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SHORT COMMUNICATION

Aerial hawking in a gleaning specialist bat (*Trachops cirrhosus*) does not involve a high-resolution buzz

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ABSTRACT

Aerial-hawking bats adjust their biosonar in the search, approach and capture phases of echolocation to guide aerial prey interception. Some bat species have secondarily evolved a gleaning strategy that relies on passive acoustic cues to detect and capture prey on vegetation. Here, we tested the hypothesis that such a gleaning specialist, the fringe-lipped bat, *Trachops cirrhosus*, must use stereotyped aerial-hunting echolocation phases, including a buzz when opportunistically capturing aerial prey. Using data from sound-recording tags on 8 individuals, we reject this hypothesis by showing that fringe-lipped bats can detect and intercept aerial prey by echolocation but do so with modest biosonar adjustments and without producing a high-resolution buzz. These findings challenge the notion that the stereotyped echolocation phases of hawking bats are required for aerial prey capture and show that echolocation is an extremely versatile sensory system that can be employed across otherwise specialized foraging niches.

KEY WORDS: Chiroptera, Echolocation, Biologging, Foraging, Behavioral ecology, Sensory ecology

INTRODUCTION

The Eocene evolution of echolocation and powered flight led to an enormous speciation of bats adapting to feeding strategies from frugivory to carnivory across the globe (Speakman, 2001). Among the animal-eating bats, two main foraging strategies exist: hawking aerial insects on the wing and gleaning food items off surfaces (Schnitzler and Kalko, 2001). Mounting evidence suggests that echolocating bats ancestrally evolved gleaning to catch prey using a sit-and-wait strategy relying on prey-emitted acoustic cues – or passive listening – to detect prey (Anderson and Ruxton, 2020). To exploit the niche of night-flying insects, some bat lineages later evolved the ability to use echolocation to catch prey in open air (Ratcliffe et al., 2013). Such aerial hawking is the most widespread foraging strategy in the Order Chiroptera, used as a specialized or opportunistic hunting strategy by ∼70% of bat species. Aerial hawking is central to how we think of bat echolocation from Donald Griffin's pioneering work (Griffin, 1958) onwards. Griffin was the first to propose that aerial hawking of prey with echolocation consists of three biosonar phases: the search, the approach and the terminal buzz phases (Griffin et al., 1960).

During the search phase, aerial-hawking bats probe their environment by calling loudly (typical SL >110 dB re. 20 µPa rms) to maximize the chances of detecting prey (Stidsholt et al., 2021a). These loud calls are enabled by a tight phase coupling to exhalations during wingbeat upstrokes (Holderied and von Helversen, 2003; Koblitz et al., 2010; Stidsholt et al., 2021b), resulting in low biosonar update rates of large sensory volumes. Once prey is detected, hawking bats gradually reduce call duration, amplitude levels and intercall intervals with decreasing range to the prey in what is termed the approach phase. These call modifications reduce the masking of prey echoes from closely preceding outgoing calls and from background clutter, facilitating prey tracking in a simplified auditory scene (Stidsholt et al., 2021a; Wilson and Moss, 2004). This culminates in the terminal buzz phase, where interception is guided by a high-repetition terminal buzz of >100 short, broadband calls per second emitted at low source levels. These rapid weak updates enable tracking of sometimes evasive prey in a very small sensory volume (Stidsholt et al., 2021a). In some species, this fast sampling is further increased in a so-called 'buzz II', characterized by even higher call rates and lowering the fundamental frequency by up to an octave (Ratcliffe et al., 2013), broadening the sonar beam and allowing for tracking of evasive prey (Jakobsen et al., 2013). The ability to buzz is not exclusive to bats but has also evolved in strong evolutionary convergence among echolocating toothed whales (Madsen and Surlykke, 2013; Wisniewska et al., 2014). Buzzes therefore appear to be an essential sensorimotor component when echolocators hunt mobile prey in open spaces. Given that all echolocators appear to buzz when tracking motile prey, it begs the question is it possible for echolocating bats to catch flying prey without buzzing?

