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Hunting bats adjust their echolocation to receive weak prey echoes for clutter reduction

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How animals extract information from their surroundings to guide motor patterns is central to their survival. Here, we use echo-recording tags to show how wild hunting bats adjust their sensory strategies to their prey and natural environment. When searching, bats maximize the chances of detecting small prey by using large sensory volumes. During prey pursuit, they trade spatial for temporal information by reducing sensory volumes while increasing update rate and redundancy of their sensory scenes. These adjustments lead to very weak prey echoes that bats protect from interference by segregating prey sensory streams from the background using a combination of fast-acting sensory and motor strategies. Counterintuitively, these weak sensory scenes allow bats to be efficient hunters close to background clutter broadening the niches available to hunt for insects.

INTRODUCTION

Hunting predators must find, pursue, and catch often fast-moving prey among myriad distracting sensory cues. Solving this sensory-motor challenge requires rapid changes in sensory attention and in motor outputs in response to both prey and environment (1). Insectivorous bats rely on echolocation to orient and catch prey on the wing under conditions of poor lighting (2), and their call patterns reveal the dynamic sensory strategies adopted to hunt successfully. During foraging, they typically follow a three-phased biosonar strategy comprising search, approach, and capture (feeding buzz) phases (audio S1). This model for how bats use echolocation to track and capture prey is based largely on laboratory experiments (3–6) and ground-based snapshot recordings in the wild as bats fly past stationary microphone arrays or cameras (7, 8). Laboratory experiments have revealed that echolocating bats can adjust both their echolocation signals (9, 10) and their flight trajectories (11, 12) to reduce acoustic background clutter when hunting or solving tasks. Much less is known about the way these adjustments are used in wild foraging where echoes return from multiple objects in different directions, creating complex acoustic scenes that require rapid auditory identification, grouping, and tracking of individual echo streams to inform prey interception. Here, we use high-resolution on-board echo- and motion-recording tags to quantify how bats adjust their sensory sampling and motor strategies when hunting aerial prey in clutter and in open space in the wild. Specifically, we sought to test the hypotheses that wild greater mouse-eared bats (i) trade sensory volumes for update rates to successfully intercept evasive aerial prey, (ii) rely on stereotyped movement patterns to enable fast motor responses during aerial prey capture, and (iii) actively seek to maximize echo information from small prey to aid auditory processing via sensory and motor adjustments.

RESULTS AND DISCUSSION

Sensory volumes traded for update rates

To investigate the sensorimotor dynamics of wild bats, we equipped 10 female greater mouse-eared bats (*Myotis myotis*) in Bulgaria with miniature biologging tags (13) that recorded synchronously the movement patterns, echolocation calls and returning echoes from aerial prey, and surroundings during a full night of foraging. The tagged bats ($n = 10$; table S1) were released after dusk and commuted to night-time foraging sites, where they gleaned insects off the ground (indicated by distinct motor patterns in the acceleration data) or caught prey in midair (indicated by emission of feeding buzzes in flight) before returning to the roost before dawn (Supplementary Materials and table S2). The bats used echolocation to detect and pursue aerial prey, transitioning through search, approach, and capture phases, during which the vocal output and corresponding sensory volumes changed markedly along with the returning echoic scene and motor patterns (Fig. 1; see summary values for all bats in Fig. 2; movies S1 and S2). We analyzed 457 aerial captures of which 371 were successful (indicated by audible chewing sounds after each feeding buzz). In the search phase, the bats emit powerful calls (Fig. 2A) with large and variable sensory volumes (fig. S7) (14) of 0.07 to 21.1 m³ (95% data range) for typical prey targets [wingspans from 5 mm (e.g., Diptera) to 50 mm (e.g., Lepidoptera)] (Fig. 2D) to maximize chances of prey detection. The large sensory volumes in the search phase highlight that wild bats generally seek to maximize the chances of detecting aerial prey by using intense calls and that they can dynamically adjust these volumes to the acoustic scenes encountered.

To efficiently track detected prey, the bats, on average, transition into the approach phase (inferred from reductions in call intervals and source levels) at 0.42 s (± 0.15 SD) before prey capture. This confirms earlier observations that bats hunting in the wild have less than 500 ms between detection and capture of prey (7). Despite a 10-fold reduction in mean sensory volumes from search to approach phase (Figs. 1C and 2D), the spatial redundancy [i.e., the number of times the bat ensonifies the same volume of air while flying forward (fig. S10)] remains constant (Fig. 2E) because the repetition rate increases (Fig. 2B). In contrast, as the bats transition into the buzz phase, the redundancy doubles (Fig. 2E) because of very high

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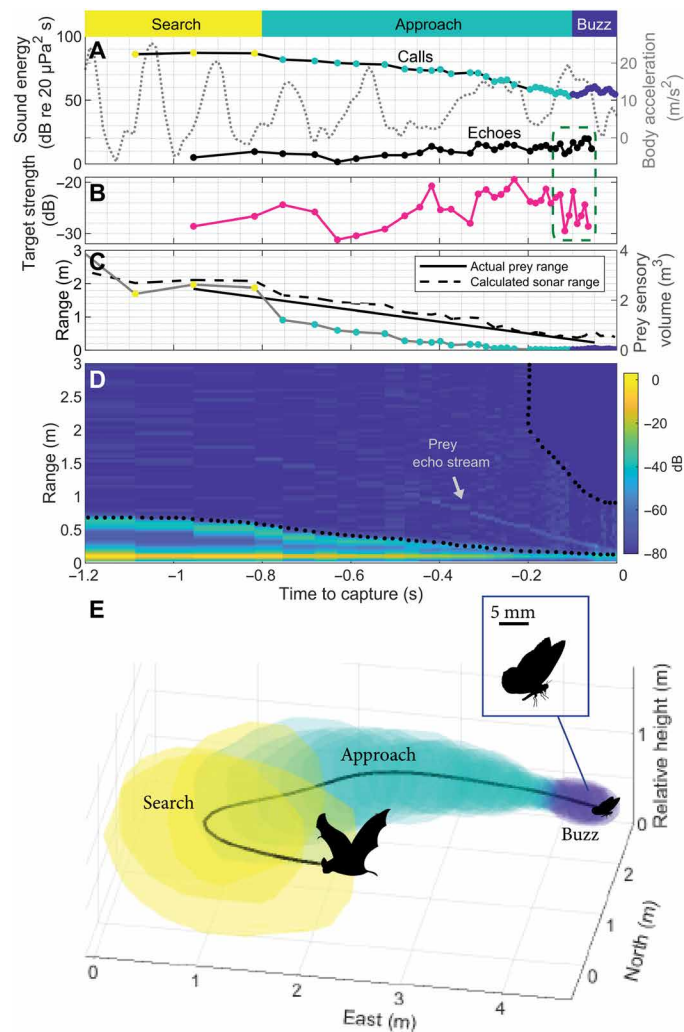


