



## Predator counteradaptations: stealth echolocation overcomes insect sonar-jamming and evasive-manoeuving defences



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Although bat–insect interactions are often described as an ‘evolutionary arms race’, conclusive evidence for bat counterstrategies to insect defences has been difficult to acquire. Previous studies have indicated that some bats use low-amplitude, ‘stealth’ echolocation to counter moth hearing. However, actual bat–insect interactions have not been documented to validate this finding. We hypothesized that the bat *Corynorhinus townsendii* uses stealth echolocation to overcome prey defences. We measured *C. townsendii* call intensities as they attacked tethered moths in the field and in a large outdoor flight cage. We also used three-dimensional videography to document *C. townsendii* and *Myotis volans*, which uses intensities more typical of aerial-hawking bats, as they attacked free-flying moths in a flight cage. Source levels of *C. townsendii* calls were  $93.6 \pm 6.1$  dB at 0.1 m in open field conditions and  $81.9 \pm 6.9$  dB in the more enclosed flight cage, values that are 20–45 dB lower than other aerial-hawking bats under similar conditions. Sound levels arriving at prey were mostly below known thresholds for eliciting late-attack defences. Free-flying moths were 49–66% less likely to exhibit evasive manoeuvring and sonar-jamming defences during attacks by *C. townsendii* compared to *M. volans*. Prey also exhibited lower peak velocities and accelerations during attacks, factors that are known to affect bat capture success. Accordingly, *C. townsendii* had 31% higher capture success against moths overall and 52% higher capture success against the sonar-jamming moth *Bertholdia trigona*. We conclude that stealth echolocation is an evolutionary counteradaptation to insect defences because there is no known benefit for *C. townsendii* to use low-amplitude calls outside of predator–prey interactions, and such calls come with considerable cost in reduced prey detection distances.

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Predator–prey interactions are often described as an ‘evolutionary arms race’ where both sides reciprocally evolve ever-more sophisticated predator and antipredator adaptations (Dawkins & Krebs, 1979). Antipredator defences in prey are numerous and varied (Edmunds, 1974; Ruxton, Sherratt, & Speed, 2004). In contrast, unambiguous examples of predator counteradaptations to prey defences are rare (but see Catania, 2009, 2014; Geffeney, Brodie, Ruben, & Brodie, 2002; Rowe, Xiao, Rowe, Cummins, & Zakon, 2013). This may result from asymmetrical selective forces on predator and prey: prey that lose encounters die, whereas predators survive to search for another meal (‘the life-dinner principle’, Dawkins & Krebs, 1979).

Bat–insect interactions are a model system for studying predator–prey interactions (Conner & Corcoran, 2012; Miller & Surlykke, 2001; ter Hofstede & Ratcliffe, 2016). Bats hunt insects

with sophisticated echolocation (Griffin, 1958), an active sensory system that allows bats to pinpoint flying insects in darkness, but also alerts prey to danger. Many insects evolved ultrasound-sensitive tympanal organs de novo or adapted existing ears to detect bats (Roeder, 1967; ter Hofstede, Goerlitz, Ratcliffe, Holderied, & Surlykke, 2013; Yack, 2004). Eared insects exhibit a variety of evasive manoeuvres that are dependent on the intensity (and sometimes calling rate) of bat echolocation calls (Miller & Surlykke, 2001; Roeder, 1962). Low-intensity calls often elicit negative phonotaxis to avoid attacks; higher-intensity calls elicit progressively stronger flight manoeuvres, including erratic spirals and dives. Moths endemic to islands that lack bat predators exhibit reduced neural and behavioural responses to ultrasound, a finding that indicates bats provide selective pressure for maintaining moth defensive responses (Fullard & Ratcliffe, 2006; Fullard, Ratcliffe, & Soutar, 2004). Some insects also produce ultrasonic clicks that either jam bat echolocation (Corcoran, Barber, & Conner, 2009; Kawahara & Barber, 2015) or warn bats of their toxicity (Barber & Conner, 2007; Dowdy & Conner, 2016; Hristov & Conner, 2005).

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Some forms of echolocation make bats inconspicuous to eared prey and are hypothesized to be counteradaptations to insect hearing. For example, unusually low or unusually high frequencies may allow some bats to avoid being detected by eared prey (Fenton & Fullard, 1979; Fullard, 1988; Rydell & Arlettaz, 1994; Schoeman & Jacobs, 2003). However, there are plausible alternate explanations for why bats echolocate at these extreme frequencies. Low calling frequencies allow bats to detect prey at further distances, and high frequencies provide better spatial resolution of echolocation scenes. Therefore, it is unclear whether these forms of echolocation evolved specifically to counter insect defences (Waters, 2003).

Bats that glean insects off surfaces use low-amplitude echolocation that is also inconspicuous to eared prey (Faure, Fullard, & Dawson, 1990). However, fruit-eating bats that forage in cluttered environments also use low-amplitude echolocation ('whispering'), and this appears to be a general adaptation for echolocating near surfaces, not necessarily an adaptation for overcoming prey defences (Brinkløv, Kalko, & Surlykke, 2010).

The best evidence for an echolocation counterstrategy to insect hearing comes from a study of the bat *Barbastella barbastellus*, which captures insects out of the air (i.e. aerial hawking), uses unusually low-amplitude echolocation calls and consumes large numbers of eared moths (Goerlitz, ter Hofstede, Zeale, Jones, & Holderied, 2010). Neurophysiological preparations of moth ears set up in the field indicate that moths detect *B. barbastellus* at much shorter distances compared to other species, and that moths would only enact evasive manoeuvring defences when bats are within 1–2 m, if at all. The authors argued that there is no other adaptive reason for an aerial-hawking bat to use low-amplitude echolocation, and therefore that 'stealth' echolocation evolved specifically to counter insect hearing (Goerlitz et al., 2010).

Goerlitz and colleagues provided a compelling argument for *B. barbastellus* using an echolocation counterstrategy, but questions remain because actual attacks on prey have not been documented. *Barbastella barbastellus* forages close to background vegetation (Sierro, 1999), a situation that favours low-amplitude calls (Brinkløv et al., 2010). Also, it is likely that *B. barbastellus*, which has low wing loading and is adapted for slow flight (Norberg & Rayner, 1987), would need to fly slowly when attacking prey that they detect at short distances. This would provide prey more time to react to the bat's echolocation calls, even if the prey detects the bat at a short distance. Escape manoeuvres that are initiated when predators are nearby (such as the 1–2 m distance modelled for *B. barbastellus*) can be highly effective, and are in the range observed for prey escaping bats in cluttered environments (Corcoran & Conner, 2016). Eared prey are frequently captured and eaten not only by *B. barbastellus*, but also by some bats that use high-intensity echolocation such as *Lasiurus borealis* (Clare, Fraser, Braid, Fenton, & Hebert, 2009). Therefore, it remains an open question to what degree low-amplitude echolocation calls prove advantageous for aerial-hawking bats.

We aimed to address this question by studying the echolocation and foraging of *Corynorhinus townsendii* (Cooper, 1837). *Corynorhinus* is closely related to *B. barbastellus* (Hoover & Van Den Bussche, 2001), has similar wing morphology (Norberg & Rayner, 1987) and peak echolocation frequency (32 kHz versus 33 kHz, respectively; Goerlitz et al., 2010) and calls at low intensity (Grinnell et al., 1963). Both species frequently capture insects out of the air in edge habitats (Fellers & Pierson, 2002; Kunz & Martin, 1982; Sierro & Arlettaz, 1997), and like *B. barbastellus*, *C. townsendii* often captures eared moths (Lacki & Dodd, 2011; Van Den Bussche et al., 2016). In addition to capturing prey out of the air, *C. townsendii* sometimes gleans prey off surfaces (Lacki & Ladeur, 2001), a trait that is common to many aerial-hawking bat species (Jones, Page, & Ratcliffe, 2016; Ratcliffe & Dawson, 2003).

