



# Mid-flight prey switching in the fringed-lipped bat (*Trachops cirrhosus*)

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## Abstract

While foraging, eavesdropping predators home in on the signals of their prey. Many prey signal from aggregations, however, and predators already en route to attack one individual often encounter the signals of other prey. Few studies have examined whether eavesdropping predators update their foraging decisions by switching to target these more recently signaling prey. Switching could result in reduced localization errors and more current estimates of prey location. Conversely, assessing new cues while already in pursuit of another target might confuse or distract a predator. We tested whether fringed-lipped bats (*Trachops cirrhosus*) switch prey targets when presented with new cues mid-approach and examined how switching and the distance between simulated prey influence attack accuracy, latency, and prey capture success. During nearly 80% of attack flights, bats switched between túngara frog (*Engystomops pustulosus*) calls spaced 1 m apart, and switching resulted in lower localization errors. The switching rate was reduced, and the localization advantage disappeared for calls separated by 3 m. Regardless of whether bats switched targets, attacks were less accurate, took longer, and were less often successful when calls were spaced at larger distances, indicating a distraction effect. These results reveal that fringed-lipped bats attend to cues from non-targeted prey during attack flights and that the distance between prey alters the effectiveness of attacks, regardless of whether a bat switches targets. Understanding how eavesdropping predators integrate new signals from neighboring prey into their foraging decisions will lead to a fuller picture of the ways unintended receivers shape the evolution of signaling behavior.

**Keywords** Eavesdropping · Call timing · Túngara · Sensory ecology · Predation · Distraction

## Introduction

Acoustically oriented eavesdropping predators exploit the intraspecific calls of other species to detect and localize their prey and regularly complete this task in the presence

background noise or of sound cues from multiple potential targets (Goodale, Ruxton et al. 2019). Prey producing sexual advertisement calls, for example, often aggregate in leks or surrounding breeding resources (Bradbury 1981). As a result, eavesdropping predators can experience the calls of multiple individual prey in short succession and are faced with decisions about which prey to pursue.

Much research has focused on the preferences and attack effectiveness of eavesdroppers choosing among prey. Studies in this area have included examinations of responses to multiple call variants (Ryan, Tuttle et al. 1982; Page and Ryan 2008; Akre, Farris et al. 2011; Aihara, de Silva et al. 2016; Lee, Kirtley et al. 2019), to multiple species of prey (Jones, Ryan et al. 2014; Trillo, Bernal et al. 2016), and to variation in the density of calling prey (Ryan, Tuttle et al. 1981; Hemingway, Ryan et al. 2018; Prakash, Greif et al. 2021; Ruether, Brady et al. 2021). They have even addressed the influence of natural and anthropogenic noise on these responses (Page and Ryan 2008; Senzaki, Yamaura et al. 2016; Allen, Hristov et al. 2021), as well as strategies for

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overcoming the challenges posed by noise, such as the use of cues from multiple sensory modalities (Gomes, Page et al. 2016).

By contrast, relatively few studies have addressed how eavesdroppers respond to another sort of variation that is present within nearly every aggregation of signaling prey: inter-individual variation in call timing. Moreover, work on this topic has focused on calls that temporally overlap or that are separated by almost no gap (Tuttle and Ryan 1982; Legett, Hemingway et al. 2020; Legett, Aihara et al. 2021). While synchronous calling is an important strategy employed by some species, most aggregations of calling prey, including many multi-species assemblages, are characterized by asynchronous calling activity. Because it can render signals more attractive to females, neighboring signalers in nature often adjust the timing of their vocalizations as not to overlap (Zelick and Narins 1983; Klump and Gerhardt 1992; Grafe 1996; Greenfield 2015).

For most eavesdropping predators, there is travel time between the decision to approach a prey individual and the moment of attack. During this time, and in the context of asynchronous calling, predators can experience new calls either from the same individual or other prey nearby and may integrate this new information into their foraging decisions. Three major factors may benefit predators who successfully integrate additional acoustic cues en route to attack. First, more recent cues are likely to provide better information about the current location of prey. If prey are moving independently of predator behavior (e.g., Desutter-Grandcolas 1998) or if they have detected the predator and are attempting to flee (e.g., Bulbert, Page et al. 2015), they may no longer be in the location from which the call that triggered pursuit behavior was emitted. In this case, it would be useful for a predator to update its assessment about the location of the original prey individual or to switch to pursue a different target. Second, a predator en route to attack a prey individual will, in many cases, be closer to the aggregation of prey when experiencing subsequent prey-emitted acoustic cues. If the angular localization acuity of the predator while flying is similar to that it possessed when responding to the initial cue, then the absolute estimate of prey location will be more precise for closer targets (Popper and Fay 2005). Finally, subsequent cues received from the same prey individual may be integrated to refine initial estimates of prey location. Generally, if some error is involved in the assessment of a cue, then exposure to additional instances of that cue will reduce uncertainty, even if the cue encodes largely redundant information (Macmillan and Creelman 2005).

