



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



Aaron J. Corcoran^{*}, William E. Conner

Department of Biology, Wake Forest University, Winston-Salem, NC, U.S.A.

ARTICLE INFO

Article history:

Received 18 February 2017
Initial acceptance 10 April 2017
Final acceptance 30 June 2017

MS. number: A17-00171R2

Keywords:

bat
coevolution
echolocation
predation
predator–prey interaction

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 ± 6.1 dB at 0.1 m in open field conditions and 81.9 ± 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.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

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).

^{*} Correspondence: Aaron J. Corcoran, Department of Biology, Wake Forest University, P.O. Box 7325, Winston-Salem, NC 27106, U.S.A.

E-mail address: aaron.j.corcoran@gmail.com (A. J. Corcoran).

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/m² versus 6.6 N/m²; 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

Download English Version:

<https://daneshyari.com/en/article/5538303>

Download Persian Version:

<https://daneshyari.com/article/5538303>

[Daneshyari.com](https://daneshyari.com)