We conducted two experiments to test the stealth echolocation hypothesis (Fig. 1). In experiment 1, we used multicamera infrared videography and a miniature ultrasound microphone suspended near tethered, live moths to document sound levels produced by *C. townsendii* and at the position of prey during attacks. We predicted that *C. townsendii* call intensities would be lower than intensities of other aerial-hawking bats in the same environments and that call sound levels at the position of the prey would be below known thresholds for insect defences. In experiment 2, we documented attacks by *C. townsendii* on a variety of free-flying moths that were released in a flight cage. For comparison, we also documented attacks by *Myotis volans* under identical conditions. This bat species was chosen because it specializes on hunting moths in cluttered habitats (Johnson, Lacki, & Baker, 2007) and uses call intensities that are more typical of aerial-hawking bats (Corcoran, Wagner, & Conner, 2013; Surlykke & Kalko, 2008). *Myotis volans* is similar in mass (10.4 g versus 10.6 g) and aspect ratio (5.8 versus 5.9) to *C. townsendii*, but has higher wing loading (8.3 N/m<sup>2</sup> versus 6.6 N/m<sup>2</sup>; Norberg & Rayner, 1987). Both bat species produce short (2–5 ms) broadband calls that sweep rapidly across a broad range of frequencies (Corcoran et al., 2013). We predicted that insect prey would exhibit fewer and less robust defensive responses to attacks by *C. townsendii* than *M. volans*, and that *C. townsendii* would capture prey at higher rates than *M. volans* and exhibit shorter prey detection distances.

## METHODS

### Animal Care

All experiments were approved by the Wake Forest University Institutional Animal Care and Use Committee (IACUC protocol A12-048). Permits for catching and holding bats were acquired from the State of Arizona Game and Fish Department (License number SP558983). For experiments conducted in the flight cage, bats were captured using mist nets and housed in wooden boxes (0.3 × 0.3 m and 0.5 m high) with ad libitum access to water. *Corynorhinus townsendii* were captured in flight corridors near a known roost; *M. volans* were captured in riparian corridors.

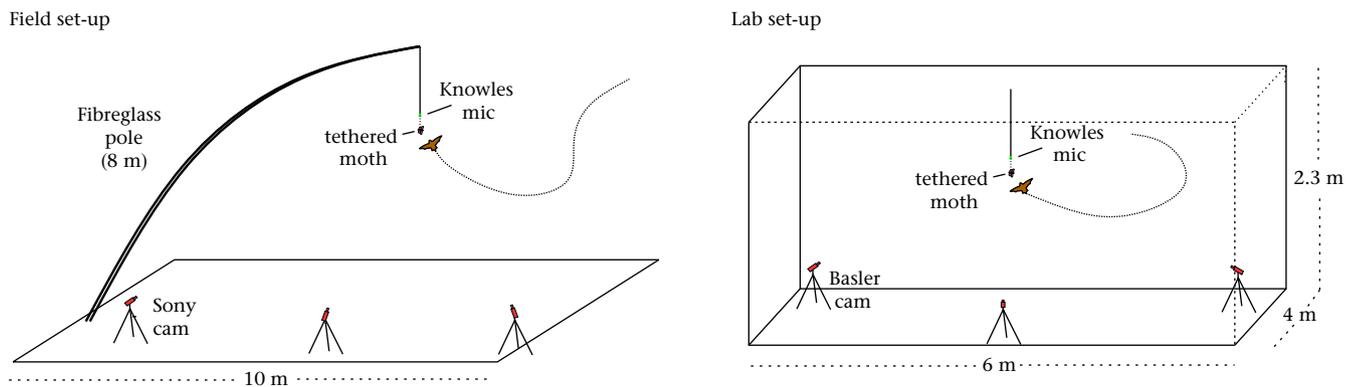
Bats were housed in groups of three to four individuals to provide social interaction, but flown alone during foraging experiments. Individuals were held in captivity for up to 7 days and released at the site of capture at the end of the experiment. The only food available to the bats were free-flying moths that had been released into the flight cage. Bats were allowed to hunt insects for 60–90 min each night of captivity until they were no longer motivated to hunt. The first two nights of captivity were used as an adjustment period to allow bats to acclimate to their new environment. Experiments began on the third night.

All moths used in experiments were caught from the wild using an ultraviolet light trap ('blacklight'; Leptraps LLC, Georgetown, KY, U.S.A.) that funnelled insects into a lumite collecting chamber 1 m tall and 0.3 m in diameter. Moths were held in a 19-litre holding chamber filled with cardboard egg cartons for up to 4 h prior to being used in experiments.

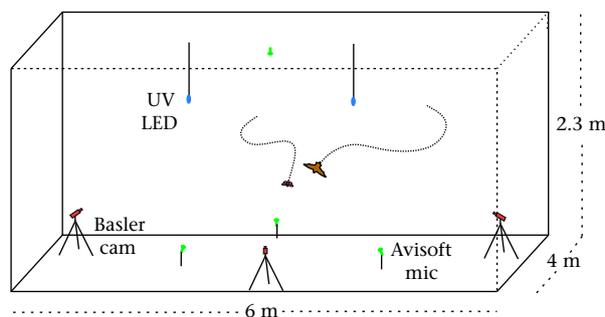
### Tethered-moth Experiments

In experiment 1, we documented the echolocation call intensities of *C. townsendii* attacking tethered moths in the field and in a large outdoor flight cage (Fig. 1a). Methods closely replicate those of Corcoran et al. (2013). Experiments were conducted during July 2010 and 2011 at the Southwestern Research Station (SWRS), Portal, AZ, U.S.A., and in the surrounding areas of the Chiricahua

## (a) Experiment 1: Measuring call intensities



## (b) Experiment 2: Attacks on free-flying moths



**Figure 1.** Experimental recording set-ups. (a) Experiment 1 was designed to measure call intensities from (1) bats in the field and (2) bats in a flight cage. The diagrams indicate the positions of Sony and Basler cameras (cam) and a miniature, calibrated Knowles microphone (Knowles Mic). Each camera was mounted directly on infrared lights (not shown). Tethered moths were suspended 0.25 m below the microphone. (b) Experiment 2 pitted individual *M. volans* or *C. townsendii* bats against free-flying moths in a large outdoor flight cage. Moths were captured from the environment and released into the enclosure with individual bats. Two ultraviolet light-emitting diodes (UV LED) were suspended from the ceiling to attract free-flying moths into the operating space of the flight room. In experiment 2, attacks were recorded by three infrared cameras, and four Avisoft microphones. As with experiment 1, cameras were mounted directly on infrared lights (not shown).

Mountains. For all tethered-moth experiments, medium-bodied (1–2 cm body length) noctuid moths were tethered 0.25 m below a calibrated Knowles microphone (Knowles Acoustics FG-3329, Itasca, IL, U.S.A.; AR100 ultrasound receiver, Binary Acoustics Technology, Tucson, AZ, U.S.A.; calibration details provided below) using a 0.1 mm monofilament line. Moths were affixed to the monofilament line by applying a superglue adhesive to the moth's descaled mesoscutum. Efforts were made to ensure moths were flying throughout the experiments.

Field recordings were made of *C. townsendii* attacking moths above open scrub habitat beside a rock outcrop. The rock outcrop was approximately 3 m from the location of tethered moths, and there was open space in the other three directions. This recording situation was chosen to match the degree of habitat openness of a previously published data set for *M. volans* (Corcoran et al., 2013), which we used for comparison. For the published study of *M. volans*, bats were recorded using the same set-up as used here, except bats attacked tethered prey in a forest gap with vegetation at a distance of 3 m on one side, and open space extending in the other three directions.