All animals have finite cognitive capacities, however, and more sound is not always better (Dukas 2004). In addition to providing useful information, added acoustic energy can also serve either to perceptually mask target cues or to distract foraging animals. For eavesdropping predators, most

work in this area has documented the detrimental effects of biotic and anthropogenic masking noises on attack effectiveness (Page and Ryan 2008; Siemers and Schaub 2011; Gomes, Page et al. 2016; Senzaki, Yamaura et al. 2016). For eavesdropping predators already en route to attack prey and who are faced with integrating new prey cues into their foraging decisions, “distraction” may be the more relevant phenomenon. As opposed to masking, where the perception of a target stimulus is obscured by the co-occurrence of additional stimuli (Fletcher 1940), distraction takes place when sounds, often those that do not overlap spectrally or temporally with target cues, reduce the listener’s performance on a task because they require time, attention, or another finite cognitive or physical resource to assess (Riddell, Rothblat et al. 1969; Parmentier, Elford et al. 2008). There is some evidence that distracting sounds can be an important obstacle for eavesdropping predators. A recent study, for example, found that Pallid bats (*Antrozous pallidus*: Vespertilionidae) are less efficient at localizing prey sounds and show longer attack flight times when distracting noise that does not spectrally overlap those calls is also present (Allen, Hristov et al. 2021).

In the study presented here, we used playback trials to test whether fringed-lipped bats (*Trachops cirrhosus*: Phyllostomidae) attend to frog calls experienced during attack flights and use this information to switch the target of their attacks. We further tested whether mid-flight exposure to calls or switching between targeted prey were associated with variation in attack effectiveness, as quantified by localization errors, attack flight times, and prey capture success. Specifically, we asked (1) do bats act on new information to switch foraging decisions mid-flight? (2) Does the distance between calling prey influence the likelihood that bats will switch targets mid-flight? (3) When bats switch targets mid-flight, does the distance between targets influence the effectiveness of their attacks? (4) When bats do not switch targets, do new, untargeted calls presented mid-flight influence the effectiveness of their attacks, either through distraction or another mechanism?

## Methods

### Study species

Fringed-lipped bats occur in neotropical lowland forests from Mexico to Brazil. A gleaning species, they eavesdrop on the calls and rustles of frogs, lizards, and large insects to locate these prey (Cramer, Willig et al. 2001; Page and Jones 2016). While they can travel several kilometers during a night, they spend much of their time making short attack flights at aggregations of foraging prey (Kalko, Friemel et al. 1999; Jones, Hämsch et al. 2017). At close ranges, under 6 m

and generally closer, they can use echolocation to pinpoint their meals, although such active acoustic signals appear to be most useful in detecting moving targets (Halfwerk, Dixon et al. 2014). *T. cirrhosus* have a long history as a model in the study of the evolutionary, sensory, and cognitive ecologies of foraging via eavesdropping on passive acoustic cues (Page and Jones 2016). Beyond the bat’s own interesting behavior, studies with this species have been instrumental in elucidating how predation pressure shapes the evolution of signal structure and signaling behavior of a preferred prey, and model organism in its own right, the túngara frog (*Engystomops pustulosus*: Leptodactylidae) (Ryan 1985).

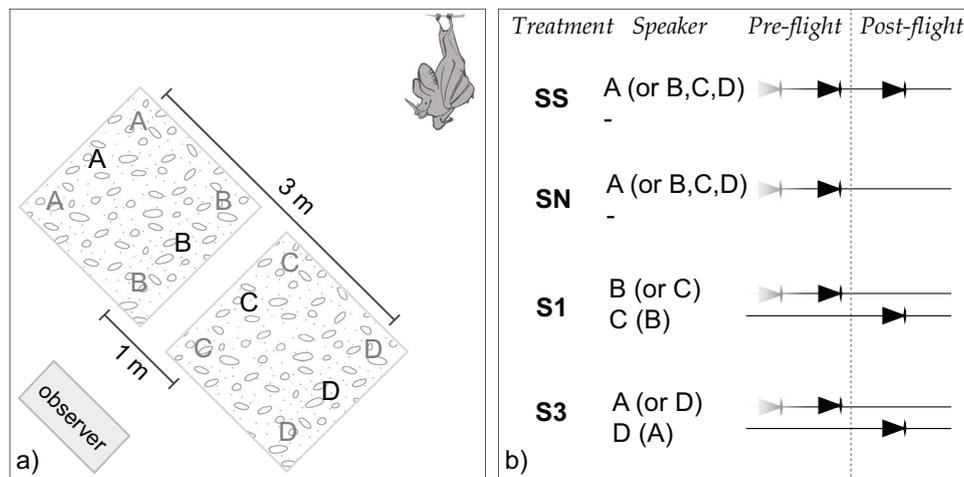
**Animal collection and care**

Trials were conducted with 14 unique adult, non-pregnant, non-lactating *T. cirrhosus* (10 males, 4 females), wild-caught using mist nets along flyways in Soberanía National Park, Panama, in June to August 2016. To ensure that they were provided sufficient food on their first night and to familiarize them with fish, a non-typical prey item, following capture, each bat was hand-fed bait fish in a small tent (2 × 1.5 × 1.5 m) and then released alone into an experimental, open air flight cage (5 × 5 × 2.5 m). Flight cages contained a single, shaded roost (60 × 60 cm) made from semi-opaque black cloth and a shallow tray of water. On the subsequent night post-capture, bats were trained to retrieve a fish reward from a single speaker on the floor of the flight cage playing calls of *E. pustulosus*. Training was considered complete when the bat regularly visited the speaker in response to call playback. Experimental trials for this study