Most phyllostomid bats are not known to buzz, as they typically glean motionless food items (i.e. insects and fruits) off surfaces by complementing their echolocation with passive acoustic, olfactory or visual cues (Schnitzler and Kalko, 2001). Their echolocation is characterized by short, broadband, low-amplitude (SL <90 dB re. 20 µPa rms; Surlykke et al., 2013) calls with a high sweep rate produced at short call intervals. This echolocation behaviour presumably acts as an adaptation to orient in the highly cluttered foliage, and supports both stereotyped and specialized echolocation (Barclay et al., 1981; Korine and Kalko, 2005). However, metabarcoding studies have detected traces of flying insects in the faeces of gleaning bats (Ingala et al., 2021), although it remains unclear whether these insects were airborne when consumed. Additionally, one field observation documented up to 170 calls s^{-1} from the presumed gleaning sword-nosed bat, *Lonchorhina aurita* (Gessinger et al., 2019). This raises the question can gleaning specialist bats deviate from their typical echolocation behaviour to target aerial prey by adopting the approach and buzz phases

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of aerial hawking? To address this question, we used onboard sound and movement recording tags on a gleaning specialist: the fringe-lipped bat (*Trachops cirrhosus*). These bats are known to eavesdrop on calls and sounds from vertebrate prey (Tuttle and Ryan, 1981), but a recent tagging study and a stable isotope analysis have demonstrated that aerial insect prey is also caught (Baier et al., 2025) and consumed (Oelbaum et al., 2019). Here, we tested the hypothesis that the fringe-lipped bat, a gleaning specialist, adopts the echolocation phases used by aerial-hawking bats to catch flying prey.

MATERIALS AND METHODS

All bat captures and experiments were licensed and approved by the Smithsonian Tropical Research Institute (IACUC no. SI-23001) and by the Government of Panamá (Ministerio de Ambiente permit ARG-078-2022).

Tags

The tags deployed in both laboratory and field experiments were equipped with an ultrasonic microphone along with a synchronized triaxial accelerometer and magnetometer. The microphone (FG-3329; Knowles Electronics, Itaska, IL, USA) recorded at 187.5 kHz with 16-bit resolution, a 10 kHz 1-pole analog high-pass filter, and a clipping level of 116 dB re. 20 µPa pk in the band where the call energy is most prominent on the tag (60–80 kHz). The accelerometer recorded with a sampling rate of 1000 Hz and 16-bit resolution with a clipping level of 8 ***g***. The acceleration data were downsampled to 100 Hz during analysis.

Field experiments

The study was performed during March and October 2023, near Gamboa, Panamá (9.1287° N, 79.6942° W). Bats, *Trachops cirrhosus* (Spix 1823), were caught from known roosts, either by hand nets during the day or in box nets during emergence. After capture, bats were scanned for subcutaneous passive integrated transponders (PIT; Biomark, Boise, IA, USA) to acquire their information. If a PIT was not present, the bat was injected with a PIT onsite. Afterwards, the bats were weighed, measured and assessed to ensure tag suitability. We tagged non-reproducing, non-lactating adult bats ≥29 g. Juveniles were identified by the presence of epiphyseal gaps in the phalanges (Brunet-Rossinni and Wilkinson, 2009). To protect the tag electronics, we enclosed the tags in balloons with the microphone exposed along with a VHF-transmitter (V5; Plecotus Solutions GmbH, Mullheim, Germany) and glued onto the fur between the scapulae using skin bond latex glue (Sauer Hautkleber, Manfred Sauer, Lobbach, Germany). Bats caught during the day were released back into their roosts, while bats caught at emergence were released immediately after tagging. We relocated the bats within 1–5 days via VHF telemetry, and removed the tag. A total of 20 bats were tagged and recaptured (12 males, 8 females). Of these, 8 were tagged during the dry season and 12 during the wet season. Depending on the mass of the bats at capture, the tag was equipped with either a 40 or 45 mA h battery. This led to a tag mass of 3–3.7 g (including VHF), corresponding to 8–10% of the bats' mass. Bats captured during the day (n=9) were equipped with tags programmed to activate at sunset, whereas the individuals captured at emergence (n=11) were instrumented with a tag that started the recording immediately. The tags recorded for ∼5.5 h, covering the first half of a full night.