Our field location for studying *C. townsendii* was approximately 100 m from a known roost home to 50–80 individual bats. Bats were observed attacking tethered moths as they left the roost for the night and commuted along a rock wall. Individual bats routinely approached the site from the direction of the roost and continued commuting along the rock wall as they left. This situation makes it highly likely that each attack that was analysed was from a different

individual bat. Species identification was confirmed using this bat's distinctive flight pattern and echolocation call structure. We analysed five attacks made by *C. townsendii* on tethered moths in the field.

Laboratory experiments were conducted in an outdoor flight cage at SWRS (Fig. 1a) that was 6 m long, 4 m wide and 2.3 m tall. The walls of the flight cage were made of hardware cloth having wires spaced at 1 cm. Six adult female *C. townsendii* were individually released into the observatory until they successfully attacked a tethered moth. One successful attack was analysed from each individual.

#### Audio and Video Recording in Tethered-moth Experiments

For all tethered-moth experiments (both in the field and in the flight cage), ultrasound was recorded using a 3 mm diameter Knowles microphone that was suspended from an 8 m fibreglass pole (in the field) or from the ceiling of the flight cage. The sampling rate was set to 250 kHz. Three infrared cameras were used to record all attacks. For the flight cage experiments, video was captured using Basler Scout sCA640-120gc cameras (Ahrensburg, Germany) recording at 60–90 frames per second and 640 × 480 pixel resolution. Three Raytec Raymax 200 (Ashington, U.K.) illuminators provided infrared lighting. Cameras were frame-synchronized using custom electronics (Innovision Systems, Columbiaville, MI, U.S.A.). An electronic trigger was used to synchronize audio and video recordings. Audio and video were recorded in a 10 s buffer,

which was triggered to save to the hard drive after attacks were observed.

Our only available site for observing foraging *C. townsendii* in the field was 3 km up a mountainous trail. The remote location precluded use of the Basler camera system and associated computer equipment. Instead, we recorded video using portable Sony cameras (Sony HDR-HC9, Tokyo, Japan) in 'nightshot' mode. Cameras operated at 30 interlaced frames per second, which were deinterlaced to provide 60 fields per second with  $720 \times 240$  pixel resolution. For this set-up, audio and video recordings were made continuously throughout the experiment. Audio and video were synchronized using an audio pulse that was broadcast from a position equidistant from each of the three cameras. This audio pulse was generated after each bat attack to provide a synchronization time point. We accounted for the time delay of the pulse arriving at the microphone slightly before it arrived at the cameras. This set-up allowed for an audio–video synchronization accuracy of 17 ms (the time interval between video fields).

### Free-flying Moth Experiments

We documented attacks on free-flying moths in the flight cage at SWRS during 18–26 July 2012 (Fig. 1b). The flight cage was the same as described above for the tethered-moth experiments, except one long interior side of the cage was covered with a thick duvetyne cloth. This cloth provided a dark backdrop for the video recordings, and it served as a landing place for moths. This provided opportunities for bats to glean moths off a soft substrate, in addition to capturing them out of the air. A mesh covering was placed over the outside of the enclosure, ensuring that only moths placed into the flight cage by the experimenters were available to the bats.

Attacks were staged between individual *C. townsendii* ( $N = 4$  individuals, all postlactating adult females ( $C_1$ – $C_4$ )) or *M. volans* bats ( $N = 4$  individuals; 3 postlactating adult females ( $M_1$ – $M_3$ ), 1 adult male ( $M_4$ )) and free-flying moths in the outdoor flight cage. Individual bats were released into the observatory and allowed to hunt moths for 60–90 min per night. After this time, bats showed signs of satiation, including reluctance to forage and enlarged abdomens. One individual bat ( $C_1$ ) showed limited interest in hunting in captivity, leading to a smaller sample size compared to other individuals.

We used two categories of prey: (1) the clicking moth species *Bertholdia trigona* and (2) a variety of silent moth species. The focal species *B. trigona* was chosen because it has evasive and clicking responses that have been well categorized (Corcoran & Conner, 2012; Corcoran et al., 2013). The second prey category was chosen to reflect a diversity of prey that would be available in the environment.

During foraging bouts, the experimenters released wild-caught moths into the enclosure at a rate that ensured one to four moths were flying continuously during the experiments. We found this necessary to keep the bats motivated to attack prey during their time in captivity. This prevented us from knowing the species identity of individual moths during attacks. One exception was *B. trigona*, whose distinctive colour, flight pattern and size, when coupled with frequent ultrasound emissions, allowed species identification during flight.

All moths that were collected in the light trap and released into the flight chamber for the experiments had body lengths of 1–4 cm. This size range was chosen to reflect the size of prey commonly eaten by *C. townsendii* (Van Den Bussche et al., 2016). Moths that are known to produce antitab ultrasound were excluded from the experiments, except for *B. trigona*, which were captured in large numbers and included in the experiment. Most moths that lack

ultrasonic hearing abilities (e.g. Lasiocampidae, Ethmiidae, Tortricidae, Saturniidae) were excluded from the experiments because they were either too small or too large to fit our size criterion.

Approximately 90–95% of moths released into the flight cage in experiments for both bat species were from superfamilies known to have ultrasonic hearing (mostly Noctuoidea, Geometroidea and Pyraloidea). We elected to include the small number of nonhearing moths that met our size criterion in an effort to replicate the diversity of prey that are available to bats in the natural environment. Efforts were made to ensure that a similar variety of moths were available to both bat species. This included collecting all moths from a single location in the field where we had been surveying moths for a 4-year period prior to this study. A list of common species used in experiments is provided in [Supplementary Table S1](#).

### Audio and Video Recording in Free-flying Moth Experiments

Video of attacks was recorded at 90 frames per second using the Basler camera system described above. Ultrasound was recorded using four Avisoft CM16/CMPA microphones that were situated around the flight cage (Fig. 1b). An Ultrasound Gate 416H recording unit (Avisoft Bioacoustics, Bradensburg, Germany) connected to a laptop computer was used to make audio recordings. Audio and video were synchronized using a custom electronic signal generator. Two ultraviolet light-emitting diodes (5 mm diameter, 20 mA) were suspended 1 m from the ceiling using 1 mm diameter electrical wires. This provided a small visual stimulus that attracted moths to fly in the operating space of the flight cage. Synchronized 90 s audio–video recordings were made throughout foraging bouts. These 90 s recordings were separated by 15 s gaps in time that allowed video to be transferred from the computer's memory to its hard drive. This allowed synchronized audio–video recordings of 85% of the time bats were foraging. All attacks that were captured on video were analysed and are reported here. Moths were removed from the observatory after unsuccessful attacks to avoid pseudoreplication.

### Video Analysis of Free-flying Attacks

We examined videos of bat–moth interactions to find all bat attacks on prey. An attack was defined as a deviation in the bat's flight path towards a moth that was accompanied by an increased calling rate. Capture was defined as a bat making contact with the prey, regardless of whether the prey was eaten.

Thirty attacks for each bat species were selected for reconstruction of bat and moth flight trajectories (details on reconstructions are provided below). To select these attacks, we first identified all interactions that occurred within view of multiple cameras. We then used a random number generator to select thirty attacks, while ensuring that attacks were evenly distributed across individual bats. Peak moth flight kinematics (velocity, linear acceleration and radial acceleration) were determined for the last 0.5 s of each attack, and for a control period from 0.5 to 1 s before the beginning of each attack. Methods for measuring flight kinematics are reported elsewhere (Corcoran & Conner, 2016). Based on our quantitative analysis, we established criteria for determining whether or not moths exhibited evasive manoeuvres in attacks. Moths were considered to exhibit an evasive manoeuvre if during the bat's approach it increased either radial or linear acceleration by at least  $5 \text{ m/s}^2$ . A data set of videos where prey either met or did not meet these criteria were used to train an observer who was blind to the purposes of the experiment. This blind observer then scored the remaining videos for presence or absence of prey evasive manoeuvring.