Fig. 1. Bats adjust their vocalizations to receive unmasked prey echoes from gradually smaller sensory volumes to guide prey capture. (A) During the chase, the bat reduces the outgoing energy (colored dots) of its calls by ~40 dB and increases call repetition rate. Returning prey echoes (black) are very weak and cover a dynamic range of ~20 dB. Wingbeats (gray line) were derived from oscillations in the body acceleration. (B) The estimated target strength (TS) of the prey insect fluctuates between -30 and -20 dB at 0.1 m. The fast fluctuations in TS and EL at the end of the chase (green dashed box) are probably caused by wingbeats from the prey. (C) The measured range of the bat to the prey is shorter than the estimated maximum range over which the bat can hear the insect (dashed black lines). The sensory volumes of each call decrease during the capture (gray lines). (D) The echogram visualizes the sensory scene during the capture. Here, the prey echo stream consisting of ~35 echoes is clearly visible during the entire last second of the chase. The bat approaches the insect with a constant speed of 1.8 m/s in an open environment, as no clutter echoes are recorded by the tag. The dashed black lines mark the zone between two consecutive calls where the bat listens for returning echoes, i.e., the overlap free zone. (E) The dead-reckoned track (black line) and the calculated sensory volumes [colored shapes marking the three phases from (A): search, approach, and buzz] show how the bat maneuvers and adjusts its sensory volume to capture the insect (movie S2).

repetition rates (Fig. 2B) despite the more than 45-fold drop in prey sensory volume down to 0.005 to 0.46 m³ (95% data range; Fig. 2D). Thus, only before capturing the prey, bats narrow their acoustic gaze to focus on a single echo stream from their prey target by using

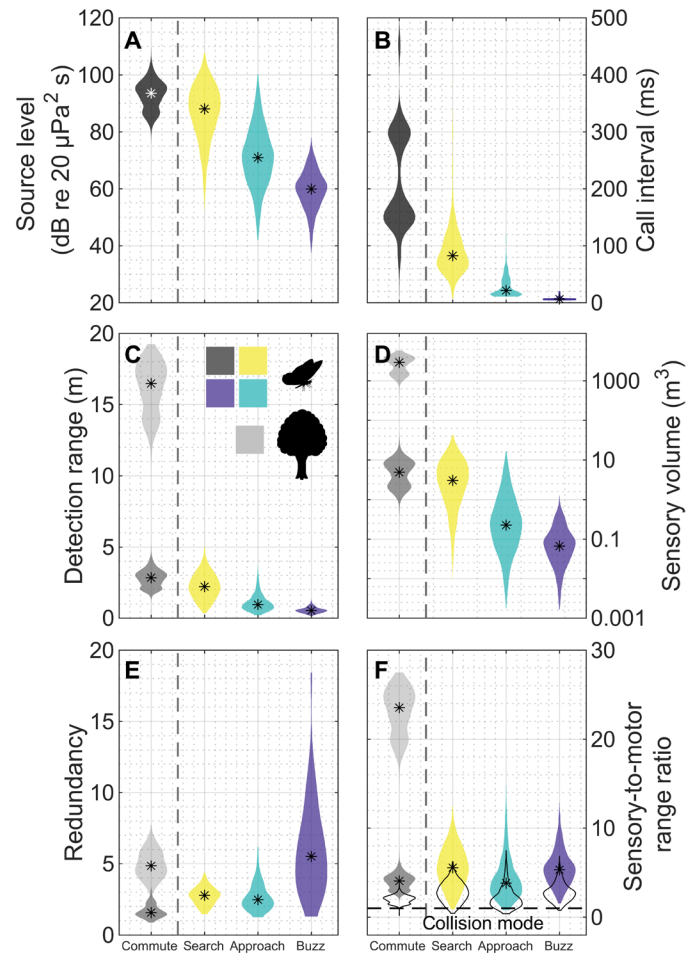


Fig. 2. Bats switch from a deliberate to a reactive sensorimotor mode upon prey detection. (A to E) Bats actively adjust their biosonar parameters to different targets (i.e., prey or large background structures such as a tree) (A and B) to regulate the detection distance (C), sensory volume (D), and spatial redundancy (E) during commuting flight and three stages of aerial capture. (F) The sensory-to-motor range ratio is the relationship between the detection range (C) and reaction range of the bats using a reaction time of 100 ms (solid violins) or 200 ms (black outline violins). All plots depict the *k* means distribution (shaded area) and means (stars) of the data. *n* = 10 bats, 121 captures (4 to 15 random prey captures per individual to balance the study because the individual bats attack prey between 4 and 103 times per night), 4562 foraging calls, and 4092 commuting calls.

high-speed sampling of a small absolute sensory volume. The strategy of using high-resolution information of prey acquires at fast update rates seems to be functionally similar to how visually guided predators such as predatory swallows and diurnal raptors focus on the frontal area of their field of view (15) at high resolution (16).

From deliberate to reactive sensory modes

It has been hypothesized that bats, because of their short inferred prey detection ranges and fast flight speeds, must use a highly reactive sensory-motor operation with little or no time between prey detection and required adjustments to flight patterns to successfully intercept prey. Here, we tested that hypothesis to investigate whether wild bats indeed use a rapid and less informed (i.e., reactive mode) or a slower and more informed (i.e., deliberate) sensory strategy when hunting (14).

When bats commute to/from their foraging sites, they emit high-intensity echolocation calls forming sensory volumes of 2800 m^3 ($\pm 1300 \text{ SD}$) (Fig. 2D) for large targets such as trees. Because the sensory range (16 m) is much larger than the motor response range (0.7 m) [i.e., the range over which bats can react based on a reaction time of 100 ms (17) and flight speed of 7 m/s], the bats operate at high ($>>10$) sensory-to-motor range ratios (SMRs) for landmarks (Fig. 2F). This means that bats have a comparatively long time for movement planning despite high flight speeds, indicating a deliberative sensory-motor mode (14) during commuting. In contrast, the detection ranges and sensory volumes for small prey (Fig. 2, C and D) are generally much smaller because of their much poorer target strength (TS) (poor backscattering) resulting in small spatial overlaps between successive beams (Fig. 2E). Hunting bats therefore have comparatively little time to react to sensory information returning from within small sensory volumes and operate in a highly reactive sensory-motor mode during all stages of aerial prey captures (low SMR of ~ 5 using flight speeds of 4, 2.5, and 1 m/s for search, approach, and capture phases, respectively; Fig. 2F).