Data analysis

Acoustic recordings were manually analysed in MATLAB R2023b or R2025a (MathWorks®, Natick, MA, USA), using custom scripts. To find aerial prey captures, we manually visualized all tag recordings via three synchronized windows *sensu* Baier et al. (2025): (1) audio data high-pass filtered at 60 kHz to show echolocation calls, (2) a full bandwidth spectrogram to visualize the acoustic scene of the bat, and (3) triaxial acceleration data to identify flight and movement (as seen in Fig. 1).

Quantification of behaviours

The behaviour of the bats was divided into flight, chewing and gleaning attempts based on acceleration, orientation and acoustic features *sensu* Baier et al. (2025). Aerial captures were identified by orientation, acceleration and echolocation patterns. The orientation and acceleration patterns associated with an aerial capture were defined as disruptions of normal wingbeat patterns and rapid shifts in body orientation, followed by the presence of mastication sounds mid-flight after the capture. We therefore only analysed successful aerial captures, and our estimates of aerial hawking events are therefore likely to be an underestimate.

Biosonar parameters

For each capture, we determined the time of capture as the last echolocation call in a sequence of relatively low call interval, followed by mastication sounds. All calls within the last 10 s before capture were detected by an automatic call detector *sensu* Stidsholt et al. (2021a) and afterwards visually inspected to remove false positives and add undetected calls to the analysis. For each call, we calculated call interval, call duration, call output level AOL, dB re. 20 µPa, rms and centroid frequency. Call duration was calculated as the −6 dB endpoint relative to the peak of the envelope (Fig. S2). To account for possible measurement artefacts caused by a low signal-to-noise ratio (SNR), calls with a duration of more than 2.5 ms were excluded from the analysis of all parameters except for call interval, which was derived from envelope peaks. Apparent output levels (Madsen et al., 2005) were measured as the root mean square (rms) level over the duration, and as energy flux density by adding $10\log_{10}$(duration) (in seconds) to the rms level. The centroid frequency was calculated as the weighted mean of frequencies present in the signal, corrected for the background noise spectrum from a time-averaged spectrogram with a 183 Hz binwidth.

RESULTS AND DISCUSSION

We tagged 20 bats across the dry and wet season, resulting in 106 h and 23 min of recordings. The bats spent 11% of their time in flight capturing prey via passive gleaning or aerial hawking (Fig. 1A). Most of this time was spent gleaning, with only 11 of 20 recordings having identifiable aerial captures (Fig. 1B) resulting in 62 aerial captures (Table S1). Because of poor SNR of the audio data, 40 aerial captures were excluded, yielding a total sample size of 22 across 8 bats (ranging from 1 to 6 captures per bat).

To test the hypothesis that a gleaning specialist adopts the echolocation phases used by aerial-hawking bats to catch flying prey, we examined the temporal dynamics of calls emitted by the fringe-lipped bats during the last second before capture (Fig. 2). Our results show that the dynamic range of source levels during the last 1 s to prey capture is ∼9 dB (Fig. 2A) with an average slope of $-2.2\log_{10}$(time to prey capture) (Table S2). Call duration decreased from a median of 0.9 to 0.6 ms (Fig. 2B), while call interval decreased from 55 to 20 ms (Fig. 2C).