took place over 1 or 2 consecutive nights per individual. At the end of the study, each bat was marked using a subdermal PIT tag (t-Tag100, Trovan LTD., Isle of Man) and released at its point of capture. All experimental procedures were consistent with ABS/ASAB guidelines (2020) and were approved by the Smithsonian Tropical Research Institute IACUC committee (protocol 2014–0101-2017) and the Panamanian Ministerio de Ambiente (permits SE/AH-2–16 and SE/AH-2–17).

**Experimental arena**

Bats were tested in the same flight cage in which they were housed. On the arena floor were two 2 × 2 m platforms, consisting of wooden frames across which acoustically transparent plastic window screening was stretched. The bat’s roost was in the corner of the flight cage, such that one platform lay to each side (Fig. 1a). Under each platform, we placed an array of six speakers (Fostex FE103En, Foster Electronic, Tokyo) in a 1 m grid. These were powered by a 2-channel amplifier (PCA2, Pyle Audio, Brooklyn), and the signal was provided by a laptop computer (T460, Lenovo, Hong Kong). An experimenter in the corner of the flight cage opposite the roost controlled stimulus presentation. Two infrared video cameras (HDRCX900/B, Sony, Tokyo) were mounted beside and above the experimenter and were focused on the roost and screens, respectively. In addition to the cameras’ onboard LED illuminators, the flight cage was lit with two high-power LED IR lights (80AIR, Okba Industries) and a dim 25 W incandescent red light.



**Fig. 1** Experimental setup and experimental stimuli: **a** positioning of speakers (A, B, C, and D) under leaf litter covered mesh platforms, human observer, and bat (not to scale) within the flight cage. Black letters show one of three possible distances for each playback stimulus, and gray letters show the other two distances. **b** The four experimental treatments. Complex, “whine-chuck” túngara frog calls, rep-

resented in the figure by simplified waveforms, were played from a starting speaker until the bat took flight, and then one more call was played from the same speaker (SS), no additional calls were played (SN), or a new call was played from a location 1 or 3 m away (S1 and S3). When call locations were switched, new calls were always played at the same distance from the roost

To interfere with the bats' ability to use echolocation to locate fish rewards, the entire surface of each platform was covered in dry, curled leaves (Arlettaz, Jones et al. 2001). This strategy, combined with the small size of the fish pieces ( $< 1 \text{ cm}^2$ ), proved effective, as the bats were never observed collecting food without landing, a behavior commonly observed for frog-sized targets on less structurally complex surfaces (M.C. pers obs.). A previous study similarly found that leaf litter increased the flight time for *T. cirrhosus* attempting to locate frog-sized prey in a comparable experimental setup (Gomes, Page et al. 2016). To facilitate the measurement of localization errors from recorded video of trials, each platform was marked with small pieces of retroreflective tape ( $\sim 1.5 \times 1.5 \text{ cm}$ ) to form a 25 cm grid. This grid could not be seen under the dim red light in the arena but shone brightly in video recordings due to the cameras' onboard light sources.

### Trial procedure and experimental stimuli

All trials were conducted between 1900 and 0300 h. Bats spent most of their time hanging from the roost, but if not in the roost before the beginning of each trial, they were encouraged to return by the experimenter, who slowly approached the bat while snapping their fingers. The bat was then presented with one of four experimental treatments. All treatments consisted of an identical base stimulus — a synthetic complex túngara frog call, consisting of a “whine” with a single “chuck,” constructed to have mean acoustic characteristics of the local population of this frog (Ryan and Rand 1990), and played at 75 dB SPL (re. 20  $\mu\text{Pa}$ , C-weighted, max, fast response) at 1 m, which is within the range of call amplitude of these frogs in the wild (Ryan 1985). The spatial and temporal arrangement of this call varied between the four experimental treatments as follows (see Fig. 1b for general speaker positions): *SS*, a call was played from one speaker pre-flight and then again from the same speaker during flight; *SN*, a call was played from one speaker pre-flight, and no call was played during flight; *S3*, a call was played from one speaker pre-flight, and during flight, a call was played from a speaker 3 m from the first; *S1*, a call was played from one speaker pre-flight, and during flight, a call was played from a speaker 1 m from the first.

Before each trial, a fish reward was placed over the speaker to play the pre-flight call and over the mirror of that location on the other platform, which may or may not have played a mid-flight call, depending on treatment. The experimenter also touched the other speaker locations in a haphazard order, so that the bat could not use the experimenter's behavior to identify reward locations. The experimenter then monitored the bat through the camera trained on the roost, and the initial pre-flight call was repeated in each trial every 2–5 s until the bat dropped from its perch,

at which point the mid-flight call, if any, was immediately played. Latencies between the bat alighting from the roost in response to the pre-flight call and playback of the mid-flight call were dependent on the reaction time of the experimenter and fell between 200 and 1000 ms, at which point the bat was between  $\sim 0.5$  and 2 m from the roost. Each bat was presented with 15 repetitions of all four stimuli in random order (60 trials total). To control for any side bias within the arena, half of the trials began with the pre-flight stimulus on the right platform and half on the left platform, in random order. For each bat, each stimulus was played at each of the three distances from the roost five times, also in random order. After each trial, the experimenter recorded whether the fish reward had been collected from the platform where the bat landed.