### Video Calibrations

Cameras were calibrated for three-dimensional reconstruction of bat, moth and microphone positions using a 'wand' calibration method (Theriault et al., 2014). Two infrared markers were fixed on the ends of a rigid rod (the wand) that was moved throughout the space visible to all three cameras. We digitized 1000–2000 frames per calibration using the MatLab packages DLTdv5 and easyWand5 (Hedrick, 2008; Theriault et al., 2014). Digitized bat and moth positions were added as 'background points' to fill out the calibrated volume. Calibrations had good accuracy, with typical reprojection errors of <1 pixel and 'wand scores' (standard deviation of reconstructed wand lengths) of <1% (Theriault et al., 2014). A ball that was dropped in the calibrated volume had a measured acceleration within 1% of gravitational acceleration. Reconstruction accuracy was slightly lower for calibrations using the Sony cameras (1–2 pixel reprojection errors and 1–2% wand scores). These results indicate that estimated distances between bats, moths and microphones have an error <1–2%.

### Audio Calibrations

We calibrated the Knowles microphone used in tethered-moth experiments to determine absolute peak equivalent sound pressure levels (peSPL) re. 20  $\mu$ Pa (Stapells, Picton, & Smith, 1982) at 0.1 m in front of the bat's mouth. The microphone calibration procedure is reported elsewhere (Corcoran et al., 2013). The frequency response of the microphone was nearly flat ( $\pm 1.5$  dB) from 20 to 40 kHz, followed by a decrease in sensitivity of approximately 0.5 dB per kHz from 40 to 100 kHz. The directionality of the microphone was calibrated for increments of 22.5° and varied by less than 4 dB. We used known frequency-specific attenuation of sound caused by spherical and atmospheric attenuation (Bazley, 1976), based on average site conditions of 15 °C and 80% relative humidity. We were unable to account for the fact that the microphone was at a slightly different position in the bat's sonar beam compared to the target. However, in most cases, the angular deviation between the two objects was small (typically <20°) until very late in attacks. This indicates that we may have slightly underestimated the intensities of calls near the end of feeding buzzes.

### Modelling Prey Detection Distances

We developed a model of bat sonar detection distance and compared predictions of this model with measured detection distances from actual attacks. We measured prey detection distances from attacks on tethered moths (Fig. 2). Prey detection is followed rapidly by an increase in calling rate, a change in the bat's flight path and an increase in call intensity at the position of the prey as the bat localizes the prey with its directional sonar beam (Corcoran et al., 2013; Ghose & Moss, 2003).

We compared measured detection distances from actual attacks with predicted values based on a model using the sonar equation (Möhl, 1988):

$$DT = SL - 2TL + TS, \quad (1)$$

where DT is the detection threshold (minimum detectable sound level by the receiver), SL is the source level, TL is the one-way transmission loss and TS is the target strength (amount of sound reflected by the target). While bats are capable of detecting sounds as low as 0 dB in ideal captive situations (Kick, 1982), we used a DT of 20 dB, which is more likely to reflect a bat's abilities under natural conditions (Stiltz & Schnitzler, 2012). TL is the sum of frequency-specific losses caused by spherical spreading and

atmospheric attenuation (Bazley, 1976). We used mean peak calling frequencies (32 kHz for *C. townsendii*; 62 kHz for *M. volans*) and average atmospheric conditions during experiments (15 °C and 80% humidity). SL was measured from attacks. The moths used in our experiments were similar in size to *Agrotis segetum*, which has a 0.1 m TS of –26 dB at the frequencies used by the bats in our experiments (Waters, Rydell, & Jones, 1995).

### Statistics

Statistical analyses were conducted in MatLab (Mathworks, Natick, MA, U.S.A.). Distributions were checked for normality by viewing histograms and conducting Kolmogorov–Smirnov tests. All tests assume two-tailed distributions. Alpha was set to 0.05.

We separately analysed call intensities of bats prior to and after they began decreasing call intensity as part of their 'gain control' mechanism (Hartley, 1992). The distance at which bats began decreasing call intensity was estimated visually based on plots of call intensity versus bat–insect distance (Fig. 3). Linear regression was used to estimate the rate of reduction in call intensity with respect to distance once bats began reducing call intensity.

We used log-linear analysis to determine whether variation between individuals within a species affected prey escape behaviour or capture success. Because individual variation was not a statistically significant predictor of capture success or evasive behaviour (see Results), we lumped data from all individuals of each species for further analysis. We then used chi-square tests to determine whether capture success and rates of prey defensive behaviour differed in attacks between the two bat species. Paired *t* tests were used to determine whether predicted and actual prey detections differed. One-way analysis of variance (ANOVA) and Tukey's post hoc tests were used to determine whether predicted and actual prey detection distances differed between bat species and habitat. Mann–Whitney *U* tests were used to compare moth kinematic variables measured prior to and during attacks by the two bat species.

## RESULTS

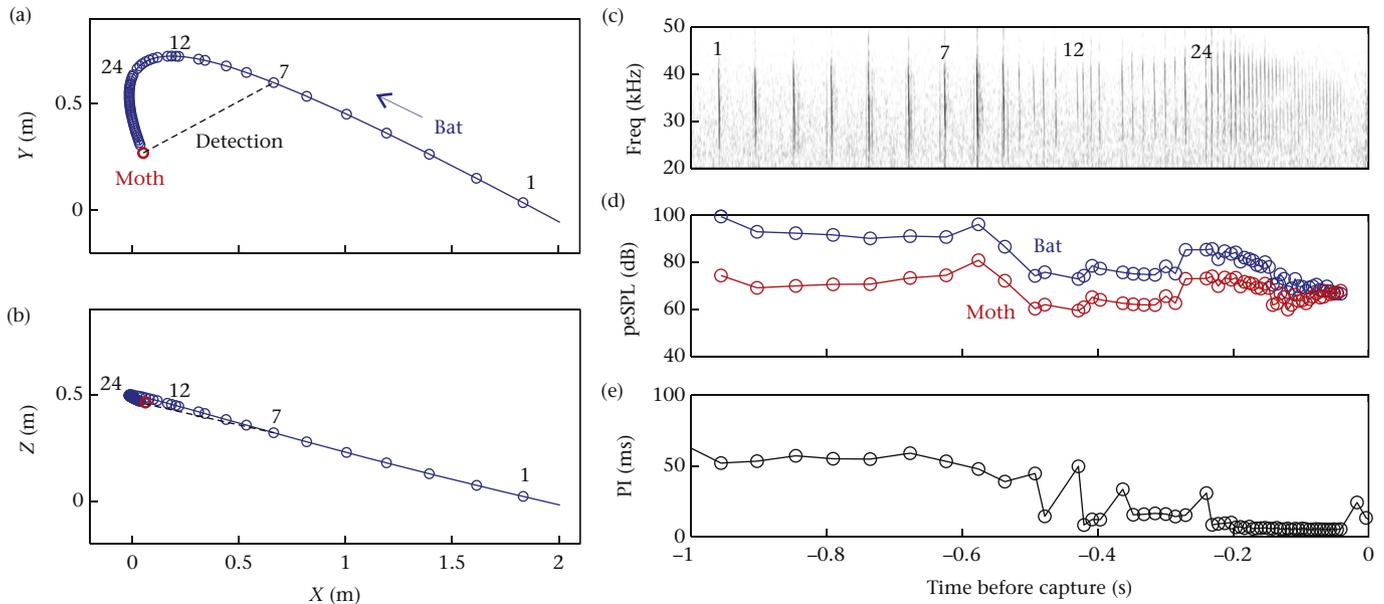
### Experiment 1: Echolocation Call Intensities during Attacks on Tethered Moths