We next tested the hypothesis that during the final stages of the prey capture, fringe-lipped bats emit a terminal buzz characterized by call intervals <10 ms and beam broadening via a

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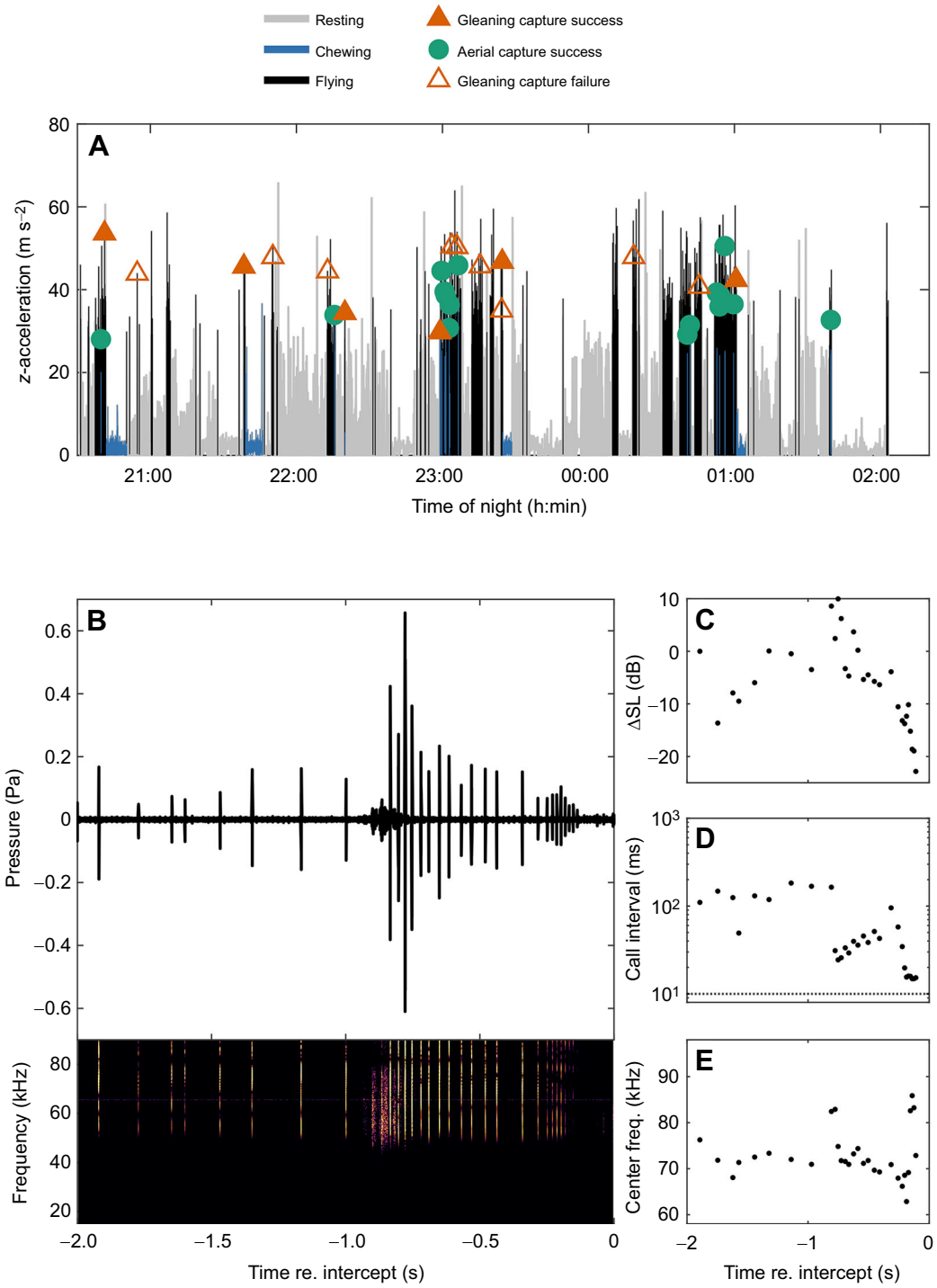