Different playback locations within our arena were slightly different distances from the overhead roost. Some locations were also closer to the flight cage walls, which could have introduced acoustic reflections. We used Kruskal–Wallis and Mann–Whitney *U* methods to test for any differences in localization errors or flight times for trials at different positions on the platforms (between the three rows of speakers and between the inside and outside columns of speakers) using responses to the SS stimulus and found no such biases.

### Scoring of videorecorded trials

Responses to each trial were scored from roost and platform video recordings by trained observers blind to treatment and blind to experimental design. To facilitate error checking, two observers independently scored each trial. They recorded the flight time of bats between the moment they dropped from the perch to the moment they landed on a platform, which platform the bat landed on, and the coordinates on the platform of the landing. From videos, observers were able to record coordinates at  $\sim 2 \text{ cm}$  resolution. These coordinates were later used to calculate localization errors from the speaker on that platform which produced sound. If bats failed to land on the platform or landed somewhere else before visiting the platform, those trials were excluded from analysis.

### Statistical analyses

We tested for inter-stimulus variation in the rate at which bats switched targets mid-flight and in the effectiveness of attacks using a series of generalized mixed models in SPSS (v.28, IBM corporation, Armonk), as described below. In general, to test whether inter-call distance, switching, or an interaction between the two affected attack effectiveness (localization accuracy, attack flight time, or food capture success), we compared responses to the 1 m (*S1*)

and 3 m (S3) spacing treatments. To determine whether a distraction effect altered attack effectiveness, we compared responses to the SN treatment, where bats experienced only a pre-flight call, to S1 and S3 trials where bats heard a mid-flight call, but did not switch to attack it. To further examine whether mid-flight information influenced attack effectiveness, we compared responses to the SN stimulus with those to the SS stimulus, where both a pre- and mid-flight calls were played from the same speaker.

Occasionally, bats ignored the SN and SS stimuli and landed on the platform with no playback. Similar behavior likely occurred in S1 and S3 trials but would not have been detectable and likely added additional random variation to our data, working to obscure any patterns. To avoid confusion in presentation of the results, these SN and SS trials have been excluded from all but the first model, which focuses on the effect of treatment on switch rates. We did, however, construct alternate versions of each model including these data in several conservative ways (e.g., scoring such trials as resulting in the maximum possible localization error). Likely due to the small number of these trials, all alternate models were consistent with the results presented below:

- GLMM1: binomial distribution with logit link. Individual bat is entered as a random effect. Effects of inter-call distance treatment (S1, S3, SN, SS) on whether bats landed on the platform where the pre-flight call was played during each trial.
- GLMM2: gamma distribution with log link. Individual bat is entered as a random effect. Effects of inter-call distance treatment (S1, S3), whether bats switched targets mid-flight (switch, no switch), and the interaction between these two factors (inter-call distance\*switched) on localization error.
- GLMM3: gamma distribution with log link. Individual bat is entered as a random effect. Effects of inter-call distance treatment (S1, S3, SN, SS) on localization error. In order to study any effects of mid-flight information not acted upon (SN vs. S1 and S3) and to test whether flight times varied with the presence of mid-flight information (SN vs SS), this model includes only bats that did not switch platforms in response to mid-flight playback.
- GLMM4: gamma distribution with log link. Individual bat is entered as a random effect. Effects of inter-call distance treatment (S1, S3), whether bats switched targets mid-flight (switch, no switch), and the interaction between these two factors (inter-call distance\*switched) on attack flight times.
- GLMM5: gamma distribution with log link. Individual bat is entered as a random effect. Effects of inter-call distance treatment (S1, S3, SN, SS) on attack flight times.

This model includes only bats that did not switch platforms in response to mid-flight playback.

- GLMM6: binomial distribution with logit link. Individual bat is entered as a random effect. Effects of inter-call distance treatment (S1, S3), whether bats switched targets mid-flight (switch, no switch), and the interaction between these two factors (inter-call distance\*switched) on food capture success.
- GLMM7: gamma distribution with log link. Individual bat is entered as a random effect. Effects of inter-call distance treatment (S1, S3, SN, SS) on food capture success. This model includes only bats that did not switch platforms in response to mid-flight playback.

We report sequential Bonferroni adjusted significances for all post hoc Z tests and use 2-tailed P values throughout.