Beyond a distance of 0.75 m from prey, *C. townsendii* produced calls with source levels of mean  $\pm$  SD of 93.6  $\pm$  6.1 dB in the field ( $N = 130$  calls from 5 bats; Supplementary Video S1) and 81.9  $\pm$  6.9 dB in the flight cage ( $N = 28$  calls from 6 bats; Supplementary Video S2, Figs. 2 and 3). These calls arrived at moth prey with intensities of 70.7  $\pm$  4.7 dB in the field and 60.9  $\pm$  6.6 dB in the flight cage. Within 0.75 m of prey, *C. townsendii* decreased calling intensities by 8.9 dB per halving of distance in the field and 4.1 dB per halving of distance in the laboratory. These values were fairly close to the 6 dB reduction in call intensity per halving of distance that is required to keep sound levels constant at the position of the prey (Hartley, 1992). Excluding a small number of calls made early in attacks at low intensity, call intensities at the position of the prey were independent of bat distance both in the field (Linear regression:  $F_{1,385} = 0.18, P = 0.67$ ) and in the flight cage (linear regression:  $F_{1,498} = 0.402, P = 0.53$ ).

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.anbehav.2017.08.018>.

### Corynorhinus has Reduced Prey Detection Distance

Both predicted (ANOVA:  $F_{2,13} = 45.4, P < 0.0001$ ) and actual prey detection distances (ANOVA:  $F_{2,13} = 5.77, P = 0.02$ ) differed

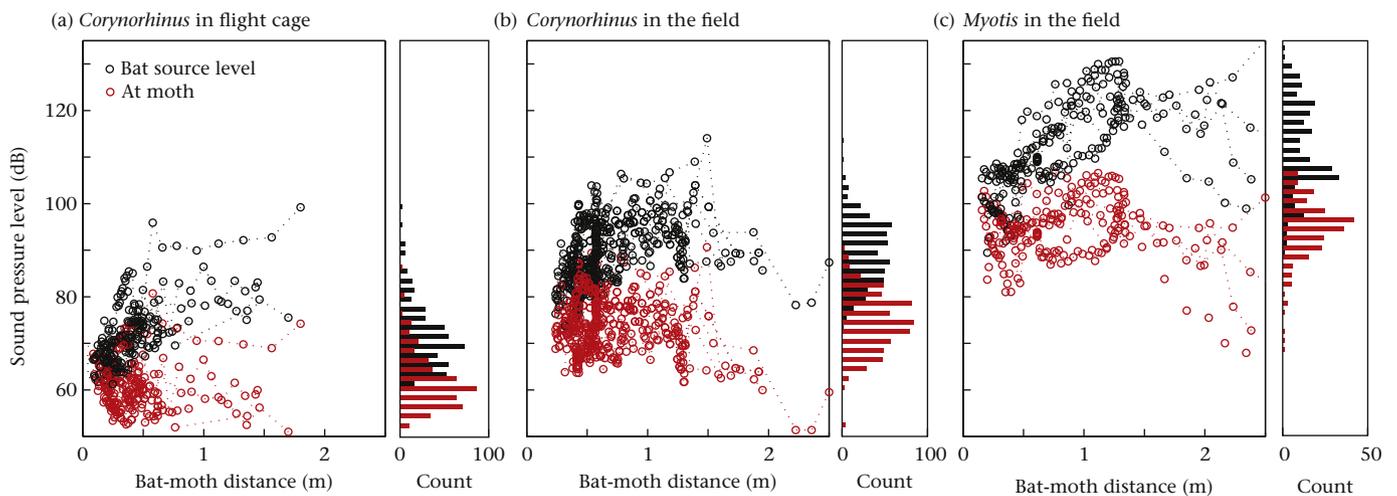


**Figure 2.** Example three-dimensional reconstruction and acoustic analysis of *Corynorhinus townsendii* attacking a tethered moth in captivity. (a) Overhead and (b) profile views show the flight trajectory of a bat attacking a tethered moth. Blue circles indicate bat echolocation calls. Numbers designate specific echolocation calls for reference between panels. The position where the bat appears to detect the prey, based on flight and acoustic behaviour, is indicated. (c) Spectrogram of the audio recording made by a microphone placed 0.25 m above the moth. (d) Estimated call levels 0.1 m in front of the bat's mouth, and at the position of the moth. (e) Echolocation pulse intervals. Audio and video of the attack are provided as Supplementary Video S2.

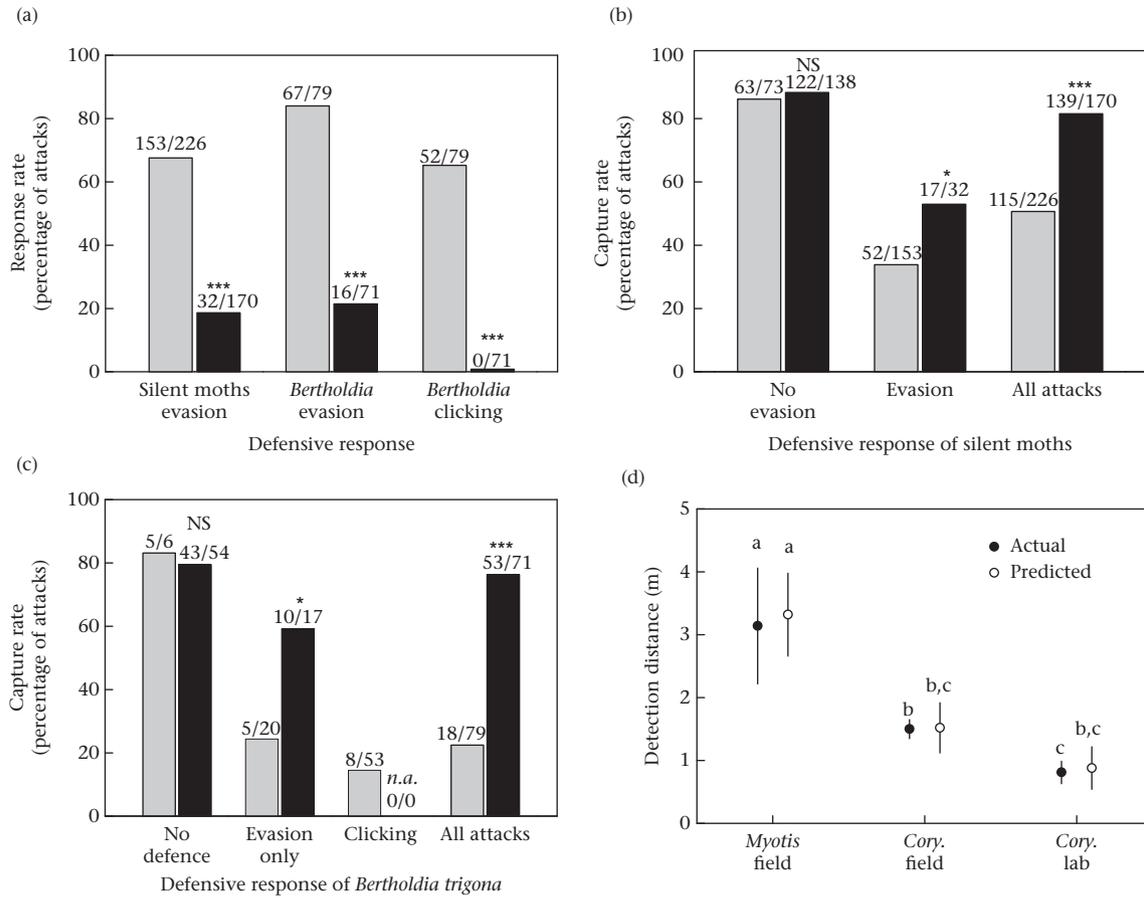
between bat species and between laboratory and field settings (Fig. 4d). Under similar settings in the field, *C. townsendii* had a 52% lower prey detection distance compared to *M. volans*. Prey detection distance was reduced even further for *C. townsendii* attacking tethered prey in the laboratory (Fig. 4d). Prey detection distances that were predicted using the sonar equation were in good agreement with measured detection distances from actual attacks (paired *t* test: *Myotis* field:  $t_4 = 0.34$ ,  $P = 0.74$ ; *Corynorhinus* field:  $t_4 = 1.25$ ,  $P = 0.28$ ; *Corynorhinus* lab:  $t_5 = -2.21$ ,  $P = 0.08$ ), although we had relative low power for detecting small differences in distributions because of the small sample sizes used.