Fig. 1. Fringe-lipped bats, *Trachops cirrhosus*, supplement gleaning with opportunistic aerial hawking. (A) The nightly activity of a fringe-lipped bat with movement quantified as *z*-acceleration. Gleaning is the preferred foraging strategy, but epochs of aerial hawking occur. Failed aerial capture attempts could not be quantified in the current study. (B–E) A capture event: the waveform (B, upper), corresponding spectrogram (B, lower), relative source level (SL; C), call interval (D) and centre frequency (E). While call level and interval decrease, intervals are above the buzz threshold of 10 ms, and the centre frequency does not drop by an octave in a 'buzz II'.

lowering of call frequency by about an octave. While call interval did decrease during terminal intercept and seemingly asymptote at ∼20 ms for the last 100 ms (Fig. 2C), it never dropped below 10 ms and was not accompanied by a drop in centre frequency (Fig. 2D). This shows that the bats do not use beam broadening via lowering of the fundamental frequency prior to prey capture (Fig. 2D).

Since Griffin's discovery >80 years ago, the active sensing of echolocation has been studied extensively in both bats and toothed whales (Au, 1993; Griffin, 1958; Griffin and Galambos, 1941). When intercepting prey in open spaces, most echolocators go through the search, approach and buzz phases of echolocation (Griffin et al., 1960; Madsen and Surlykke, 2013). However, in contrast to this echolocation-based hunting strategy, some bats

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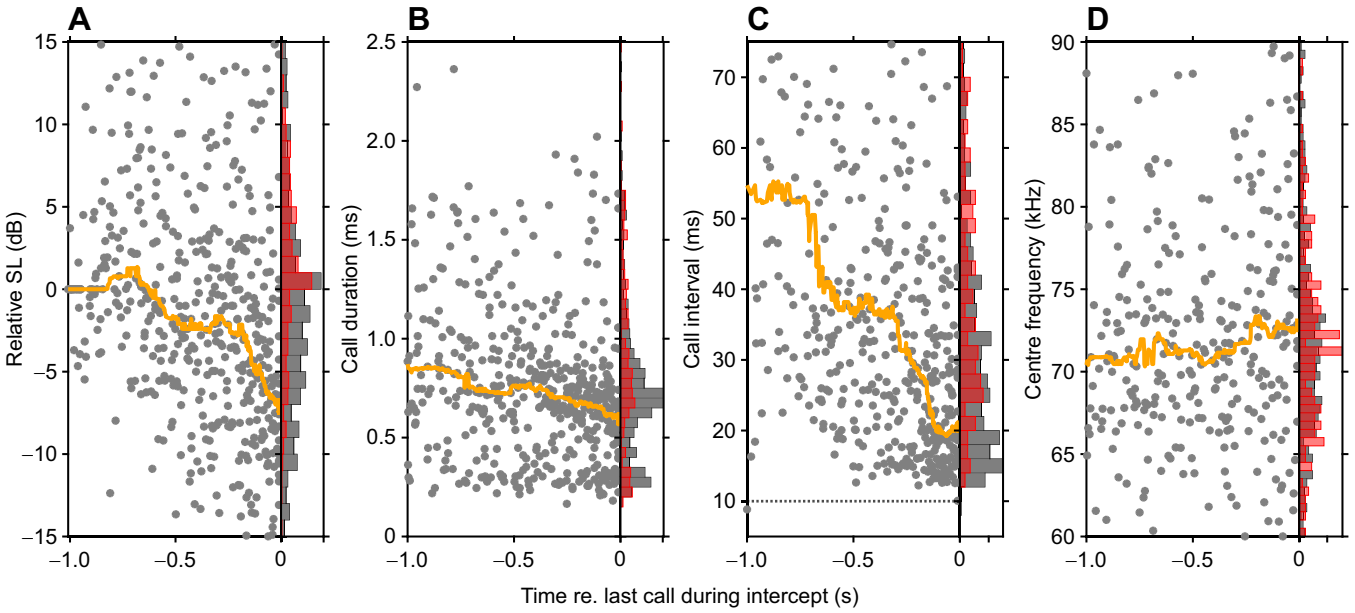