## Results

### Did bats switch foraging decisions mid-flight?

Bats readily flew to speakers playing frog calls in our arena, and the likelihood that they switched foraging choices depended on whether they were presented with additional information mid-flight (GLMM1,  $\chi^2_{(3,603)}=57.2, P<0.001$ ) (Table 1). When calls were played from a speaker on only one of the two platforms, bats rarely approached silent speakers on the other platform (doing so in 6.5% of SS trials

**Table 1** Rates at which bats switched targets mid-flight in response to new information about prey location: SS, a call was played from one speaker pre-flight and then again from the same speaker during flight. SN, a call was played from one speaker pre-flight, and no call was played during flight. S3, a call was played from one speaker pre-flight, and during flight, a call was played from a speaker 3 m from the first. S1, a call was played from one speaker pre-flight, and during flight, a call was played from a speaker 1 m from the first. Z test results are shown for post hoc pairwise contrasts following GLMM. Significance values have been adjusted using the sequential Bonferroni method

Stimulus	Switch rate		
SS	6.5% (10 of 155 trials)		
SN	16.1% (18 of 112 trials)		
S3	54.9% (78 of 142 trials)		
S1	78.2% (133 of 170 trials)		
Pairwise contrasts	Z	df	Adj. Sig
SS vs. SN	2.18	603	0.029*
SS vs. S1	18.44	603	< 0.001*
SS vs. S3	9.45	603	< 0.001*
SN vs. S1	14.71	603	< 0.001*
SN vs. S3	7.65	603	< 0.001*
S1 vs. S3	-4.35	603	< 0.001*

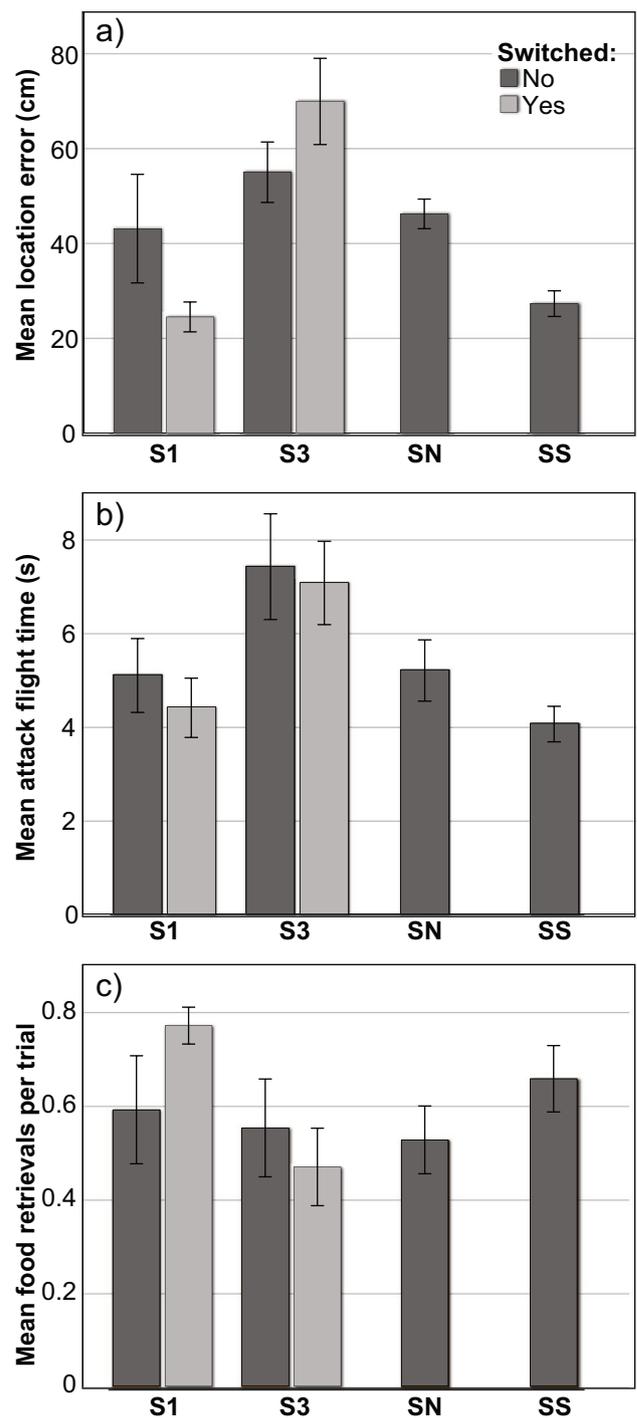
and 16.1% and SN trials) (Table 1). In these cases, it is notable that the rate at which bats approached the other, “incorrect,” platform was lower when a second call was played mid-flight from the same speaker.

By contrast, when presented with a second, mid-flight, call played from a speaker 1 or 3 m away from the speaker which played the call that initiated a foraging flight, bats often switched to approach the second call (Table 1). When the mid-flight call originated from a position 1 m from the first call, bats switched to the new target in 78.2% of trials. When the mid-flight call originated 3 m from the original call, bats switched targets at a lower rate (54.9%, S1 vs. S3) (Table 1).