#### Experiment 2: Defensive Behaviour and Capture Success during Attacks on Free-flying Moths

Four individual *C. townsendii* were documented attacking 170 silent moths and 71 *B. trigona*. Four individual *M. volans* bats were documented attacking 226 silent moths and 79 *B. trigona*. Aerial-hawking attacks were much more common than gleaning attacks, which were only observed seven times (four successful) for *C. townsendii* and never for *M. volans*. This was despite the presence of numerous moths that were available on the ceiling and walls of the enclosure during experiments. Gleaning attacks were excluded from further analysis.



**Figure 3.** Echolocation call intensities of bats attacking tethered moths. Echolocation call intensities 0.1 m in front of the bat (black circles) and at the position of the prey (red circles) were determined for attacks made by *Corynorhinus townsendii* (a) in a flight cage and (b) in the field, and for (c) *Myotis volans* in the field. Data from (c) were reanalysed from a previous study (Corcoran et al., 2013) and are reproduced with permission. Call levels are shown relative to the distance between the bat and the moth. Histograms of call intensities are also displayed. Note the relatively low call levels of *C. townsendii* compared to *M. volans*.



**Figure 4.** Results of bat–insect predator–prey interactions. Comparisons are made between attacks made by *Myotis volans* (grey bars) and *Corynorhinus townsendii* (black bars). Data shown include (a) percentage of prey exhibiting defences, (b) capture rates on silent moths, (c) capture rates on *B. trigona*, and (d) measured and modelled distances at which bats detected prey. Numbers above bars in (a)–(c) indicate sample sizes of attacks; n.a.: not applicable because data were not available. For each bat species, attacks were combined from four individuals. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$  (chi-square test). See Results for full details of tests. (d) Comparison of actual and predicted prey detection distances from attacks on tethered moths (*Myotis*: *M. volans*; *Cory*: *C. townsendii*). Predicted distances were based on a model using the sonar equation (Møhl, 1988). Values are means  $\pm$  SD. Letters indicate significantly different means (see Methods for more details on statistical tests).

We examined three categories of defensive responses from free-flying moths: (1) frequency of evasive manoeuvres made by silent moths; (2) frequency of evasive manoeuvres made by *B. trigona*; and (3) frequency of *B. trigona* clicking responses. Prey defensive response rates were fairly consistent between individuals within each species (Table 1), differing by 0–25%. These differences were not statistically significant (Supplementary Table S2), and therefore data were lumped between individuals of each species for further analysis.

Moth defences were much more common in attacks by *M. volans* (66–85% response rate; Supplementary Video S3) compared to attacks by *C. townsendii* (0–23% response rate; Fig. 4a; Supplementary Video S4). Both silent moths (chi-square test:  $\chi^2_1 = 178.0$ ,  $P < 0.0001$ ) and *B. trigona* ( $\chi^2_1 = 58.7$ ,  $P < 0.0001$ ) exhibited higher rates of evasion in response to attacks by *M. volans* than in response to attacks by *C. townsendii*, and *B. trigona* also clicked more frequently during attacks by *M. volans* ( $\chi^2_1 = 85.1$ ,  $P < 0.0001$ ). Differences in prey defensive response rates were considerably

**Table 1**  
Results of individual bats from two species attacking free-flying moths in a flight cage

Bat species	Individual	Silent moths			<i>Bertholdia trigona</i>			
		$N_s$	Evasion	Captures	$N_b$	Evasion	Clicking	Captures
<i>Myotis volans</i>	M <sub>1</sub>	87	38 (43.7%)	39 (44.8%)	21	16 (76.2%)	13 (61.9%)	9 (42.9%)
	M <sub>2</sub>	25	11 (47.8%)	14 (56.0%)	10	10 (100%)	7 (70.0%)	1 (10.0%)
	M <sub>3</sub>	31	17 (54.8%)	17 (54.8%)	12	9 (75.0%)	10 (83.3%)	2 (16.7%)
	M <sub>4</sub>	92	61 (66.3%)	49 (53.3%)	36	32 (88.9%)	21 (60.0%)	6 (16.7%)
<i>Corynorhinus townsendii</i>	C <sub>1</sub>	5	1 (20.0%)	5 (100%)	3	1 (33.3%)	0 (0%)	2 (66.7%)
	C <sub>2</sub>	91	19 (20.9%)	76 (83.5%)	34	7 (20.6%)	0 (0%)	26 (76.5%)
	C <sub>3</sub>	29	2 (6.8%)	24 (82.8%)	10	3 (30.0%)	0 (0%)	6 (60.0%)
	C <sub>4</sub>	50	10 (20.0%)	38 (76.0%)	25	6 (24.0%)	0 (0%)	20 (80.0%)

$N_s$  and  $N_b$  indicate the total number of silent moths and *B. trigona* attacked by each bat, respectively. Evasion and clicking indicate the number (and percentage) of moths exhibiting these defensive behaviours; captures indicate the total number (and percentage) of attacks resulting in capture for each individual bat.

smaller between individuals of the same species than between individuals of different species (Table 1), which indicates that the differences observed were likely a result of species-level adaptations.

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.anbehav.2017.08.018>.

Quantitative analysis of moth flight kinematics during attacks compared to control periods (Fig. 5) also indicates that moths exhibited greater evasive manoeuvring in response to attacks by *M. volans* compared to *C. townsendii*. Prior to attacks, moth kinematics did not differ between moths attacked by the two bat species (Mann–Whitney *U* test: velocity:  $U = 371$ ,  $N_1 = N_2 = 30$ ,  $P = 0.25$ ; linear acceleration:  $U = 420$ ,  $N_1 = N_2 = 30$ ,  $P = 0.66$ ; radial acceleration:  $U = 413$ ,  $N_1 = N_2 = 30$ ,  $P = 0.59$ ). However, all three moth flight parameters were higher during attacks by *M. volans* than during attacks by *C. townsendii* (velocity:  $U = 177$ ,  $N_1 = N_2 = 30$ ,  $P = 0.0001$ ; linear acceleration:  $U = 185$ ,  $N_1 = N_2 = 30$ ,  $P = 0.0001$ ; radial acceleration:  $U = 210$ ,  $N_1 = N_2 = 30$ ,  $P = 0.0004$ ). When moths did exhibit evasive manoeuvres (21 of 30 digitized attacks for *M. volans* and 10 of 30 digitized attacks for *C. townsendii*), they did so at approximately three times the distance for *M. volans* (median  $\pm$  interquartile range =  $0.89 \pm 0.51$  m) compared to *C. townsendii* ( $0.29 \pm 0.17$  m), a highly significant difference ( $U = 79$ ,  $N_1 = 21$ ,  $N_2 = 10$ ,  $P = 0.0007$ ).