Fig. 2. Echolocation call parameters preceding a capture event. (A) Relative source level (binwidth: 1 dB), (B) call duration (binwidth: 0.05 ms), (C) call interval (binwidth: 2 ms) and (D) centre frequency (binwidth: 0.5 kHz). Yellow lines represent moving medians (window size: 20% of data). The horizontal line in C is the buzz threshold. Histograms on the right of each panel illustrate the distribution of data points: grey denotes the final second before capture, while red represents 9–8 s prior.

exploit prey-emitted cues to passively localize their targets from surfaces instead of from open space – a foraging strategy known as gleaning (Griffin, 1958; Norberg and Rayner, 1987). Here, we tested the hypothesis that the search, approach and buzz phases are pre-requisites for aerial hawking by using acoustic tags on gleaning fringe-lipped bats to quantify their biosonar strategy during aerial prey attacks in the wild.

Fringe-lipped bats hawk flying insects, but are constrained by their short-range sonar

Fringe-lipped bats are known for eavesdropping on ground-dwelling prey, but we show here that they also capture flying insects (Fig. 1). We used such aerial captures to investigate whether they follow the stereotyped echolocation pattern observed in hawking bats. When searching for prey during commuting or foraging flights, true aerial hawkers use calls of long duration that are produced at high intensity, coupled to the wingbeats in a one-to-one fashion (Holderied and von Helversen, 2003; Stidsholt et al., 2021b). These loud, long duration calls, in concert with a stapedial reflex (Suga and Jen, 1975), aid bats in detecting weak echoes from distant prey in open spaces. In stark contrast, our tagged fringe-lipped bats used calls with short duration (mean: 0.75 ms, inter-quartile range IQR: 0.5–0.9 ms), low apparent output level (mean: 30 dB re. 20 μPa^2 s, IQR: 26–34 dB re. 20 μPa^2 s; Fig. S1) and short call interval (43 ms, IQR: 20–53 ms) just prior to prey capture and during their commuting flights (Fig. 2A,B). Fringe-lipped bats therefore – like most other studied Phyllostomids, but in contrast to typical aerial hawkers – employ a short-range biosonar with high update rates during commuting and searching, probably as an adaptation for navigating cluttered environments. In contrast to aerial hawkers, this aerial searching strategy limits their ability to detect flying insects at long ranges, probably adding greater search effort and leaving less time to plan and execute an attack when they opportunistically detect and target aerial prey.

When tracking prey during the approach phase, true aerial hawkers shorten call duration by up to 80% to reduce forward masking of returning echoes, decrease source level by 30–40 dB to reduce clutter and decouple calls from wingbeats to achieve higher update-rates on prey location (Stidsholt et al., 2021a). In contrast, we found that fringe-lipped bats made more modest adjustments in their approach: call duration decreased by ∼30% (from 0.9 to 0.6 ms), source level dropped by ∼9 dB [mean slope: $-2.2\log_{10}$(time to prey capture); Table S2] and call interval gradually decreased from about 55 to 20 ms (Fig. 2A–C, yellow lines). This consequently resulted in weakly changing sensory volumes (Stidsholt et al., 2021a) when approaching prey with more marked increases in the temporal resolution of their echolocation facilitating prey tracking. Thus, while fringe-lipped bats employ an approach phase resembling that of true aerial hawkers, they execute this behaviour within a smaller dynamic range. This limitation probably stems from their short-range, high update rate biosonar already being tuned for aiding close-range navigation in acoustically cluttered environments. This reduces the dynamic range available to adjust call levels and rates with range to the prey, and a further reduction in source level might make vital prey echoes undetectable to the bats. Consequently, this clutter-adapted echolocation precludes a traditional search phase and constrains the extent to which the bats can adjust their biosonar, resulting in a reduced yet apparently functional approach phase strategy.