### Was localization error affected by information presented mid-flight?

Target localization errors were strongly influenced by calls played during foraging flights, and this effect was dependent on the distance between the speakers playing the pre- and mid-flight calls. There was a significant interaction between inter-speaker distance treatment and whether or not bats switched targets mid-flight in their effect on localization error (GLMM2 inter-call distance\*switched,  $\chi^2_{(1,308)} = 8.33$ ,  $P = 0.004$ ). When pre- and mid-flight calls were played 1 m apart, bats that switched targets mid-flight showed lower localization errors (S1 switch,  $24.53 \text{ cm} \pm 11.4 \text{ SD}$ ,  $N = 13$  bats, 133 trials; no switch,  $43.17 \text{ cm} \pm 42.9$ ,  $N = 14$  bats, 37 trials;  $Z = -2.57$ ,  $P = 0.041$ ) (Fig. 2a). The advantage of switching disappeared and trended in the opposite direction, when pre- and mid-flight calls were played 3 m apart (S3 switch,  $55.1 \pm 23.9 \text{ cm}$ ,  $N = 14$  bats, 78 trials; no switch,  $28.4 \pm 12.7 \text{ cm}$ ,  $N = 14$  bats, 64 trials;  $Z = 1.67$ ,  $P = 0.096$ ) (Fig. 2a). There was also an overall effect of call spacing on localization errors, with less accurate localization in response the calls spaced by 3 m versus those spaced by 1 m, regardless of whether or not bats switched between targets (GLMM2 inter-call distance,  $\chi^2_{(1,308)} = 39.8$ ,  $P < 0.001$ ).

When focusing on trials where bats did not switch away from the platform from which pre-flight calls were played, again localization errors were strongly affected by stimulus treatment (GLMM3,  $\chi^2_{(3,364)} = 10.34$ ,  $P < 0.001$ ). Compared to their responses to a pre-flight call played alone, bats did not show any significant reduction in localization performance when they were also exposed to mid-flight calls that they did not attack (SN vs. S1,  $Z = 1.42$ ,  $P = 0.432$ ; SN vs. S3,  $Z = -0.883$ ,  $P = 0.432$ ) (Fig. 2a). Localization errors were lower, however, when bats experienced both a pre- and mid-flight call from the same speaker, as compared to when they were presented with a pre-flight call alone (SS,  $27.3 \text{ cm} \pm 10.1$ ,  $N = 14$  bats, 155 trials; SN,  $46.3 \text{ cm} \pm 11.7$ ,  $N = 14$  bats, 112 trials;  $Z = -3.97$ ,  $P < 0.001$ ) (Fig. 2a).



**Fig. 2** Attack effectiveness of bats ( $N = 14$ ) in response to acoustic stimuli varying in the presence and relative spacing of additional frog calls played mid-flight. Responses where bats switched to attack calls spaced 1 m ( $n = 133$  trials) and 3 m ( $n = 78$  trials) from pre-flight calls are displayed separately from responses where bats attacked the source of the pre-flight call (1 m,  $n = 37$  trials; 3 m,  $n = 64$  trials). Shown are **a** means of mean localization errors exhibited by each bat. **b** Means of mean attack flight latencies exhibited by each bat and **c** means of mean rate of successful food retrieval exhibited by each bat

## Were flight times affected by information presented mid-flight?

The latency between the moment a bat dropped from its perch to landed on the platform varied with presence and type of information presented mid-flight. Bats showed longer flight times when targets were separated by 3 m vs. 1 m (3 m,  $7.2 \text{ s} \pm 3.7 \text{ SD}$ ,  $N = 14$  bats, 142 trials; 1 m,  $4.8 \text{ s} \pm 2.6 \text{ SD}$ ,  $N = 14$  bats, 170 trials; GLMM4 inter-call distance,  $\chi^2_{(1,308)} = 15.88$ ,  $P < 0.001$ ). Flight times were not, however, significantly influenced by switching or the interaction between switching and call separation.

Our GLMM that focused on attack flight times during trials where bats did not switch away from the platform where pre-flight calls were played showed a significant effect of stimulus treatment (GLMM5 treatment,  $\chi^2_{(3,364)} = 9.67$ ,  $P = < 0.001$ ). This was largely driven by shorter flight times in the single speaker stimuli (SN and SS) as compared to flight times for bats that did not switch targets when calls were presented 3 m apart (SN vs S3,  $Z = -3.15$ ,  $P = 0.009$ ; SS vs. S3,  $Z = -4.34$ ,  $P < 0.001$ ) (Fig. 2b). In non-switching trials, there was no significant difference between any of the other pairwise comparisons.

## Was capture success affected by mid-flight information?

The likelihood that a bat was successful in retrieving a food reward was dependent on the presence and type of information presented mid-flight. Regardless of whether they switched targets mid-flight, bats were more likely to retrieve food from a speaker playing frog calls if the distance between pre- and mid-flight calls was 1 m than if the calls were separated by 3 m (1 m, 129 of 170 successful attacks; 3 m, 80 of 142 attacks; GLMM6 treatment,  $\chi^2_{(1,308)} = 9.34$ ,  $P = 0.002$ ). Neither whether the bat switched targets nor the interaction between inter-call distance and switching significantly affected prey capture success. There was, however, a non-significant trend that mirrored that for localization error and flight time, with food retrieved more often when bats switched targets in the 1-m separation treatment and less often when they switched targets in the 3-m separation treatment (Fig. 2c). Among trials where bats landed on the platform from which pre-flight calls were played, we found no significant effect of stimulus treatment on food retrieval success (Fig. 2c).