Although the SMRs during prey interactions are approximately constant across all four stages (i.e., commute, search, approach, and buzz), the bats achieve this in different ways. During commuting flight, when bats opportunistically encounter prey, and during prey search, the bats operate with low information flow rates (Fig. 2B) but long prey detection ranges (Fig. 2C, dark gray and yellow) that can support fast flight speeds. Conversely, in the buzz phase, prey detection ranges are so small ($<1 \text{ m}$) that a $\text{SMR} > 1$ [i.e., allowing some reaction to prey movements as opposed to a collision mode (14)] is only maintained by decreasing flight speed. This is in contrast to most other predators that operate at much higher SMRs (18, 19) and therefore hunt in a more informed, deliberate sensory-motor mode, allowing for prey selection and planning of a greater range of complex motor patterns during most of the hunt (14).

We then tested the hypothesis that bats hunting in this highly reactive mode with a direct coupling between sensory input and necessary motor action rely on stereotyped movement patterns when catching aerial prey. To our surprise, we found large variations in the relative bat-prey approach speeds [1.4 to 4.9 m/s (95% data range), derived from the slopes of the echo streams; fig. S1], indicating that bats used nonstereotypic motor approaches when tracking prey with potentially different evasive strategies (20). Some of the typical aerial prey types targeted by greater mouse-eared bats belong in families with ears (e.g., *Geometridae*, *Notodontidae*, and *Noctuidae*), allowing these moths to perform evasive maneuvers. This shows that despite hunting over extremely short time scales, bats use versatile motor patterns that are supported by ultrafast echo-informed sensory-motor responses to catch evasive prey (17).

Weak prey echoes in a simplified auditory scene

To successfully hunt prey in a reactive mode over short time scales, bats must rely on efficient stream segregation of echoes to guide their motor patterns (1). We hypothesized that bats actively shape their auditory scene to facilitate stream segregation by controlling the timing and level of their calls and, therefore, the relative timing and level of echoes from prey and background (21). To test this, we used echograms to visualize and quantify auditory streams of the bats while hunting ($n = 451$ captures; see example capture in Fig. 1D). We show that the bats control their call timing to receive echoes in an overlap-free zone (i.e., a time window after the emitted

call and before the next vocalization) (22, 23) in which echo ranging is unambiguous (Fig. 1D, dashed black lines).

This confirms laboratory experiments suggesting that bats seek to place echoes of interest between their so-called outer and inner windows (22). It may be hypothesized that bats would seek to maximize the received echo levels from their small prey to be well above hearing thresholds to facilitate auditory streaming. However, despite a wide range of back-calculated TSs (at 0.1 m) (Fig. 3, A and B), the received aerial prey echo levels were consistently extremely low with a dynamic range of 5 to 29 dB re $20 \mu\text{Pa}^2\text{s}$ (95% data range) for the echoes that we could extract (Fig. 3D, black) (fig. S6). The remaining echo streams (58%, 267 of 451 echo streams) were below the noise floor of the tag microphone, suggesting echolocation based on echo levels below 5 dB re $20 \mu\text{Pa}^2\text{s}$ or 30 dB rms (root mean square).

Bats have been reported to have echo detection thresholds from 0 (24) to 55 dB re 20 Pa (25) in laboratory experiments. Here, we show that wild greater mouse-eared bats echolocate prey for capture using echo levels that are only of use to them if they have an acute hearing sensitivity. This sensitivity must exceed the sensitivity reported for many bats in the laboratory but can be supported by auditory sensitivities comparable to those of gleaning bats (down to -27 to -39 dB re $20 \mu\text{Pa}^2\text{s}$, using an integration time of 125 ms) (26, 27) and nocturnal predators such as owls and cats that have similarly evolved very sensitive hearing (-26 to -27 dB re $20 \mu\text{Pa}^2\text{s}$, using a 100-ms signal duration) (28, 29).

Thus, bats deliberately only use the lowest part of their auditory dynamic range for processing of prey echoes by actively reducing their call levels during approach and capture (Fig. 3). This raises the

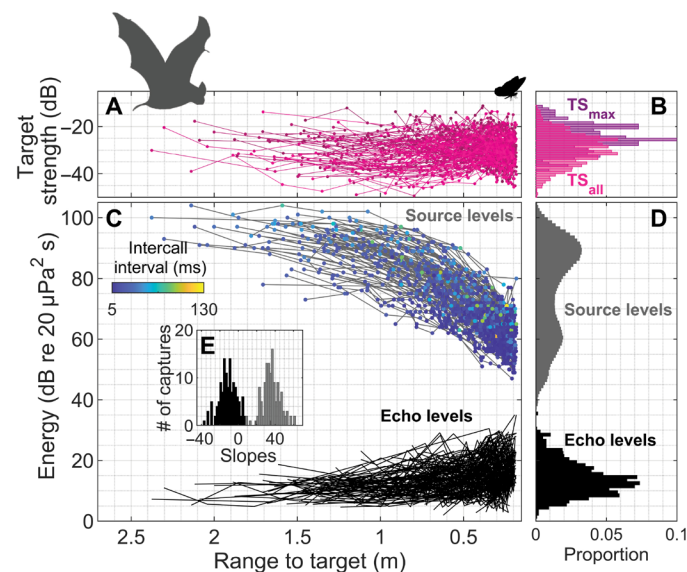


Fig. 3. Hunting bats actively generate weak prey echoes from a large range of prey items. (A and B) Estimated TSs of aerial prey vary over a dynamic range of approximately 30 dB. (C and D) Source levels (gray) and prey echo levels (black) change as bats approach their target. (A to C) $n = 1387$ calls, 204 captures with visible prey echoes. (D) $n = 10$ bats; 43 recording hours; 1,200,368 calls; 1387 echoes. (E) Distribution of the slope for the distance-dependent change in source level (gray) and received echo level (black). Source levels followed a logarithmic fit to target range with a slope of 29 dB ($\pm 11 \text{ SD}$; $R^2 = 0.79$); echo levels followed a slope of -10 dB ($\pm 10 \text{ SD}$; $R^2 = 0.35$). $n = 123$ captures. This means that call source levels reduce by an average of 8.7 dB [i.e., $29 \times \log_{10}(2)$] per halving of distance while echo levels tend to increase by 3 dB over the same distance.