Individual bats within each species had fairly consistent capture success rates for both silent moths and *B. trigona* (Table 1), with individual capture rates typically differing by less than 12–25%. These differences were not statistically significant (Supplementary Table S3). One individual *M. volans* ( $M_1$ ) appeared to capture *B. trigona* at a higher rate than other individuals of the same species

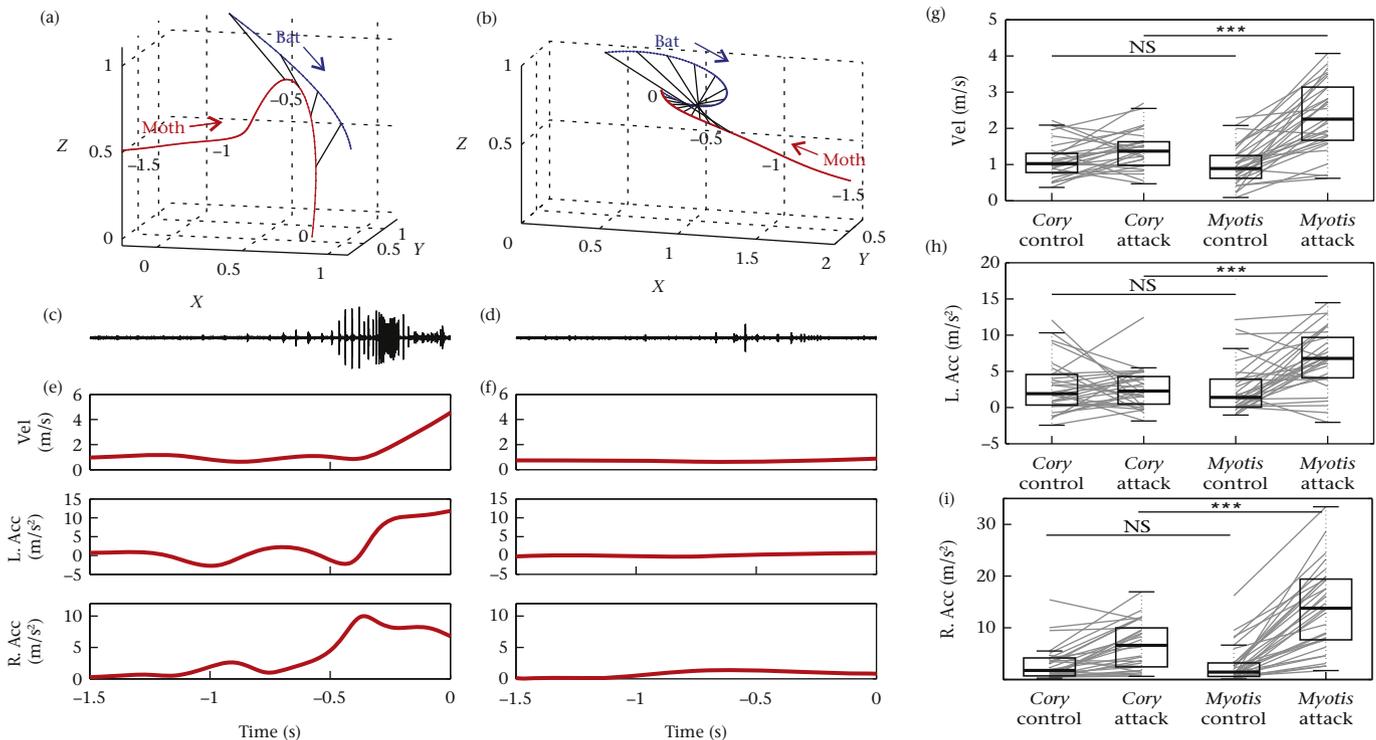
(42.9% versus 10–16.7%), but this difference was not significant (Supplementary Table S3). There were no obvious differences between  $M_1$  and other individuals. Because individual differences in capture success were not statistically significant, data were lumped between individuals of each species for further analysis.

Compared to *M. volans*, *C. townsendii* had 30.9% higher overall capture success for silent moths (chi-square test:  $\chi^2_1 = 40.2$ ,  $P < 0.0001$ ; Fig. 4b) and 51.9% higher capture success for *B. trigona* ( $\chi^2_1 = 40.3$ ,  $P < 0.0001$ ; Fig. 4c). For both prey categories, *C. townsendii* capture success was higher than *M. volans* for evasive prey (silent moths:  $\chi^2_1 = 4.2$ ,  $P = 0.04$ ; *B. trigona*:  $\chi^2_1 = 4.4$ ,  $P = 0.04$ ) but not for nonevasive prey (silent moths:  $\chi^2_1 = 0.19$ ,  $P = 0.66$ ; *B. trigona*:  $\chi^2_1 = 0.05$ ,  $P = 0.83$ ). Capture rates on clicking *B. trigona* could not be compared because the moths never produced sonar-jamming clicks when attacked by *C. townsendii*.

## DISCUSSION

To demonstrate that predators have coevolved with their prey, it is necessary to show that not only does an adaptation allow the predator to overcome a defence, but that it has evolved specifically for that purpose (Janzen, 1980). Several features of bat echolocation, including especially high- and low-frequency calls and low-intensity calls of gleaning bats, meet the first criterion while failing the second (ter Hofstede & Ratcliffe, 2016; Waters, 2003). These adaptations all provide bats benefits outside of predator–prey interactions and could have evolved for a purpose other than capturing prey.

Stealth echolocation by the aerial-hawking bat *B. barbastella* has been proposed as an adaptation that serves bats in predator–prey



**Figure 5.** Moth kinematics before and during bat attacks: (a, b) three-dimensional plots; (c, d) bat ultrasound recordings; (e, f) plots of moth flight kinematics for an example attack by *Myotis volans* (left column) and *Corynorhinus townsendii* (middle column). Note the increase in moth kinematic parameters that accompanies the increase in calling rate and intensity during the attack by *M. volans* (c, e), but the relatively low and constant moth flight parameters in the attack by *C. townsendii* (f). In (d), the low call intensities of *C. townsendii* make it difficult to discern some calls from background noise levels. (g, h, i) Moth flight kinematics (velocity, linear and radial acceleration) are compared between control time periods before attacks and peak values during attacks for *C. townsendii* ('Cory',  $N = 30$  attacks) and *M. volans* ('Myotis',  $N = 30$ ). Note the larger increase in moth flight kinematics during attacks by *M. volans* compared to attacks by *C. townsendii*. \*\*\* $P < 0.001$  (Mann–Whitney *U* test). Audio and video of the attacks shown in (a) and (b) are provided as Supplementary Videos S2 and S3.

interactions, but for no other purpose (Goerlitz et al., 2010). It has been noted as the best evidence to date of a bat counteradaptation to insect defences (ter Hofstede & Ratcliffe, 2016). However, actual predator–prey interactions between stealth bats and insects have not been documented, leaving room to question this conclusion. Furthermore, during echolocation recordings, *B. barbastella* was recorded flying close to the ground and close to background objects such as the microphones (see Fig. 1A in Goerlitz et al., 2010), a factor that could have partially caused the low calling intensities that were recorded (Brinkløv et al., 2010). Here, we used controlled field and laboratory experiments to provide a direct test of predictions made by the stealth echolocation hypothesis.

