

Research



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Inconspicuous echolocation in hoary bats (*Lasiurus cinereus*)

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Echolocation allows bats to occupy diverse nocturnal niches. Bats almost always use echolocation, even when other sensory stimuli are available to guide navigation. Here, using arrays of calibrated infrared cameras and ultrasonic microphones, we demonstrate that hoary bats (*Lasiurus cinereus*) use previously unknown echolocation behaviours that challenge our current understanding of echolocation. We describe a novel call type ('micro' calls) that has three orders of magnitude less sound energy than other bat calls used in open habitats. We also document bats flying close to microphones (less than 3 m) without producing detectable echolocation calls. Acoustic modelling indicates that bats are not producing calls that exceed 70–75 dB at 0.1 m, a level that would have little or no known use for a bat flying in the open at speeds exceeding 7 m s⁻¹. This indicates that hoary bats sometimes fly without echolocation. We speculate that bats reduce echolocation output to avoid eavesdropping by conspecifics during the mating season. These findings might partly explain why tens of thousands of hoary bats are killed by wind turbines each year. They also challenge the long-standing assumption that bats—model organisms for sensory specialization—are reliant on sonar for nocturnal navigation.

1. Introduction

Echolocation is a key adaptation that allowed bats (except most Pteropodidae) to radiate into diverse ecological niches [1]. Echolocating bats exhibit numerous physiological, neural and behavioural adaptations that facilitate their refined echolocation abilities [2,3]. This makes them useful model organisms for understanding animal sensing [4]. Familiarity with the environment [5,6] and availability of cues from other sensory modalities [7,8] can allow bats to reduce their reliance on echolocation; however, they rarely forgo it entirely. Known cases of bats not using echolocation involve situations where echolocation is ineffective and where additional auditory cues are available, such as sounds from conspecifics [9] or prey [10,11].

The high-intensity echolocation calls of bats make them subject to eavesdropping by prey and conspecifics [12,13]. This has shaped ecological interactions. For example, many insects use bat echolocation as a cue to initiate defensive behaviours [14,15], and some bats have responded over evolutionary time by producing 'stealth' calls that are difficult for prey to detect [16,17].

Humans also eavesdrop on bats [18]. Extensive monitoring efforts use long-term ultrasonic recording inventories to quantify and track bat activity levels over time. This method is, of course, dependent on bats producing echolocation calls that can be recorded and detected using available equipment. Some authors have speculated that bats might sometimes navigate night skies without using echolocation, which could make them more susceptible to fatal collisions with wind turbines [19,20]. Previous efforts to test this hypothesis have not used methods that allow determination of bat positions relative to microphones [21]. Therefore, it is not clear whether previous field recordings that lacked echolocation calls were a result of bats being out of range of microphones, or bats being silent or echolocating at low intensities.

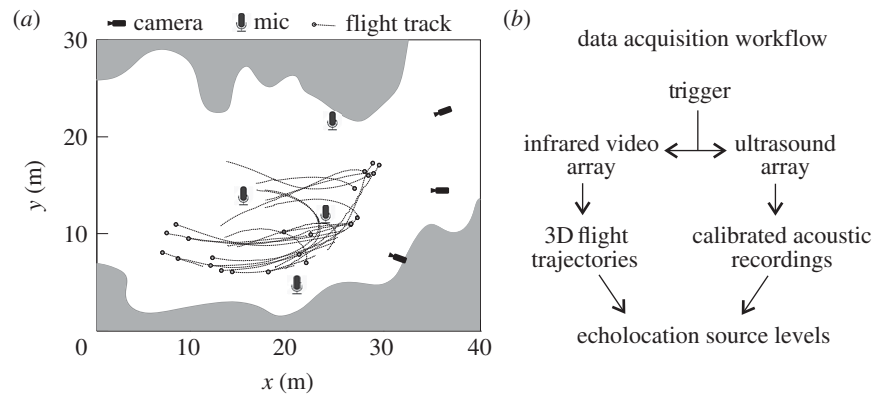


Figure 1. Experimental methods. (a) Example experimental set-up shows locations of cameras, microphones and bats flying through a riparian corridor (grey shaded area indicates vegetation boundaries). (b) Overview of data acquisition workflow. Bats were recorded using time-synchronized arrays of infrared cameras and ultrasonic microphones. Cameras were calibrated for three-dimensional reconstruction of bat flight paths. The directionality and frequency-specific absolute sensitivity of each microphone was measured. Together, this information allowed estimation of bat echolocation source levels. Full three-dimensional data from all recording nights are presented in electronic supplementary material, figure S1.