## Discussion

Results from this study provide clear answers to each of the questions that we initially posed. Fringed-lipped bats do act on new information mid-flight by switching to attack

alternative targets (Table 1). When calls were separated by 1 m, bats switched to target new prey in over 78% of trials. The distance between calling prey affected the likelihood with which bats switched, dropping to a rate of only 55% when prey were separated by 3 m. Furthermore, all three measures of attack effectiveness we quantified varied with the presence and relative source location of calls experienced mid-flight.

## Switching and attack effectiveness

Switching targets strongly influenced localization accuracy, but this depended on the distance between calling prey. Bats that switched targets in response to mid-flight calls spaced 1 m from the pre-flight call benefited in terms of reduced localization errors compared to those that did not switch. Bats that switched between targets separated by 3 m, however, suffered increased localization errors compared to those that did not switch (Fig. 2a). Localization benefits seen at closer inter-call distances may be due to the simple geometry of localization. For an animal with a consistent localization acuity, assessing targets at closer distances (i.e., when the mid-flight call was played) will result in smaller linear localization errors. This explanation is consistent with reduced localization errors that resulted from trials where the pre- and mid-flight calls were played from the same speaker (SS). On the other hand, in trials where speakers were separated by 3 m, bats would not have experienced as great a decrease in the distance to the source of the mid-flight call, because they had already traveled some distance towards the location of the pre-flight call. Furthermore, the pinnae of *T. cirrhosus* are remarkably directional for sound frequencies in the range of frog calls (Obrist, Fenton et al. 1993), which presumably improves localization acuity for sounds originating from the forward direction. During attack flights, bats' heads and pinnae were likely oriented towards the first call, especially if ensonifying the area from which the call was emitted (Surlykke, Jakobsen et al. 2013). As a result, they would have experienced mid-flight calls in the 3-m separation treatment at greater angles relative to the forward direction of the head than those in the 1-m separation treatment, potentially impairing their ability to localize those sound sources.

Angular localization acuity for passive sound signals has not been quantified for *T. cirrhosus*, but previously reported behavioral measurements of open-loop localization errors (Page and Ryan 2008) are remarkably consistent with open-loop localization errors (SN) reported here. Intuitively, localization errors in response to the SS stimulus in our study, where a single mid-flight call was played, were intermediate to open-loop and closed-loop localization errors reported in the 2008 study. Taken together, these results suggest that prey localization is an iterative task in fringed-lipped bats,

who take advantage of repeated calls from the same source to improve their location estimates. Similar strategies are employed by both eavesdropping barn owls (Konishi 1973) and female frogs attempting to locate mates (Caldwell and Bee 2014).

Switching targets did not affect flight times. It is interesting that no additional assessment or travel times were associated with switching prey targets. We believe that this is likely due two factors. First, most of the variation in attack flight times was due to assessment and searching behaviors rather than time spent in directed travel towards the sound source. The bats in our trials commonly took arcing trajectories or hovered above the platforms, apparently either actively echolocating or waiting for additional prey cues. Second, the bats may have spent additional time in assessment when pre- and mid-flight cues were spatially separated, regardless of whether they ultimately switched to target a new call. *T. cirrhosus* are known to take more arcing trajectories towards a target when faced with auditory scenes of increasing complexity (Rhebergen, Taylor et al. 2015). Barn owls similarly show increased attack flight times when exposed to mid-flight prey rustling sounds, due to changes in speed and posture while assessing sounds mid-flight (Konishi 1973).

While we saw no significant effects of switching on food capture success due to high variance among bats that did not switch targets, mean capture rates were approximately 20% higher in bats who switched to attack mid-flight calls presented 1 m away from initial calls, compared to those who did not switch from their initial target when presented with the same treatment (Fig. 2c). If this pattern is reflective of the natural behavior of these bats, it would be consistent with the lower localization errors seen in those same trials.

### Does exposure to new prey cues mid-flight result in a distraction effect?

Our most direct assessment of whether bats experienced mid-flight calls as distracting (Riddell, Rothblat et al. 1969; Parmentier, Elford et al. 2008) was comparisons of attack effectiveness in trials where they were played a pre-flight but no mid-flight call (SN) versus trials where bats were played mid-flight calls at other locations (S1 and S3) but did not switch to attack these calls. The clearest pattern that emerged from these analyses was increased attack flight times when bats experienced, but did not act on, mid-flight calls played 3 m from the original target of attack. This result suggests that bats were, in fact, distracted by playback of the distant calls, resulting in additional search time before landing.

Fringed-lipped bats also showed a very consistent pattern of higher localization errors, increased attack flight times, and reduced capture success when responding to calls spaced

at larger distances, regardless of whether they switched targets or continued to target the pre-flight call. This suggests that assessment of distantly spaced calls is either cognitively or physically more demanding than mid-flight assessment of calls more closely situated to the bat's original target. This result involved comparisons of performance between treatments in which the same sound stimuli were played in different spatial arrangements. In previous investigations of distraction effects, a single stimulus was played either alone or in the presence of a second distracting sound (e.g., our own comparison of SN vs. S3 trials) (Parmentier and Elford et al. 2008; Allen and Hristov et al. 2021). Nevertheless, these findings again appear to indicate distraction by the more challenging stimulus.