question of why bats opt for such weak echoes spanning a relatively low echo dynamic range if they can increase echo levels for auditory processing by producing louder calls. At long ranges, call intensity may already be maximized (30), and the low echo strength is a consequence of small prey items and high absorption of ultrasound in air. However, as wild bats approach their prey, they produce calls that are well below their maximum intensity, resulting in extremely low echo levels close to the hearing threshold. Bats pursuing aerial prey in the laboratory decrease their output levels logarithmically with target range (R), roughly halving call source level for each halving of range [an intensity adjustment of $\sim -20\log_{10}(R)$ dB] (31–33). This compensates for about half of the decreasing acoustic propagation loss as targets are approached, resulting in echo levels that double for every halving in range, presumably to avoid very loud echoes when approaching prey (34). Our wild bats actively lower the energy of their calls over the course of captures by ~ 30 dB (Fig. 3C) corresponding to an average logarithmic decrease of $29 (\pm 12)$ dB per decade of reduction in range to prey (Fig. 3E, gray). This leads to consistently weak but increasing echo levels of 10 dB (± 10) per decade of reduction in range to prey (Fig. 3, C and D, black) across all prey ranges (Fig. 3, A and B). Over the course of a capture, echo levels therefore generally increase but with large variations likely caused by both the fluctuating TSs from insect wing movements and the use of different call source levels for the same ranges (Fig. 3A).

Thus, wild bats hunting small prey reduce their source levels markedly when within 2 m of their prey to consistently receive weak echo levels across all prey ranges that are sufficient for auditory processing but that fall in an unexpectedly low and narrow distribution just above their hearing threshold. These results support the recent suggestion that bats use a dynamic range compression strategy (35) to avoid receiving loud echoes (36) and perhaps in concert with call-induced stapedial reflexes (31) to maintain a large number of neurons in a nonrefractory state available for auditory processing. To process these weak echoes, bats may have dedicated a large part of their auditory neurons to fire at low levels (37) so as to maximize detection volumes of small prey despite low-intensity calls and, hence, to maximize time to execute complex motor plans for capture. We consequently posit that bats actively adjust call levels during close approaches to keep prey echo levels in a fairly narrow dynamic range close to their hearing thresholds that, in turn, maximizes the overall sensory-motor performance.

Vocal and motor responses reduce clutter

An alternative driver for, or additional benefit of, using low source levels during approach and buzzing may be to minimize clutter from farther objects (fig. S3) that would otherwise complicate the auditory stream segregation of prey. To test that hypothesis and to uncover how bats hunt prey in such cluttered habitat, we first tracked clutter echo streams in echograms of aerial capture attempts and then compared the acoustic and movement behavior during captures both with (57% of the captures; $n = 260$ of 457), and without, detectable clutter (fig. S2 and movie S2). Within the last 3 s before prey capture, prey echoes appear within about 2-m range of the bat, whereas clutter appears at up to 8-m range due to the higher TS of clutter-generating structures (Fig. 4). The clutter echoes disappeared just before prey capture [-0.4 s (± 0.3 SD); Fig. 4B, gray], resulting in simplified auditory scenes during the final moments of prey capture. The continued presence of clutter echoes during the pursuit

indicates that the tagged bats flew alongside large background objects, such as forest edges, at ranges of 1.9 to 7.8 m (Fig. 4). By keeping a minimum range to the clutter sources of about one prey detection range, the bats temporally separate clutter echo streams from the echoes of potential prey, thereby facilitating auditory stream segregation of the weaker prey echoes.

We next investigated how the source levels and flight paths varied before and after prey detection in the different habitats (cluttered versus uncluttered) to test whether bats use motor and sensory adjustments to aid in clutter rejection. Before prey detection (i.e., >2 s before captures), we found that bats increased call source levels, used less variable flight paths [GLMM (generalized linear mixed-effect model); $P < 0.01$, R^2 (coefficient of determination) = 0.6; table S3], and used longer call intervals (t test; $t = -11.5$, $P < 0.001$) in cluttered versus uncluttered conditions. This is counter to what has been found in microphone array recordings in the wild where bats have been shown to call weaker (38, 39) and at higher rates (23) to maintain sufficient updates to navigate in cluttered environments while avoiding range ambiguity. In contrast, the wild bats in our study emitted intense calls at slower rates perhaps to keep unambiguous clutter streams audible even in situations where the bats fly up to tens of meters away from background structures (Fig. 4), while still retaining overlap between successive sensory volumes (Fig. 2E).

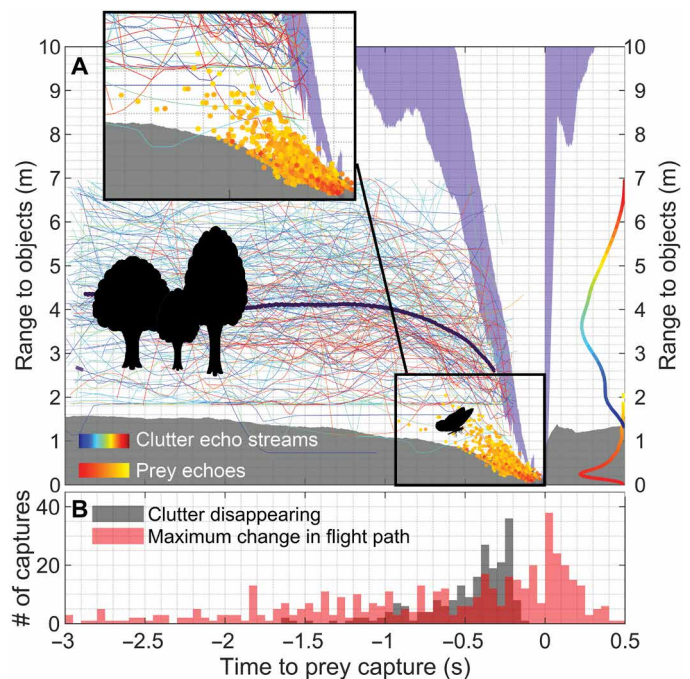


Fig. 4. Bats separate prey and clutter echo streams by acoustic gaze and motor pattern adjustments. (A) The durations of the current call and the following call determine the inner (gray) and outer (purple) window, which together determine the overlap-free perceptual zone. The echo streams of prey (colored dots) and clutter (colored lines, according to each individually tagged bat; the black line depicts mean clutter distance) are located within the overlap-free zone. Histograms on the right axis show that prey and clutter echoes are spatially separated. (B) Timing of the disappearance of clutter from the auditory scenes (gray) and the maximum change in the flight path (red). The bats approach their prey with flexible nonstereotypic flight patterns, as their maximum change in flight paths span a large time scale (~ 2 s).