We aimed to test the hypothesis that bats fly without using echolocation by studying hoary bats (*Lasiurus cinereus*) flying close to the ground (less than 10 m height) in their natural habitat. We developed a model of the detection range of our microphones and predicted that this model would fail to explain cases where bats flew over our microphones without producing detectable calls. Hoary bats were selected as study species because previous reports suggested that they might not echolocate [20,21] and because they are the species killed most frequently by wind turbines [22]. We provide strong evidence that under some conditions hoary bats fly without producing detectable echolocation calls. These findings challenge our existing understanding of the sensory capabilities of bats.

2. Material and methods

(a) Experimental overview

We studied hoary bats flying through the Bull Creek riparian corridor in Humboldt Redwoods State Park in California, USA between 24 September and 21 October 2016. Data were collected at three field sites that were separated by distances of 0.5–1.9 km. Water flows were low during the study, allowing for deployment of equipment in the mostly dry river channel. We conducted experiments on multiple nights to ensure a variety of environmental conditions (e.g. moon phase, cloud cover); however, we did not have sufficient sample size to determine whether these factors affected bat acoustic behaviour.

Figure 1 provides an overview of the experimental set-up, which was used to conduct three experiments: (i) natural observations of bats flying alone or interacting with conspecifics; (ii) bats responding to a mist-net obstacle; and (iii) bats responding to echolocation playbacks. In all three experiments, bats were recorded using time-synchronized arrays of infrared cameras and ultrasonic microphones. Cameras were calibrated to allow three-dimensional reconstruction of bat flight trajectories. This information was used together with known position, sensitivity and directionality of the microphones to determine the source levels of all recorded echolocation calls (electronic supplementary material).

In experiment 1, we recorded bats flying under natural conditions on five nights (Blue Slide, 2 nights; Albee, 2 nights; Big Tree, 1 night). Recordings began 1 h after sunset and continued for 2 h each night. In experiment 2, a large mist net (12 m wide, 7.5 m tall) was stretched across the riparian corridor to test the bats' responses to a novel obstacle. This experiment was repeated on two nights at the Big Tree field site, which we chose because of its relatively narrow corridor width (approx. 15 m).

In experiment 3, we documented bat reactions to playbacks of conspecific echolocation calls, heterospecific echolocation calls or silence (control). We chose *Eptesicus fuscus* for our heterospecific species because this bat's calling frequency is similar to *L. cinereus*. Therefore, the effective range and directionality of conspecific and heterospecific playbacks should be similar. Playbacks were broadcast at 95 dB peak-equivalent sound pressure level (peSPL) at 1 m. The objectives of this experiment were to determine whether hoary bats are attracted to echolocation and whether hoary bats behave differently in response to conspecific or heterospecific echolocation. More details on the experimental protocol are provided in the electronic supplementary material.

(b) Recording equipment

Bats were recorded using three Ace acA2000-50gc infrared video cameras (Basler, Highland, IL, USA) recording at 50 Hz and 2000×1080 -pixel resolution. Custom electronics synchronized shutter exposures of all three cameras. Infrared illumination was provided by three Raymax 200 infrared illuminators (Raytec, Ashington, UK). Video was captured on a field desktop computer running Streampix 6 video acquisition software (Norpix Inc., Montréal, QC, Canada).

Ultrasound was recorded using a 4-channel USGH 416 h recording unit (Avisoft Bioacoustics, Glienicke, Germany) and Avisoft CM16/CPA microphones. Preliminary experiments demonstrated that 40DP microphones (GRAS Sound and Vibration, Holte, Denmark), which are more omnidirectional and have a flatter frequency response than our Avisoft microphones, had too high of a noise floor to reliably detect micro calls. Our microphone calibration procedure is described in the electronic supplementary material, Microphone Calibrations section.