*Corynorhinus* produces calls with unusually low intensities while aerial-hawking insects. When attacking flying prey under mostly open field conditions, *C. townsendii* produced calls with source levels that were 26.8 dB lower than *M. volans* (120.4 versus 93.6 dB mean values; Fig. 3) and 22–45 dB lower than other aerial-hawking bats (116–138 dB; Holderied & von Helversen, 2003; Hulgard, Moss, Jakobsen, & Surlykke, 2016; Surlykke & Kalko, 2008). The call intensity of *C. townsendii* is nearly identical to that of *B. barbastella*, with both bats calling at average intensities of 94 dB in the field (Goerlitz et al., 2010). In a flight cage, *C. townsendii* called at even lower levels (81.9 dB mean), which are 20–30 dB lower than other aerial-hawking bats recorded in captivity (Waters, 1995). Overall, *C. townsendii* calls at much lower levels than other aerial-hawking bats (except *B. barbastella*) under similar conditions.

Insects typically exhibit graded responses to bat echolocation calls. Small changes in flight direction are often observed in response to relatively low-level bat calls, and progressively larger changes in flight are observed at higher levels (Corcoran & Conner, 2012; ter Hofstede & Ratcliffe, 2016). For the first time, data were collected that allows direct comparison of bat call levels at the position of prey throughout actual attacks (Fig. 3). The strongest insect defensive responses, including evasive manoeuvring and clicking defences, are elicited by bat sound levels in the range of 76–94 dB (Table 2). This indicates that *M. volans*, a fairly typical aerial-hawking bat whose calls arrive at prey with mean values of 94.5 dB, should elicit most or all insect defences. In contrast, the lower sound levels of *C. townsendii* (70.7 dB at prey's position in the field and 60.9 dB in the flight cage) should elicit only the weaker defences of most insects. These are usually negative phonotactic responses aimed at avoiding attacks. However, low-intensity calls would ensure that *C. townsendii* detect prey before prey detect the bats (Goerlitz et al., 2010), rendering these negative phonotactic responses ineffective.

Quantitative analysis of moth flight trajectories supports the prediction that *C. townsendii* calls elicit weaker prey defensive responses. Prey of *M. volans* exhibited defences much more frequently (Fig. 4) and they flew with approximately twice the

speed and accelerations compared to prey of *C. townsendii* (Fig. 5g–i). These factors are known to increase the likelihood that insects escape bats (Corcoran & Conner, 2016). Accordingly, *C. townsendii* had 31% higher capture success when attacking silent moths and 52% higher capture success attacking the sonar-jamming moth *B. trigona*. The 81.7% capture success rate of *C. townsendii* (Fig. 4b) is the highest rate reported for any bat species attacking flying insects (reviewed in Corcoran & Conner, 2012). These findings provide a direct demonstration that stealth echolocation allows *C. townsendii* to overcome insect defences.

#### *Stealth Echolocation Likely Evolved to Counter Insect Defences*

Low-amplitude calls give bats a clear advantage in predator–prey interactions, but did they evolve for this, or another purpose? As noted above, *C. townsendii* calls at considerably lower levels than other bats in similar habitats. Therefore, their low calling intensity does not appear to be a result of bats flying close to background vegetation (Brinkløv et al., 2010). Another hypothesis is that *C. townsendii* uses low-amplitude echolocation while gleaning prey off surfaces (Lacki & Dodd, 2011) but is unable to switch to a higher amplitude when aerial hawking. Our results indicate that *C. townsendii* prefers capturing prey out of the air rather than gleaning. Furthermore, a recent study found that the bat *Otonycteris hemprichii*, which is an avid gleaner and close relative of *C. townsendii* (Hoofer & Van Den Bussche, 2001), dramatically increases calling intensity from 75 dB when gleaning to 119 dB when capturing insects out of the air (Hackett, Korine, & Holderied, 2014). This demonstrates that bats are capable of changing call intensity while switching foraging strategies and that *C. townsendii* should not be constrained to call at low intensity because it sometimes gleans prey.

Another hypothesis is that stealth echolocation is aimed at preventing conspecifics from eavesdropping and stealing prey (kleptoparasitism). For example, *Tadarida brasiliensis* produces specialized sonar-jamming calls to interfere with the foraging of conspecifics (Corcoran & Conner, 2014). While we cannot rule out this hypothesis entirely, it seems just as likely that eavesdropping is beneficial to bats as it is likely that eavesdropping is costly. Bats benefit from being able to find food sources by hearing conspecific feeding buzzes (Cvikel et al., 2015; Dechmann et al., 2009; Gillam, 2007), and often this comes at no cost to other bats (Reddy & Fenton, 2003).

The low-intensity calls used by *C. townsendii* come with the cost of substantially reduced prey detection distances. Whereas *M. volans* detect prey in the field at distances of 3 m, *Corynorhinus* typically detect prey at 1.5 m in the field and 0.8 m in more enclosed settings (Fig. 4d). Reduced prey detection distances indicate that *C. townsendii* would have a lower encounter rate with prey. However, they are able to compensate for this by having higher capture success during individual attacks.

**Table 2**  
Ultrasound intensity thresholds for late-attack insect defences

Species	Defensive response	Call intensity thresholds <sup>a</sup>	Reference
Dogbane tiger moth ( <i>Cycnia tenera</i> )	Clicking	72–76 dB	Ratcliffe, Fullard, Arthur, and Hoy (2009)
Grote's bertholdia ( <i>Bertholdia trigona</i> )	Clicking	92–94 dB	Corcoran et al. (2013)
Greater waxmoth ( <i>Galleria mellonella</i> )	Flight cessation	72–94 dB	Skals and Surlykke (2008)
Death's head hawkmoth ( <i>Acherontia atropos</i> )	Flight cessation/Clicking	80–90 dB	Göpfert and Wasserthal (1999)
Green lacewing ( <i>Chrysopa carnea</i> )	Flight cessation	55–86 dB	Miller (1975)
Praying mantis ( <i>Parasphendale agrionina</i> )	Diving	64–85 dB	Yager, May, and Fenton (1990)
Bushcrickets ( <i>Neoconocephalus ensiger</i> )	Flight cessation	76–85 dB	Libersat and Hoy (1991)

<sup>a</sup> Studies included here are only those where thresholds were determined for late-attack evasive manoeuvring and clicking defences. Thresholds for negative phonotactic responses are not included. The range of thresholds shows variability between individuals and between stimulus parameters and in the strength of the response. Higher thresholds within the ranges shown often elicited more robust defensive responses.

## Conclusion

We conclude that because there is no other known benefit, yet considerable cost in prey detection ability, that the low-intensity echolocation used by *C. townsendii* during aerial-hawking attacks is an evolutionary countermeasure to insect hearing. It would be beneficial to confirm this finding in the future with studies of hunting bats in the field and with larger numbers of bats. This study provides the first direct demonstration that lower calling intensities allow aerial-hawking bats to overcome insect defences. Our findings are in agreement with a previous study (Goerlitz et al., 2010), which came to the same conclusions for *B. barbastellus* using a different approach.

Stealth echolocation appears to be an example of predators functioning as 'rare enemies' (Dawkins, 1982). Both *C. townsendii* and *B. barbastella* are sympatric with numerous aerial-hawking bats that echolocate at higher intensities (e.g. 19 species coexist with *C. townsendii* in Arizona, U.S.A.; Harvey, Altenbach, & Best, 2013). These higher-intensity bats have driven the evolution and sensitivity of insect ears (ter Hofstede & Ratcliffe, 2016). The relative rarity of stealth bats, and the inability of prey to respond appropriately to their attacks, suggests that there has not been sufficient selective pressure for prey to evolve responses to these rare predators. We propose that predator counteradaptations to prey defences may be more common than has previously been recognized, particularly in systems where many predators attack the same prey species.

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## Supplementary material

Supplementary material related to this article can be found at <https://doi.org/10.1016/j.anbehav.2017.08.018>.

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