We thus argue that bats searching for prey actively keep clutter streams in their auditory scenes by maintaining long call intervals and large sensory volumes to use clutter as echo acoustic flow (40, 41) or as a spatial anchor for navigation. Furthermore, this sensory strategy maintains long detection ranges and therefore allows time for reactions while avoiding range ambiguity. Thus, in search and approach phases, the bats operate at a high sensory-to-motor ratio and therefore likely plan the motor patterns necessary to maximize detection of prey against clutter and to intercept their prey.

During the last stage of prey capture, clutter echoes disappeared just before prey capture [-0.4 s (± 0.3 SD); Fig. 4B, gray], resulting in even simpler auditory scenes close to prey interception. The vocal and motor patterns when hunting in open space or in cluttered habitats at this stage remained the same. This suggests that the mean $29\log_{10}(R)$ reduction in call source levels (Figs. 3 and 4) is sufficient to eliminate interference from clutter only before interception (i.e., on average over the last 0.4 s before prey capture; Fig. 4B, gray). Furthermore, at this late stage in the capture, the bat's movement is likely dominated by maneuvering to intercept prey and not to avoid collision with large background structures: In the absence of clutter echoes, collision avoidance must be achieved by spatial memory rather than sensory feedback. This result suggests that the motor patterns have already been planned at an earlier stage further supporting our notion that bats operate in a highly reactive sensory mode (Fig. 2F) close to prey capture.

Thus, we conclude that adjustments of both sensory (vocal) and motor (flight trajectory) patterns at an early stage of the hunt increase the efficiency of prey capture in complex environments. This strategy serves both to counter insects that seek refuge in vegetation as a predator-abatement strategy and to expand the niches available to foraging bats.

In conclusion, we found that bats actively adjust call intensity to generate weak prey echoes with a low dynamic range. This may be a consequence of gaze adjustments aimed at simplifying the natural auditory scene, thereby easing tracking of prey echo streams in cluttered environments.

These results show how wild bats adjust their sensory sampling and flight motor planning during foraging so as to separate clutter and prey sensory streams in time and space. Doing so may critically facilitate perceptual organization of their sensory inputs to inform echo-guided captures in less than 0.5 s. Bats are therefore extreme examples of predators that have evolved a flexible and rapid control over their dominant sensory system and motor actions to hunt fast, evasive prey efficiently in highly dynamic and complex scenes.

MATERIALS AND METHODS

Experimental procedure

All experiments were carried out under the following licenses: 721/12.06.2017, 180/07.08.2018, and 795/17.05.2019 from MOEW (Ministry of Environment and Water)–Sofia and RIOSV (Regional Inspectorate of Environment and Waters)–Ruse. During the field seasons of 2017, 2018, and 2019, we tagged and recaptured 10 female *M. myotis* with on-board sound and movement tags. The acoustic tag used for these studies recorded audio with a Knowles ultrasonic microphone (FG-23329) and sampled the bat's behavior by synchronized triaxial accelerometers and magnetometers. The audio was recorded at a sample rate of 187.5 kHz (16 bit) and a clip level of 121 dB re 20 μ Pa. A one-pole, 10-kHz high-pass filter and an

anti-aliasing filter of 80 kHz were filtering the output of the microphone. The accelerometers were sampled at 1000 Hz (16 bit, 8 g) with a 250 Hz anti-alias filter, while the magnetometers were sampled at 50 Hz. The tags weighed between 3.5 and 3.9 g including radio transmitters to locate the bats (table S1).

The bats were caught with a harp trap at Orlova Chuka cave, close to Ruse, North east Bulgaria, in the early mornings as they returned to the roost. The bats were kept at the Siemers Bat Research Station in Tabachka to measure the forearm lengths, CM3, and body weights (table S1). Bats weighing above 29 g were tagged and released the following night between 10 and 11 p.m. at a field 8 km from the roost (decimal degrees, 43.622097 and 25.864917). The tags were wrapped in balloons for protection and glued to the fur on the back between the shoulders with skin bond latex glue (Ostobond). The bats on average spend 2 to 14 days equipped with the tags until we recaptured the bats at the cave or until the tags were detached from the bats and fell to the ground below the colony. Upon recapture, the bats were weighed and checked for any sign of discomfort from the tagging before they were released back to the colony.

The tags weighed 11 to 14% of the body mass of the bats, which is higher than the 5% rule. The bats on average lost ~ 2.5 g during the tagging, which is less than the average diurnal loss in body mass of 5.5 g during the 1 day spent at the station before release (table S1). In addition, these bats caught prey up to several hundred times per night with high success rates (table S2), indicating that the tags did not have large, if any, effects on their ability to maneuver and catch prey (42). The bats were weighed and inspected after instrumentation for any sign of discomfort before they were released back to the colony.

Categorization of behaviors

All wild tag recordings were manually analyzed by displaying both the acoustic and the inertial sensor data in 7-s segments with an additional option of playing back audio data. The visualization included three separate windows with synchronized data: an envelope of audio data filtered by a 20-kHz four-pole high-pass filter to detect the echolocation calls. A spectrogram of audio data filtered by a 1-kHz one-pole high pass filter to visualize the full-bandwidth acoustic scene showing echolocation calls, conspecific calls, chewing sounds, wind noise, etc. The final window showed triaxial accelerometer and magnetometer data aiding the identification of wingbeats, landings, etc. Aerial capture attempts were identified in the wild data by comparison to the data from the prey capture study in the flight room. An aerial prey capture attempt was marked if the bat was flying both before and after a buzz.

The aerial captures were divided into search, approach, and buzz phases. The buzz phase was defined as the time interval where all call intervals were below 10 ms. In this study, we used the end of the buzz as the time of prey capture. The approach phases were defined by five participants manually marking the beginning of the approach phase based on call intervals and source levels plotted against time to prey capture. Whenever three of the five participants marked the transition into the approach phase in the same time interval (± 120 ms), the mean value was used as the onset of the approach phase. The onset of the approach phase was on average 0.42 s (± 0.15 SD) before prey capture. The approach phase ended when the first call was below 10 ms, indicating that the bat had transitioned into the buzz phase. We used the last 10 calls before the approach for analyzing search phase behaviors.