Audio and video were each recorded into a 10 s buffer on the computer. During experiments, an experimenter observed these feeds. Any time a bat was detected, the observer waited several seconds, and then triggered acquisition of the previous 10 s of recording. It took approximately 20 s for the recording to be saved to the computer's hard drive, at which point the experimenter was free to make additional recordings.

3. Results

(a) Hoary bats use a previously undocumented form of echolocation

We recorded a total of 79 hoary bat flights over our recording equipment on five nights. The minimum bat–microphone distance during these flights ranged 2.2–8.6 m. Surprisingly,

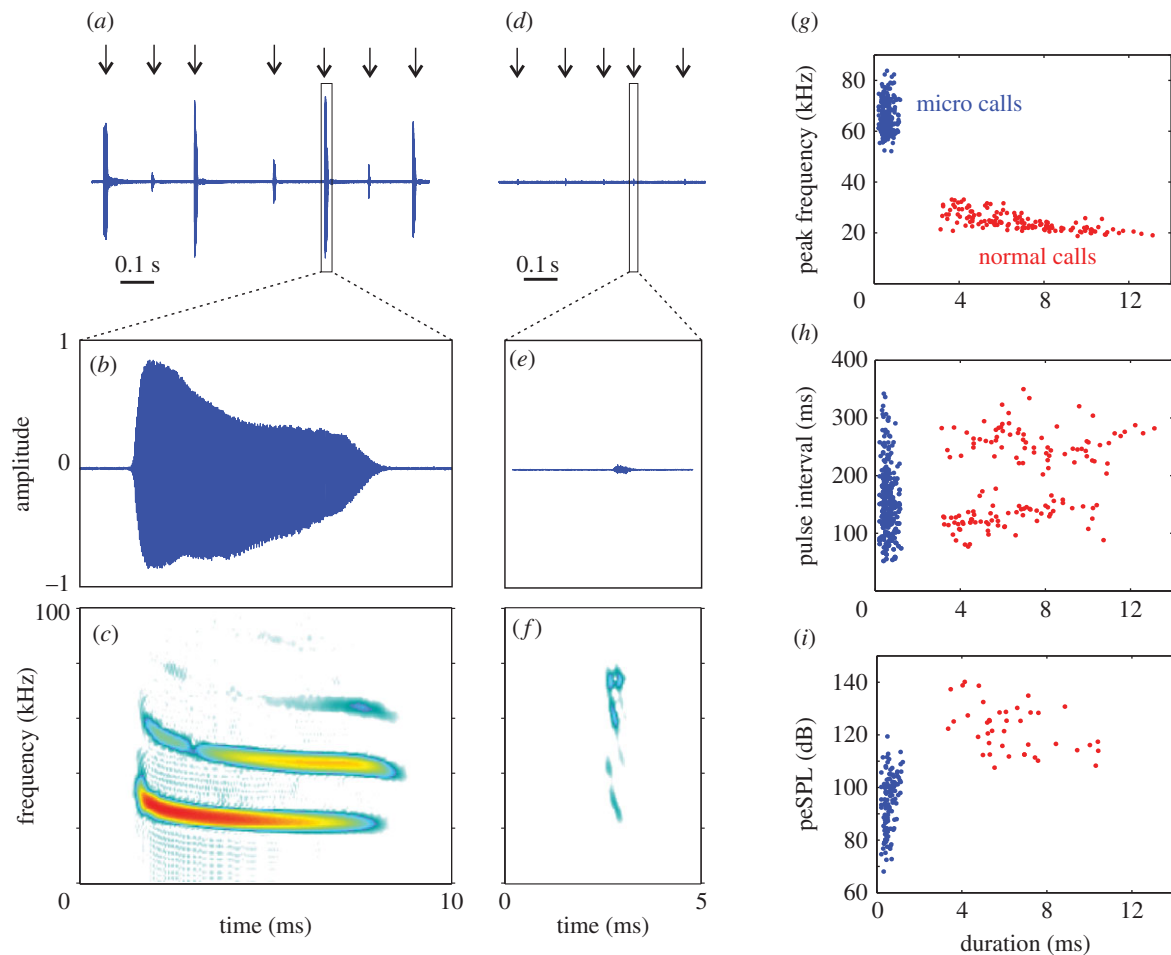


Figure 2. Comparison of hoary bat (*Lasiurus cinereus*) echolocation call types. (a–f) Oscillograms of call sequences (a,d) and oscillograms (b,e) and spectrograms (c,f) of individual calls are shown for normal calls (a–c) and micro calls (d–f). Arrows indicate calls in (a,d). (g–i) Scatter plots are shown for select call parameters. See table 1 for statistical comparisons. Note the non-overlapping distributions of multiple call parameters, which indicate that normal and micro calls are discrete call types. (Online version in colour.)

‘normal’ hoary bat echolocation calls (those falling within the range of acoustic parameters documented in previous studies [23,24]) were recorded in only 6 of 79 flights (7.6%). By contrast, normal echolocation calls were always recorded when other bat species flew through the recording location ($n = 23$ flights from five bat species). Normal calls were recorded from all eight hoary bats that were captured and released at the same recording locations used in experiment 1 (electronic supplementary material, figure S1c,g). When normal calls were recorded from hoary bats (figure 2a) or from other species, these calls were recorded continually on all microphones whenever bats were within the calibrated volume of our cameras (figure 3a).

