responses to the experimental stimuli. We found an effect of trial number in populations and included this variable as a fixed effect in all models to account for the fact that bats responded more quickly as the night progressed. Unfortunately, we lacked sufficient power to detect whether the previous stimuli affected the behaviour of the next trial because we did not have large enough sample sizes to run the models on each trial independently. Despite this overall pattern in trials within a night, some individuals were always fast (bat 153, 0.2–2 min), others were always slow (bat 34, ~13–20 min) and some bats showed wide variation in their latency to land on the platform (bat 141, ~1–20 min). Wide variation in responses may have also contributed to marginal effects observed across various tested stimuli. Because Jamaican fruit bats must sometimes travel long distances to find fruit sources (at most 0.6 km for BCI bats: Morrison, 1978a; 10 km for mainland bats in Mexico: Morrison, 1978b), we expect that bats can utilize many different strategies to not only find these fruit resources, but also to evade predation during travel time. One form of this evasion may be the time bats take to approach food sources and/or how they approach them (flight paths). Morrison (1978b) remarked upon differences in commuting strategies between male and female Jamaican fruit bats, but these differences were not observed in our study, perhaps because bats were not competing for the platform during testing. Previous work has shown variation in flight paths of Jamaican fruit bats to food sources in response to odour cues (Brokaw et al., 2021) and variation in flight paths of numerous bat species under artificial light at night (Barré et al., 2023). Bats in our study may have used different approaches to the platform in different stimulus trials, but we were limited in our resources to effectively track flight paths.

Our experimental design had several limitations because we only quantified two responses of adult bats: whether bats landed on a food platform and their latency to land on the platform. Bats have a suite of behaviours they could display in response to environmental or predator cues, such as alarm calling (González-Palomares et al., 2021; Huang et al., 2015; Russ et al., 1998), mobbing (Knörnschild & Tschapka, 2012; Lučan & Šálek, 2013) or changing their flight path (Barré et al., 2023) as well as physiological changes (stress hormones; Song et al., 2020). While we did not observe alarm calling in response to stimuli tested, we were not able to quantify other potential antipredator responses. Although infrequent, we did observe one female in Gamboa and one male on BCI appear to approach the owl model. It would be interesting to investigate whether this is fear-induced behaviour, as seen in Caribbean cleaner fish, which show heightened cortisol levels but nevertheless inspect predatory fish (Soares et al., 2012). Future studies would benefit from utilizing devices that can quickly record rapid physiological changes in small mammals.

Previous studies have demonstrated that response to fear is state dependent, and animals are capable of overcoming fear aversions to engage in risk-prone behaviour when hungry (Anholt & Werner, 1995; Caraco, 1981). Future work could test whether aversion to full moonlight can be overcome by hunger. Such investigations should be conducted with caution, however, as bats in the wild have access to a wide variety of food choices, and captive experiments may not fully capture the range of behavioural shifts one might find in nature in response to perceived increases in predation risk. Jamaican fruit bats, for example, eat other fruits besides figs when figs are not as readily available (Teixeira et al., 2009), in addition to nectar, pollen and occasionally insects (Kunz & Diaz, 1995; Rodríguez-Durán & Vázquez, 2001; Teixeira et al., 2009). Different food resources may be linked to different degrees of potential predation risk. While bats may show risk-prone behaviour in captive experiments, in the wild, they may shift to safer food resources, for example those found closer to their roosts. Interpretation of responses to environmental variation should consider foraging habits, predation risks in those areas, food availability and trade-offs associated with these variables.

Overall, antipredator behaviour can result in decreased time spent foraging (Lima, 1985), increased caution to approach food sources (Smith et al., 2017) or shifting to less energy-rewarding food sources (Caldwell, 1986). More studies in predator–prey dynamics would benefit from experiments done from the perspective of the predator. We know that nonvisually oriented prey are light aversive and that many visually oriented predators become more vigilant during full moon nights (Prugh & Golden, 2014). To better understand the relationship between bats and their nocturnal visually orienting predators, we need increased investigation of predator hunting behaviour and how it fluctuates in different environmental conditions, such as increased moonlight. We might predict two outcomes: predators are more active during full moon nights and are more successful during increased light availability. Different types of predators are active in different environmental conditions and habitats, and prey adjust their foraging behaviour depending on the activity of their predators and the availability of food at various temporal and spatial scales (Bouskila, 1995). Studying predator–prey dynamics can reveal how animals interact within their environment to either find or avoid each other and can explain the mechanisms by which prey species adapt to mitigate predation risk.

Author Contributions

Briana A. Sealey: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft, Writing – review & editing. **Logan S. James:** Formal analysis, Methodology, Software, Visualization, Writing – review & editing. **Gregg Cohen:** Funding acquisition, Investigation, Methodology, Project administration, Resources. **Michael J. Ryan:** Conceptualization, Formal analysis, Funding acquisition, Supervision, Visualization, Writing – original draft. **Rachel A. Page:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Data Availability

Data set and code are available on Texas Data Repository (https://doi.org/10.18738/T8/OKCFHW).

Declaration of Interest

The authors declare no conflicts of interest.

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