To compare the aerial captures to another operational mode (spatial orientation), we identified 100 s of each tag recording, where the bat was performing “commuting flight.” This was defined as a time period with no prey capture attempts, regular flight pattern, a wingbeat frequency between 6 and 7 Hz, and stable output levels.

Biosonar parameters

All calls in the tag recordings were automatically detected by a call detector and visually inspected to ensure correct extractions. Call energy of the off-axis calls (AOLs) were estimated in energy flux density (EFD) over a -6 -dB energy window. The 14 -dB offset between AOLs and source levels in the target approach experiment (fig. S4) was added to AOLs to estimate source levels from the on-board recordings. On the basis of the technique developed from the aerial prey captures in the flight room, we tracked echo streams on all echograms of the aerial captures to extract echo levels (ELs) and the range to target, R (figs. S5 and S6). The beginning and end of the prey echo streams were manually marked. The parameters, SL, EL, and R , were used to calculate TS at 0.1 m of the insect for each call-echo pair. The slope of the tracked prey echo streams corresponded to the speed at which the bat was homing in on the insect (i.e., the approach speed). The tagged bats in this study used approach speeds between 1.4 and 4.9 m/s (95% data range) (fig. S4). It was only possible to detect echo streams from the echograms in 45% of all the captures ($n = 204$ of 457), meaning that we could only extract approach speeds from half of the captures.

Clutter extractions

To understand how clutter interferes with prey captures, clutter echo streams from the surroundings were identified and tracked on the echograms. Clutter echoes were distinguished from prey echoes based on the time over which they returned. Large clutter echoes from, e.g., vegetation, return over a longer time interval compared to the single prey echoes from small aerial prey (fig. S4). The clutter detector was tracking the closest stream of echoes above a threshold of 0.5% of the maximum amplitude in a time window from 3 s to 200 ms before the beginning of the buzz and above a distance corresponding to the length of the call in meters in front of the bat to the next call emission.

A tracked echo stream was as categorized as a clutter echo stream if these two criteria were fulfilled:

- 1) More than six echoes were extracted in a sequence.
- 2) The distance to the reflecting object did not vary by more than 0.5 m from call to call. For two individuals, we set a 0.7 -m threshold.

The range to clutter over successive calls was interpolated using cubic Hermite interpolation [pchip (MATLAB 2019a) to a sampling rate of 30 Hz] and smoothed with a moving mean of 0.16 s.

Movement

We defined motor range as the minimum distance flown from sensory input until a motor reaction in response to this sensory input can occur. The motor range is calculated by multiplying the reaction time [100 ms (17) and 200 ms as a more conservative estimate, taking the processing time into account] with the velocity of the bat. Here, we used flight speeds of 7 m/s for commuting flights and 4, 2.5, and 1 m/s for the three different phases of foraging behavior, resulting in motor ranges of 0.7, 0.5, 0.25, and 0.1 m. The motor range was used to calculate SMRs. The three-dimensional flight

paths of the bats were reconstructed by calculating the dead reckoning tracks (DRTs). The DRTs were calculated on the basis of the orientation of the bat recorded by the accelerometers and magnetometers and on assuming a flight speed for the bat (43). The accelerometer and magnetometer data were downsampled to a sample rate of 25 Hz and low-pass filtered by a delay free finite impulse response filter with a cutoff frequency of 3 Hz to reduce the high-frequency motion accelerations. This method is not accurate (44) but suitable to measure the relative angular changes in flight paths used in this study. The angular changes in the flight paths were measured every 40 ms (corresponding to every sample using a sample rate of 25 Hz) by calculating the vector between every successive samples of the DRT. The angle between two successive vectors was calculated for all data points along the flight path. To estimate the angular turns in a time interval over where the bats would likely be able to make a full reaction (reaction time between 80 and 120 ms), the angles were summed every 120 ms.

Calculations of sensory volumes

To study how the changes in output level affected the spatial volume that the bat ensonified per call (i.e., the sensory volumes) and the number of times the same volume was ensonified (i.e., the sensory redundancy), we modeled the sensory beams per call along the three-dimensional flight path of the bats (figs. S7 to S10). The air volume that the bat ensonified per call varied according to source level, beam shape, hearing threshold, and the size of the target of interest. Here, we used source levels measured from on board the tag, the piston model to estimate the radiation pattern of the call, and a point target with TS of -30 dB at 0.1 m indicated from our recordings to model the prey sensory volume. To model the navigation sensory volumes, we chose a mirror target with TS of -10 dB for the commuting flights. We used a hearing threshold of 0 dB re $20 \mu\text{Pa}^2\text{s}$, as we could observe acoustic reactions to echoes returning at and below this level in our field data.

Statistical analysis

All statistical analyses were conducted using R version 4.0.3. We investigated the relationship between the presence of clutter in the auditory scenes of the bats and their acoustic and movement behavior. We used the presence of clutter as a response variable (hereafter named “clutter”) and the change in source levels and flight paths as predictor variables (table S3) because laboratory studies have shown that bats adjust both the energy of their calls and their flight path when hunting in clutter. To explore this relationship, we tested the hypothesis that the presence of clutter in the echograms is explained by the slope of the six closest call source levels at 0.4 and 2 s before capture and by the maximum change in angle at 0.4 and 2 s before capture.

This time interval was chosen because the clutter on average disappeared 0.4 s before prey capture. We used the individual tagged animal (AnimalNo) as random effect.

We examined potential collinearity between predictor variables using variance inflation factors. No collinearity was found. After examining the response variable, we fitted a GLMM (glmer in R package “lme4”) to the data using binomial distribution with a “logit” link. We used model selection procedures (dredge in R package “MuMIn”) to examine the best-fitted model using the AICc (corrected Akaike information criterion). The best-fitted model included the maximum change in angle ($MA_{2\text{sec}}$) and the

slope of the call source levels (SL_{2sec}) at 2 s before capture. This was chosen as our best-fitted model. The residuals were examined and showed slight deviations from the expected distribution (using “simulateResiduals” in the “DHARMA” R package). The model was refit with a “cauchit” link function, which slightly improved the patterns.

Overall, the model including fixed and random effects explained 49% of the deviance in the clutter presence (using `rsq` in the “rsq” R package). Subtracting the random effect from the model decreased the explained deviance by 2%.