During 34 of 79 hoary bat flights (43.0%), we only recorded a previously undocumented call type that we term ‘micro’ calls (figure 2d–f). Compared to normal calls, micro calls have strikingly shorter duration, lower sound pressure level and higher frequency, but on average are produced at only a slightly faster rate (table 1). The distributions of normal and micro call durations and frequencies do not overlap (figure 2g–i), indicating that the call types are discrete, not a continuum. The lower level and shorter duration of micro calls provide three orders of magnitude (36 dB) less sound energy than normal calls. Bats flew slightly (but significantly) faster when producing micro calls (mean $\pm$ s.d., 8.7 ± 1.2 m s⁻¹) compared with normal calls (7.7 ± 0.5 m s⁻¹; Student’s *t*-test; $t = 2.215$; d.f. = 40; $p = 0.03$).

(b) Hoary bats appear to fly without using echolocation

In 39 of 79 (49.4%) hoary bat flights over our microphone array over five nights, no calls were detected. To determine whether this resulted from our microphones failing to detect the relatively faint micro calls, we developed a micro call detection model (see the electronic supplementary material). We used logistic regression to test the accuracy of this model in differentiating 200 ms time intervals when micro calls were detected versus matched intervals when calls were absent. This model included all flights where at least one micro call was detected on one microphone. Bat–microphone distance and the angle separating the bat’s flight trajectory and the direction from the bat to the microphone were used as predictors (see the electronic supplementary material). The micro call detection model performed well, correctly classifying 1308 of 1393 (93.9%) 200 ms time intervals. Micro calls were detected in 92 of 97 time intervals (94.8%) where bats flew within the modelled micro call detection range. The microphones reliably detected micro calls at distances up to 7.0 m when bats were flying directly towards the microphones in the horizontal plane, and at distances up to 4.5 m when bats were flying off-axis horizontally by 45° (figure 3d).

We applied our micro call detection model to the 39 flights where no calls were detected. If flights lacking calls resulted from the microphones’ limited detection range, then these flights should mostly occur outside the known micro call detection volume. To the contrary, bats flew