### Mid-flight prey switching and preference for complex calls

An important driver of research interest in the foraging behavior of fringed-lipped bats is their preference for complex, rather than simple, call variants produced by túngara frogs (Ryan, Tuttle et al. 1982). Because complex calls are also preferred by female túngara (Ryan, Akre et al. 2019), this pairing of predator and prey is a key model in our understanding of the balance between ecological and sexual selective forces that shape the evolutionary trajectory of mating signals (Ryan 1985). One major hypothesis for why *T. cirrhosus* prefer complex túngara calls is that such calls are correlated with high-density calling aggregations (number of calling frogs within 1 m) (Bernal, Page et al. 2007). Our results suggest that in these same, high-density contexts, bats are likely to enjoy benefits, in terms of lower localization errors and higher capture success, if they experience and switch to attack the calls of other nearby frogs during foraging flights. That is, it may make sense to approach a complex calling túngara frog, because that frog is likely to be closely spatially associated with other calling frogs that will signal during the attack flight, rendering themselves particularly vulnerable to the eavesdropping bat.

### Implications for prey calling behavior

Mid-flight prey switching behavior by fringed-lipped bats should exert pressures on both the spatial arrangement and relative call timing of their prey. While there is a general tendency for females to prefer clustered males in lek forming species (Isvaran and Ponskhe 2013; Stratman, Oldenhoeft et al. 2021), predators may show similar preferences. *T. cirrhosus*, for example, prefer to attack high-density aggregations of prey (Hemingway, Ryan et al. 2018), a foraging tactic shared with other gleaning bats (Prakash, Greif et al. 2021). As is also seen in the evolution of signal structure (Tuttle and Ryan 1981; Endler 1983; Zuk and

Kolluru 1998; Trillo, Athanas et al. 2013), this sets up a balance between selection by conspecifics and selection imposed by eavesdropping heterospecific enemies. Our results indicate that for the prey of fringed-lipped bats, the degree to which frogs spaced 1 m apart influence the risks they each face is relatively higher than the degree to which the fates of prey spaced by 3 m are intertwined. That is, bats are more likely to switch prey targets at the shorter distance and when they do switch are quicker and more accurate in their attacks. From the perspective of signaling prey, optimal inter-individual spacing will therefore depend upon an interplay between the effects of male density on female attraction and those on predation risk.

Predators that switch targets en route to attack will also exert selective pressures on the relative call timing of their prey. Our results indicate that, generally, more recent calls are preferred by *T. cirrhosus*, at least for prey closely spaced at distances typical of natural aggregations (Bernal, Page et al. 2007). In terms of predation risk, this puts the final prey to signal in a train of calls at a selective disadvantage and may be partially responsible for the rapid rate at which cessation of calling in response to predator cues spreads through a local aggregation of túngara frogs (Tuttle, Taft et al. 1982; Dapper et al. 2011). Such silence is likely an effective antipredation tactic and has been demonstrated both for túngara frog and katydid prey of *T. cirrhosus* (Tuttle, Taft et al. 1982; Jennions and Backwell 1992; ter Hofstede, Kalko et al. 2010). Falling silent, however, almost certainly results in reduced mate attraction. Female túngara frogs en route to a perspective partner, for example, adaptively update their mating decisions, and like their bat predators, switch to approach more attractive calls played from another location (Baugh and Ryan 2010).

Attraction of eavesdroppers to more recent calls may interact with other sorts of preferences measured through two-choice experiments in captivity and in the field. Eavesdropping enemies initially attracted and en route to a given call may shift their attention to a second call, even if that call would not have been initially preferred. This pattern would be consistent with “collateral damage” from eavesdropping parasites suffered by less attractive neighboring frogs in nature (Trillo, Bernal et al. 2016; Trillo, Benson et al. 2019). While collateral damage effects have not been documented as resulting from predation by *T. cirrhosus*, the relevant experiments have been conducted using “closed-loop” methods, where playback repeats every few seconds (Trillo, Bernal et al. 2016; Ruether, Brady et al. 2021), and as mentioned above, *T. cirrhosus* excel at localization when allowed to repeatedly assess prey location as they approach a target. As our current results indicate, bats are likely to integrate information from nearby calling prey and alter their foraging decisions if the initial target falls silent.

## Conclusions

Given the high density of frog choruses where fringed-lipped bats feed in nature, they inevitably experience multiple calls emanating from prey gathered in close spatial proximity, even after targeting a single individual for attack. Our findings suggest these bats commonly switch targets mid-flight, are more likely to switch to target closely neighboring signalers, and that this strategy should allow them to maintain high attack effectiveness even if the initially targeted prey falls silent. It is likely that other acoustically oriented eavesdroppers employ similar strategies. Moreover, these strategies are not neutral with respect to the behavior of prey. Signalers calling from dense aggregations, which are highly attractive to eavesdropping predators, should closely attend to the signaling activity of their neighbors, as risks those neighbors attract may transfer to the last prey left calling.

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## Declarations

**Competing interests** The authors declare no competing interests.

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