Fringe-lipped bats catch aerial prey without producing a terminal buzz

In echolocating bats, the aerial hawking hunting sequence usually ends in a terminal buzz (in 13 of 17 families), characterized by short calls, low source levels and call intervals below 10 ms (Ratcliffe et al., 2013). In some species, this is followed by a ‘buzz-II’ with even lower call interval down to 5 ms and a frequency drop of about an octave (Ratcliffe et al., 2013). In contrast, fringe-lipped bats do not adjust frequency in the final stage before prey capture, and only reduce call interval from 55 ms to 20 ms. This gradual reduction in call interval pales compared with the 10–100 times increase in sampling rate of other echolocators during the final stage of prey capture (Madsen and Surlykke, 2013). Accordingly, fringe-lipped

bats do not reach the short intervals of the stereotyped buzz of an aerial hawker of 10 ms (Ratcliffe et al., 2013). The lack of a buzz means that fringe-lipped bats get less than half the updates on the prey in the final moments before capture compared with aerial hawking specialists. This, along with their extremely narrow and directional sonar beam (Surlykke et al., 2013) with no beam broadening by calling at lower frequencies, should therefore make it much harder to keep track of evasive prey. The lack of buzzing is common amongst phyllostomids (Gessinger et al., 2019; Gonzalez-Terrazas et al., 2016; Weinbeer and Kalko, 2007) with the exception of the long-legged bat, *Marcophyllum macrophyllum* (Ratcliffe et al., 2013; Weinbeer et al., 2013), and has also been reported from captive constant frequency (CF) bats catching stationary larvae (Ma et al., 2025). However, these captive CF bats initiate buzzing in response to fluttering or escaping prey, supporting the hypothesis that the buzz evolved as a sensory mechanism to facilitate tracking of evasive prey (Ma et al., 2025). As such, our results offer the first direct evidence that a wild bat can catch flying and moving prey without emitting a fast buzz, demonstrating that while buzzing probably improves prey tracking, it is not a requirement for successful aerial prey capture.

The lack of a clear aerial hawking search phase with powerful wingbeat-coupled calls and buzz phase with fast update rates and beam broadening therefore leads us to reject the hypothesis that all three Griffin phases are a pre-requisite for successful aerial hunting. However, this strategy should instead come with several foraging consequences: lower amplitude calls probably lead to increased search efforts, and reduced time to execute and plan an attack in a reactive sensorimotor operation. Combined with low update rates, a narrow biosonar with no beam broadening during interception, fringe-lipped bats probably struggle to detect, track and intercept evasive prey. Thus, we predict that this leads to a lower success rate when compared with aerial hawking specialists – a hypothesis that future research should investigate. This may also explain the scarcity of these successful aerial hunting events (n=62 in ∼5 h), indicating that although fringe-lipped bats can hunt on the wing, aerial foraging is not nearly as effective or energetically rewarding as gleaning much larger prey at high success rates (Baier et al., 2025) and therefore is likely to be an infrequent strategy. We predict that this opportunistic supplement to gleaning is probably widespread but severely understudied in gleaning specialists.

In conclusion, we report the first documented aerial hawking without all three echolocation phases described by Griffin, nuancing the widely held view that these phases are essential for successful aerial prey capture. Our results emphasize that echolocation is an extremely versatile strategy, allowing fringe-lipped bats to forage in a hitherto undocumented niche. These findings probably extend to other gleaning specialists, suggesting that the remarkable flexibility of echolocation may be a widespread, yet underappreciated, trait among gleaning bats. Given that interception of motile prey can occur without the Griffin phases, we posit that the first ancestral aerial hawkers may have captured aerial prey before the evolution of a buzz and subsequently refined this echolocation behaviour to improve capture success via a high-resolution buzz.

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Competing interests
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Author contributions
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Data and resource availability
Data used in this study are available from the open science framework OSF.io: https://doi.org/10.17605/OSF.IO/PM49J. All other relevant data and details of resources can be found within the article and its supplementary information.

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