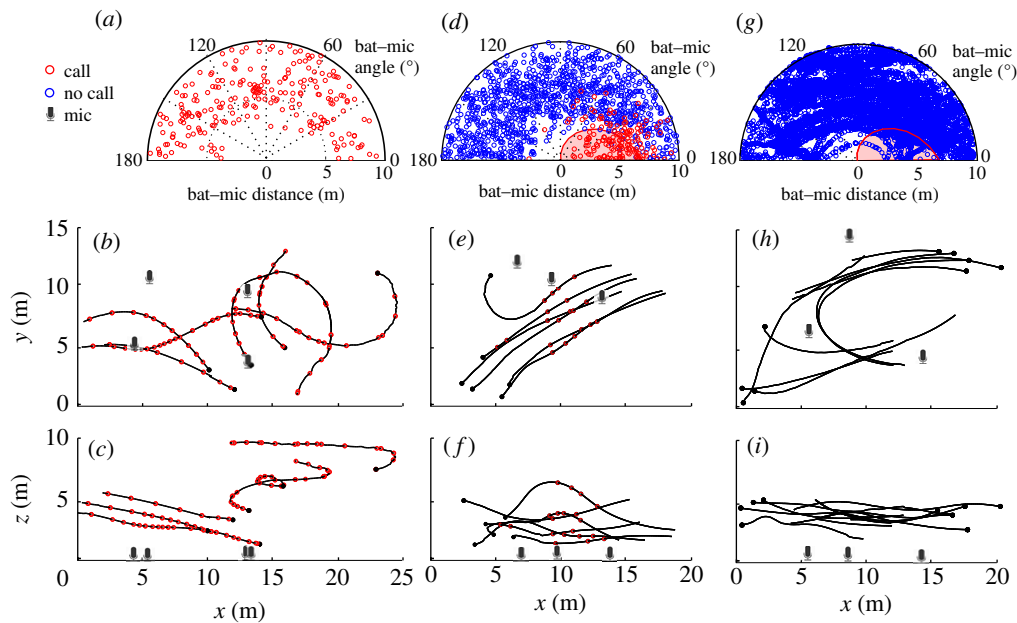


Figure 3. Call detections and example three-dimensional plots of hoary bat flights involving (a–c) normal calls, (d–f) micro calls and (g–i) no call detections. Polar plots show the distance and angle between the bat's flight trajectory and each microphone for call detections (red circles) and 200 ms time intervals where no calls were detected (blue circles). The micro call detection range is illustrated by the red shaded area in (d) and (g). Note the occurrence of bats flying within the micro call detection range in (g), despite no calls being detected. Solid black circles indicate starting positions of bats in three-dimensional plots.

Table 1. Acoustic parameters of normal and micro calls used by *Lasiurus cinereus*. Medians and 10th–90th percentile ranges are shown for call parameters. Mann–Whitney *U*-tests were used to test for significant differences between normal and micro call parameters. Stricter criteria were used for selecting calls for measurements of call intensity (*n*₂) than other parameters (*n*; see Material and methods).

	flights	<i>n</i> calls	duration (ms)	peak freq. (kHz)	high freq. (kHz)	low freq. (kHz)	pulse interval (ms)	<i>n</i> ₂ (calls)	source level (peSPL dB)
normal calls	13 ^a	188						48	
median			5.9	25.2	28.4	24.3	189.7		120.9
range			3.6–10.2	21.4–41.6	24.4–58.7	20.8–33.0	113.1–282.6		109.6–134.6
micro calls	34	318						120	
median			0.54	63.2	78.5	53.3	150.0		99.8
range			0.34–0.96	55.0–73.8	66.7–87.1	40.4–60.2	84.4–250.8		81.3–109.0
<i>U</i> -statistic			0	2274.5	863	1663.5	24241		157
<i>p</i> -value			<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		<0.0001

^aIncludes six natural flights and seven released individuals.

within the micro call detection volume in 23 of the 39 flights (59%) where no calls were detected (figure 3g). During these 23 flights, bats spent 0.2–1.1 s within the micro call detection volume, which should have resulted in one to seven micro call detections per flight (assuming median pulse interval of 150 ms). In three cases, bats flew nearly directly towards a microphone at a distance of less than 3 m. Acoustic modelling indicates that under these conditions the microphones should be able to detect calls having 0.1 m source level of at least 70–75 dB peSPL (see the electronic supplementary material).

(c) Hoary bats 'switch on' normal echolocation to avoid obstacles and interact with conspecifics

We documented 15 individual hoary bats (all adult males) flying into a mist net that was placed across their natural

flight corridor. In all 15 cases, only micro calls (*n* = 9) or no calls (*n* = 6) were detected during the bat's initial approach towards the obstacle. However, in 12 of 15 trials, hoary bats rapidly initiated normal echolocation within close proximity (2–3 m) of the net (figure 4a–c; electronic supplementary material, video S1). In all 15 trials, bats collided with the net.