The effect of the individual predictor variables was examined (using R package “hier.part”). The change in source levels and flight path 2 s before capture explained 57 and 43%, respectively, of the deviance explained by the model. The best-fitted model (table S3) indicates that there is a significant effect of source level reductions and change in flight path on the presence of clutter in the auditory scenes of the bats before prey pursuit.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/7/10/eabf1367/DC1>

[View/request a protocol for this paper from Bio-protocol.](#)

REFERENCES AND NOTES

- M. S. Lewicki, B. Olshausen, A. Surlykke, C. F. Moss, Scene analysis in the natural environment. *Front. Psychol.* **5**, 199 (2014).
- D. R. Griffin, Echolocation by blind men, bats and radar. *Science* **100**, 589–590 (1944).
- A. Surlykke, C. F. Moss, Echolocation behavior of big brown bats, *Eptesicus fuscus*, in the field and the laboratory. *J. Acoust. Soc. Am.* **108**, 2419–2429 (2000).
- L. Jakobsen, M. N. Olsen, A. Surlykke, Dynamics of the echolocation beam during prey pursuit in aerial hawking bats. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 8119–8123 (2015).
- D. R. Griffin, F. A. Webster, C. R. Michael, The echolocation of flying insects by bats. *Anim. Behav.* **8**, 141–154 (1960).
- D. A. Cahlander, J. J. G. Mccue, F. A. Webster, The determination of distance by echolocating bats. *Nature* **201**, 544–546 (1964).
- E. K. V. Kalko, Insect pursuit, prey capture and echolocation in pipestirelle bats (*Microchiroptera*). *Anim. Behav.* **50**, 861–880 (1995).
- M. W. Holderied, C. Korine, M. B. Fenton, S. Parsons, S. Robson, G. Jones, Echolocation call intensity in the aerial hawking bat *Eptesicus bottae* (*Vespertilionidae*) studied using stereo videogrammetry. *J. Exp. Biol.* **208**, 1321–1327 (2005).
- A. R. Wheeler, K. A. Fulton, J. E. Gaudette, R. A. Simmons, I. Matsuo, J. A. Simmons, Echolocating big brown bats, *Eptesicus fuscus*, modulate pulse intervals to overcome range ambiguity in cluttered surroundings. *Front. Behav. Neurosci.* **10**, 125 (2016).
- B. Mao, M. Aytakin, G. S. Wilkinson, C. F. Moss, Big brown bats (*Eptesicus fuscus*) reveal diverse strategies for sonar target tracking in clutter. *J. Acoust. Soc. Am.* **140**, 1839–1849 (2016).
- B. Falk, L. Jakobsen, A. Surlykke, C. F. Moss, Bats coordinate sonar and flight behavior as they forage in open and cluttered environments. *J. Exp. Biol.* **217**, 4356–4364 (2014).
- M. Taub, Y. Yovel, Segregating signal from noise through movement in echolocating bats. *Sci. Rep.* **10**, 382 (2020).
- L. Stidsholt, M. P. Johnson, K. Beedholm, L. Jakobsen, K. Kugler, S. Brinkløv, A. Salles, C. F. Moss, P. T. Madsen, A 2.6-g sound and movement tag for studying the acoustic scene and kinematics of echolocating bats. *Methods Ecol. Evol.* **10**, 48–58 (2019).
- J. B. Snyder, M. E. Nelson, J. W. Burdick, M. A. MacIver, Omnidirectional sensory and motor volumes in electric fish. *PLOS Biol.* **5**, e301 (2007).
- L. P. Tyrrell, E. Fernández-Juricic, The hawk-eyed songbird: Retinal morphology, eye shape, and visual fields of an aerial insectivore. *Am. Nat.* **189**, 709–717 (2017).
- J. E. Boström, M. Dimitrova, C. Canton, O. Håstad, A. Qvarnström, A. Ödeen, Ultra-Rapid vision in birds. *PLOS ONE* **11**, e0151099 (2016).
- C. Geberl, S. Brinkløv, L. Wiegrebe, A. Surlykke, Fast sensory–motor reactions in echolocating bats to sudden changes during the final buzz and prey intercept. *Proc. Natl. Acad. Sci.* **112**, 4122–4127 (2015).
- D. M. M. Wisniewska, M. Johnson, J. Teilmann, L. Rojano-Doñate, J. Shearer, S. Sveegaard, L. A. A. Miller, U. Siebert, P. T. Madsen, Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Curr. Biol.* **26**, 1441–1446 (2016).
- J. Demšar, C. K. Hemelrijk, H. Hildenbrandt, I. L. Bajec, Simulating predator attacks on schools: Evolving composite tactics. *Ecol. Model.* **304**, 22–33 (2015).
- T. Hügel, H. R. Goerlitz, Species-specific strategies increase unpredictability of escape flight in eared moths. *Funct. Ecol.* **33**, 1674–1683 (2019).
- C. F. Moss, A. Surlykke, Auditory scene analysis by echolocation in bats. *J. Acoust. Soc. Am.* **110**, 2207–2226 (2001).
- W. W. Wilson, C. F. Moss, Sensory-motor behavior of free-flying FM bats during target capture, in *Echolocation in Bats and Dolphins*, J. A. Thomas, C. F. Moss, M. Vater, Eds. (The University of Chicago Press, 2004), pp. 22–27.
- E. K. V. Kalko, H.-U. Schnitzler, Plasticity in echolocation signals of European pipistrelle bats in search flight: Implications for habitat use and prey detection. *Behav. Ecol. Sociobiol.* **33**, 415–428 (1993).
- S. A. Kick, Target-detection by the echolocating bat, *Eptesicus fuscus*. *J. Comp. Physiol.* **145**, 431–435 (1982).
- C. F. Moss, J. A. Simmons, Acoustic image representation of a point target in the bat *Eptesicus fuscus*: Evidence for sensitivity to echo phase in bat sonar. *J. Acoust. Soc. Am.* **93**, 1553–1562 (1993).
- S. Schmidt, B. Türke, B. Vogler, Behavioral audiogram from the bat, *Megaderma lyra*. *Myotis* **21–22**, 62–66 (1984).
- R. B. Coles, A. Guppy, M. E. Anderson, P. Schlegel, Frequency sensitivity and directional hearing in the gleaning bat, *Plecotus auritus* (Linnaeus 1758). *J. Comp. Physiol. A* **165**, 269–280 (1989).
- M. Konishi, How the owl tracks its prey. *Am. Sci.* **61**, 414–424 (1973).
- W. D. Neff, J. E. Hind, Auditory thresholds of the cat. *J. Acoust. Soc. Am.* **27**, 480–483 (1955).
- S. E. Currie, A. Boonman, S. Troxell, Y. Yovel, C. C. Voigt, Echolocation at high intensity imposes metabolic costs on flying bats. *Nat. Ecol. Evol.* **4**, 1174–1177 (2020).
- D. J. Hartley, Stabilization of perceived echo amplitudes in echolocating bats. II. The acoustic behavior of the big brown bat, *Eptesicus fuscus*, when tracking moving prey. *J. Acoust. Soc. Am.* **91**, 1133–1149 (1992).
- S. Hiryu, T. Hagino, H. Riquimaroux, Y. Watanabe, Echo-intensity compensation in echolocating bats (*Pipistrellus abramus*) during flight measured by a telemetry microphone. *J. Acoust. Soc. Am.* **121**, 1749–1757 (2007).
- J. C. Koblitz, P. Stilz, W. Pflästerer, M. L. Melcón, H.-U. Schnitzler, Source level reduction and sonar beam aiming in landing big brown bats (*Eptesicus fuscus*). *J. Acoust. Soc. Am.* **130**, 3090–3099 (2011).
- T. Budenz, A. Denzinger, H.-U. Schnitzler, Reduction of emission level in approach signals of greater mouse-eared bats (*Myotis myotis*): No evidence for a closed loop control system for intensity compensation. *PLOS ONE* **13**, e0194600 (2018).
- L. Stidsholt, R. Müller, K. Beedholm, H. Ma, M. Johnson, P. T. Madsen, Energy compensation and received echo level dynamics in constant-frequency bats during active target approaches. *J. Exp. Biol.* **223**, jeb217109 (2020).
- A. Denzinger, H.-U. Schnitzler, Echo SPL, training experience, and experimental procedure influence the ranging performance in the big brown bat, *Eptesicus fuscus*. *J. Comp. Physiol. A* **183**, 213–224 (1998).
- K. R. Measor, B. C. Leavell, D. H. Brewton, J. Rumschlag, J. R. Barber, K. A. Razak, Matched behavioral and neural adaptations for low sound level echolocation in a gleaning bat, *Antrozous pallidus*. *eNeuro* **4**, ENEURO.0018-17 (2017).
- S. Brinkløv, L. Jakobsen, J. M. Ratcliffe, E. K. V. Kalko, A. Surlykke, Echolocation call intensity and directionality in flying short-tailed fruit bats, *Carollia perspicillata* (*Phyllostomidae*). *J. Acoust. Soc. Am.* **129**, 427–435 (2011).
- S. Brinkløv, E. K. V. Kalko, A. Surlykke, Dynamic adjustment of biosonar intensity to habitat clutter in the bat *Macrophyllum macrophyllum* (*Phyllostomidae*). *Behav. Ecol. Sociobiol.* **64**, 1867–1874 (2010).
- M. Warnecke, W.-J. Lee, A. Krishnan, C. F. Moss, Dynamic echo information guides flight in the big brown bat. *Front. Behav. Neurosci.* **10**, 81 (2016).
- K. Kugler, H. Luksch, H. Peremans, D. Vanderelst, L. Wiegrebe, U. Firzclaff, Optic and echo-acoustic flow interact in bats. *J. Exp. Biol.* **222**, jeb195404 (2019).
- K. Egert-Berg, E. R. Hurme, S. Greif, A. Goldstein, L. Harten, L. G. Herrera, M. J. J. Flores-Martinez, A. T. Valdés, D. S. Johnston, O. Eitan, I. Borissov, J. R. Shipley, R. A. Medellín, G. S. Wilkinson, H. R. Goerlitz, Y. Yovel, Resource ephemerality drives social foraging in bats. *Curr. Biol.* **28**, 3667–3673.e5 (2018).
- R. P. Wilson, M. P. Wilson, Dead Reckoning: A new technique for determining penguin movements at sea. *Meeresforschung* **32**, 155–158 (1988).
- R. P. Wilson, N. Liebsch, I. M. Davies, F. Quintana, H. Weimerskirch, S. Storch, K. Lucke, U. Siebert, S. Zankl, G. Müller, I. Zimmer, A. Scolaro, C. Campagna, J. Plötz, H. Bornemann, J. Teilmann, C. R. McMahon, All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. *Deep Sea Res. II Top. Stud. Oceanogr.* **54**, 193–210 (2007).
- R. J. Urick, *Principles of Underwater Sound* (Peninsula Pub, ed. 3, 1983).

46. K. Ghose, C. F. Moss, Steering by hearing: A bat's acoustic gaze is linked to its flight motor output by a delayed, adaptive linear law. *J. Neurosci.* **26**, 1704–1710 (2006).

Acknowledgments: We thank A. Hubancheva for discussions and J. Goldbogen and C. Elemans for comments on the earlier version of the manuscript. **Funding:** This study was funded by the Carlsberg Semper Ardens grant to P.T.M. and by the Emmy Noether program of the Deutsche Forschungsgemeinschaft (DFG; German Research Foundation, grant no. 241711556) to H.R.G. All experiments were carried out under the following licenses: 721/12.06.2017, 180/07.08.2018, and 795/17.05.2019. **Author contributions:** L.S. was responsible for data collection, programming, analysis, interpretation, and drafting of the manuscript. S.G. was responsible for conceptualization, data collection, and interpretation of the data. H.R.G. interpreted the data. K.B. programmed and analyzed the data. J.M. programmed software for data analysis. M.J. designed and manufactured the tags and

contributed to the analysis and interpretation of the data. P.T.M. designed the experiment, analyzed, and interpreted the data. All authors contributed to the writing of the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from the authors.

Submitted 6 October 2020

Accepted 21 January 2021

Published 3 March 2021

10.1126/sciadv.abf1367

Citation: L. Stidsholt, S. Greif, H. R. Goerlitz, K. Beedholm, J. Macaulay, M. Johnson, P. T. Madsen, Hunting bats adjust their echolocation to receive weak prey echoes for clutter reduction. *Sci. Adv.* **7**, eabf1367 (2021).

Hunting bats adjust their echolocation to receive weak prey echoes for clutter reduction

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Sci. Adv., 7 (10), eabf1367. • DOI: 10.1126/sciadv.abf1367

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