We also documented 13 natural interactions between pairs of bats. In these interactions, one hoary bat appeared to chase, and sometimes make direct contact with the second hoary bat (figure 4d,e; electronic supplementary material, video S2). In all 13 cases, both bats produced normal echolocation calls throughout the conspecific interaction. In cases where the beginning of the conspecific interaction was documented, both bats began the interaction either producing micro calls or not producing detectable calls. One bat then initiated normal echolocation just as it began pursuing the other bat,

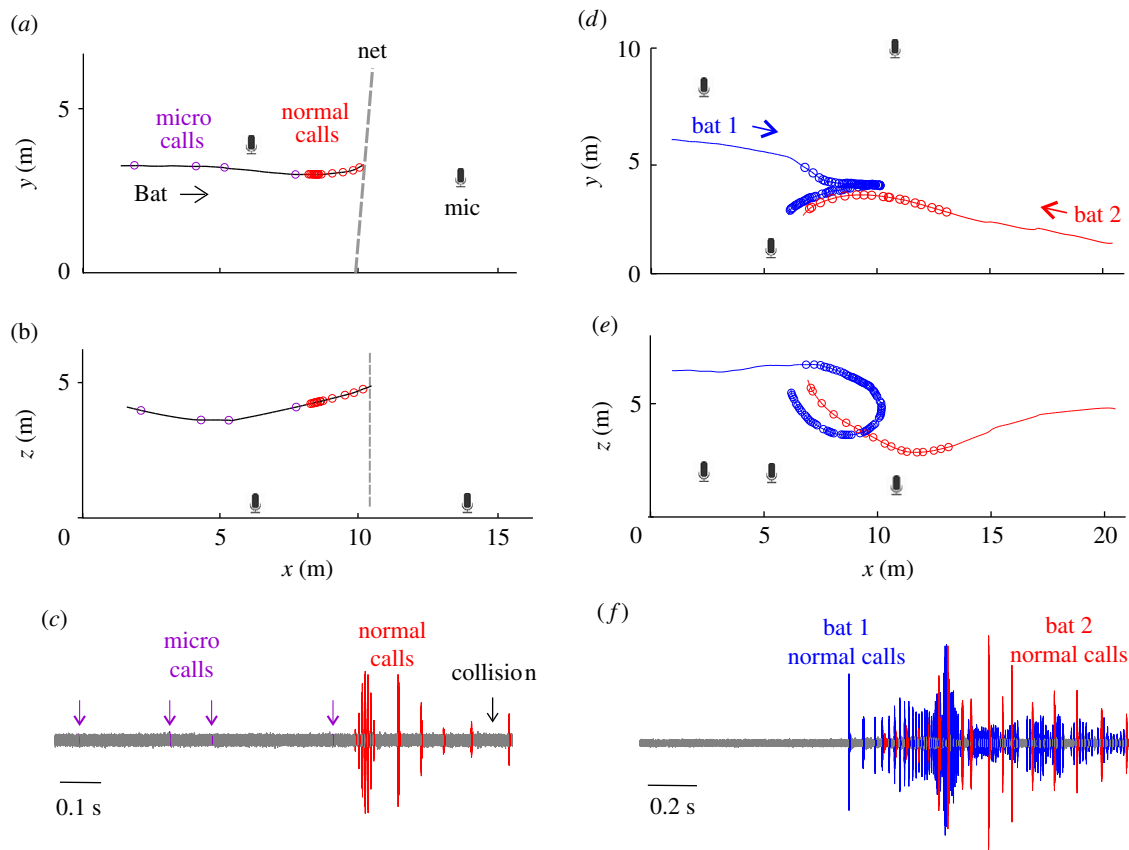


Figure 4. Hoary bats ‘switch on’ normal echolocation in response to (a–c) a mist-net obstacle in their flight corridor or (d–f) a nearby conspecific. Shown are (a,d) overhead views and (b,e) profile views of bat flight trajectories, and (c,f) ultrasound recordings. ‘Bat’ labels indicate starting positions. Circles indicate the positions where bats emitted echolocation calls. Microphone icons indicate the position of microphones. In (a–c), a hoary bat switches from producing micro calls to producing normal calls just before flying into a net obstacle. In (d–f), bat 1 commences normal echolocation just as it begins pursuing bat 2. Bat 2 commences normal echolocation shortly thereafter. Videos of interactions are available in electronic supplementary material, videos S1 and S2.

and soon after the second bat initiated normal echolocation (figure 4d–f; electronic supplementary material, video S2). These results demonstrate that hoary bats rapidly commence normal echolocation when attempting to avoid an obstacle and when interacting with conspecifics.

(d) Hoary bats are attracted to playbacks of conspecific and heterospecific calls

Hoary bats were highly attracted to playbacks of conspecific calls (17 approaches to the speaker during 13 five-minute playbacks over two nights) and calls of the heterospecific *E. fuscus* (12 approaches during matched time periods), but not to playbacks of silence (zero approaches). There was no difference in attraction between playbacks of conspecific versus heterospecific echolocation calls (Chi-square test; $\chi^2 = 0.83$; $p = 0.36$), but bats were attracted more to playbacks of calls than playbacks of silence (Chi-square test; $\chi^2 = 21.4$; $p < 0.0001$).

Hoary bats showed a high degree of interest in playbacks, frequently making several tight circles around the speaker (electronic supplementary material, video S3). During 23 of 29 approaches to the speaker, only micro calls were detected. Normal calls were detected during three approaches, and no calls were detected in the remaining three approaches. Combined with the results from naturally interacting bats, these data indicate that hoary bats use micro calls to investigate other bats and then switch on normal echolocation when a conspecific interaction ensues. Because we could not identify individuals in video recordings, we could not determine

whether the observed response resulted mainly from one individual at each site, or from multiple individuals.

4. Discussion

Here, we show that hoary bats exhibit striking reductions in echolocation call output through previously undocumented micro calls and that they navigate their natural environments either without echolocation or while producing calls with source levels less than 70–75 dB peSPL at 0.1 m. This level is 30–70 dB lower than sound levels used by other bats in open habitats [25,26], and approximately 60 dB lower than maximum levels we recorded from hoary bats (table 1).

Established sonar theory [27] indicates that switching from normal to micro calls reduces the detection range for a tree from 26.9 to 7.5 m, and reduces the detection range of a medium-sized insect (3 cm wingspan) from 6.9 to 2.1 m. Assuming average flight speeds and call parameters (table 1), switching from normal to micro calls would reduce the time available for avoiding a collision with a tree from 3.5 to 0.9 s and reduce time for capturing prey from 0.89 to 0.24 s. Bats have a sensori-motor reaction time of 0.1 s [28] in addition to time required to coordinate an evasion or capture manoeuvre. Hoary bats using micro calls should have sufficient time to detect and avoid large obstacles such as tree branches but should have difficulty avoiding smaller objects or obstacles that are difficult to detect such as our mist nets. Hoary bats using micro calls would be unlikely to have sufficient time available to capture insects.

We documented multiple cases where bats did not produce calls above 75 dB. This result could not be explained by the directionality of our microphones (see the electronic supplementary material). Calls at this low amplitude would only allow hoary bats to detect large obstacles such as a tree from a distance of 1.5 m [27]. Given average flight speeds and reaction times, it is unlikely that hoary bats could avoid a collision even with a large tree if using calls at such a low level. This suggests that calling at 75 dB or lower would be of little use for hoary bat navigation and obstacle avoidance. These data indicate that hoary bats sometimes operate entirely without the use of echolocation. This hypothesis could be tested further, for example, by deploying on-board ultrasonic recording devices to bats in the field [29].

Our results demonstrate that bats have considerably more plasticity in their use of echolocation than previously known. This is noteworthy considering the degree to which bats are specialized for using echolocation to navigate nocturnal environments [30–32]. Previous reports of silent behaviour in bats have been restricted to specific scenarios such as severe jamming from conspecifics [9], or when attending to prey-generated sounds [10,11]. In both cases, bats had additional sensory information (i.e. calls from other bats or prey sounds) to aid navigation. By contrast, hoary bats in our study substantially reduced calling output when flying alone through open habitat without additional auditory cues.

Bats typically use echolocation call structures that are adapted to the task at hand and the animal's environment [33]. However, the acoustic structure of micro calls—particularly their unusually short duration and low sound level—are poorly suited for the open habitats in which hoary bats used them (electronic supplementary material, figure S1). Bats producing micro calls incur a sharply reduced sonar range for no reason that is apparent based on sonar theory. This indicates that there must be some alternative compensating benefit to this behaviour.

Why do hoary bats reduce their calling output, and possibly even fly in silence? Echolocation has little or no energetic cost because bats couple sonar emissions with respiratory exhalations and the wing-beat cycle [34]. Therefore, reducing calling output is unlikely to provide energetic savings. Low-intensity echolocation has been proposed as a mechanism for avoiding detection by eared prey [16,17]. However, we argue that reduced echolocation is unlikely to be a foraging strategy in hoary bats. As noted above, micro calls are poorly suited for detecting prey, and are unlikely to provide bats sufficient time for insect pursuit and interception. Furthermore, hoary bats typically use normal echolocation calls when hunting prey [35,36], and they did not regularly forage during our study (see the electronic supplementary material).

Alternatively, reduced calling output could help bats avoid eavesdropping by conspecifics. Conspecific chases were common at our field site, and bats were highly attracted to echolocation playbacks. Calling at normal intensity might attract unwanted aggression from other bats. Shifting from normal to micro calls would make bats far less conspicuous to conspecifics, reducing the eavesdropping range from approximately 92 to 12 m (see the electronic supplementary material). Our study was conducted during the hoary bat reproductive period, which makes it possible that call intensity reductions are part of a broader mating strategy.

Our findings challenge the long-standing assumption that bats are reliant upon high-intensity echolocation for nocturnal

navigation [37]. We postulate that hoary bats increase their reliance on vision and spatial memory when echolocation output is reduced. The primary advantages of echolocation over vision are (i) detecting small targets such as insects and (ii) measuring target distance with high precision [38]. Bats could circumvent these limitations by not foraging and by using their underappreciated visual abilities [39,40] to detect obstacles before switching on normal echolocation for high-precision obstacle localization (figure 4).

Several important questions remain unanswered. Do females as well as males exhibit reduced echolocation behaviours? Are these behaviours restricted to the autumn mating season, or do they occur year-round? What are the proximate factors that cause bats to switch between normal echolocation, micro calls and potentially silence? Light levels, habitat structure, familiarity with the habitat and abundance of conspecifics are factors that warrant further examination. Also, what other bat species use reduced forms of echolocation? Answering these questions would help explain why bats reduce their reliance on a sensory system that has been crucial to their evolutionary success.

This study has important ramifications for the conservation and management of bats killed at wind turbines. Hoary bats comprise 40% of all bats killed at wind energy facilities in North America [22], and consequently are at increased risk of drastic population reductions [41]. Most hoary bat fatalities occur during late summer and autumn [22], which overlaps with the time period of our study. Our data are consistent with the hypothesis that bats are at increased risk of colliding with turbines because of reduced use of echolocation [19,20]. Use of micro calls around wind turbines would allow them to detect and avoid stationary turbines [20]; however, large turbine blades moving at high speed could disrupt the adaptive benefit of a micro call strategy and lead to strikes by the blades. Reduced echolocation also complicates the metrics of monitoring hoary bat activity using passive acoustic monitoring. Acoustic monitoring is used widely to assess fatality risk prior to construction of wind turbines [42], but these efforts have uneven results in their ability to predict post-construction fatalities [43,44]. Additional caution is warranted before assuming bats are always detectable using standard acoustic monitoring techniques.

Ethics. Bat capture and handling were carried out in accordance with guidelines of American Society of Mammologists under permit with the California Department of Fish and Wildlife (no. SC-002911). Our methods were approved by the Institutional Animal Care and Use Committee of the USGS Fort Collins Science Center (FORT IACUC 2014-08).

Data accessibility. The computer code, audio files and three-dimensional flight data supporting this article are available at Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.pc1q122>) [45].

Authors' contributions. A.J.C. and T.J.W. jointly designed the experiments. A.J.C. conducted experiments, analysed results, and wrote the initial draft of the manuscript. T.J.W. made initial observations leading to the study, provided logistical support for collecting data and revised the manuscript.

Competing interests. We declare we have no competing interests.

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