

REVIEW

Evolutionary escalation: the bat–moth arms race

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ABSTRACT

Echolocation in bats and high-frequency hearing in their insect prey make bats and insects an ideal system for studying the sensory ecology and neuroethology of predator–prey interactions. Here, we review the evolutionary history of bats and eared insects, focusing on the insect order Lepidoptera, and consider the evidence for antipredator adaptations and predator counter-adaptations. Ears evolved in a remarkable number of body locations across insects, with the original selection pressure for ears differing between groups. Although cause and effect are difficult to determine, correlations between hearing and life history strategies in moths provide evidence for how these two variables influence each other. We consider life history variables such as size, sex, circadian and seasonal activity patterns, geographic range and the composition of sympatric bat communities. We also review hypotheses on the neural basis for anti-predator behaviours (such as evasive flight and sound production) in moths. It is assumed that these prey adaptations would select for counter-adaptations in predatory bats. We suggest two levels of support for classifying bat traits as counter-adaptations: traits that allow bats to eat more eared prey than expected based on their availability in the environment provide a low level of support for counter-adaptations, whereas traits that have no other plausible explanation for their origination and maintenance than capturing defended prey constitute a high level of support. Specific predator counter-adaptations include calling at frequencies outside the sensitivity range of most eared prey, changing the pattern and frequency of echolocation calls during prey pursuit, and quiet, or ‘stealth’, echolocation.

KEY WORDS: Insects, Echolocation, Nocturnal, Bat-detecting ears, Arms race, Predator–prey interaction

Introduction: the evolutionary history of a predator–prey model system

As a well-known predator–prey model system, the interactions of bats and moths have long fascinated scientists (Roeder, 1967), university students (Alcock, 2013) and children alike (Oppel, 1997). Insect-eating bats detect and track moths using echolocation and attempt to capture and consume these insects in flight. In turn, some moths listen for bat echolocation calls to avoid being captured. Although the phrase ‘co-evolutionary arms race’ is often used to describe the moths’ anti-bat defences (which include bat-detecting ears, sound-evoked defensive flight and sound production), there is no evidence of reciprocal adaptations between bats and moths at the species level, nor are the causes and effects of this arms race

exclusive to the interactions between bats and moths. Most adaptations that make bats better moth hunters also make them more effective hunters of other insects, and such adaptations are therefore not moth specific. Likewise, some moths use their ears to detect not only bats but also insect-eating birds or mates (Conner, 1999; Nakano et al., 2015).

The evolutionary histories of predator and prey also differ. The order Lepidoptera (moths and butterflies) originated ~150 million years ago (mya; Misof et al., 2014), long before the origin of bats, which first took to the wing sometime between 60 and 95 mya (Bininda-Emonds et al., 2007). Although powered flight is a defining characteristic of bats, laryngeal echolocation may have evolved only ~50 mya (Simmons et al., 2008; Teeling, 2009; Veselka et al., 2010). The distinctive combination of echolocation and powered flight allowed bats to first exploit, then dominate the foraging niche of night-flying insects. Bat predation drove selection for both bat-detecting ears and non-auditory means of avoiding bats in a variety of insects, including moths and butterflies that never evolved ears and remain deaf to bats (Fullard and Napoleone, 2001; Barber et al., 2015).

The earliest adaptations in the arms race, laryngeal echolocation in bats and tympanal ears in moths, were not necessarily singular events – possibly not in bats, certainly not in moths. For bats, there are two equally parsimonious hypothetical time lines for the origination of laryngeal echolocation; it evolved either once (and was subsequently lost in the Pteropodidae) or twice (once in each of the two suborders Yinpterochiroptera and Yangochiroptera; Fig. 1). Ears have evolved numerous times independently in divergent lepidopteran groups, with bats as the apparent driver in every instance. Today, some lepidopteran lineages remain earless, having evolved other defences against bats. Interestingly, bats, which originated after insect-eating birds, may have driven some previously nocturnal lepidopteran lineages, including some extant butterflies (Yack and Fullard, 2000) and tiger moths (Ratcliffe and Nydam, 2008), into being diurnal.

The interactions of bats and moths do not meet a strict definition of co-evolution in which two species demonstrate reciprocal adaptations (Janzen, 1980; Jones and Rydell, 2003; Jacobs et al., 2008; Ratcliffe, 2009). Co-evolutionary relationships are most common between host and parasite species or mutualistic partners such as plants and pollinators, but are rarely observed between predator and prey. Dawkins and Krebs (1979) suggest that the rarity of co-evolution between predators and prey is due to the ‘life–dinner principle’ – the cost of a mistake being death for the prey versus only a lost meal for the predator – resulting in more specific antipredator defences than predator counter-strategies. Here, we concentrate on the traits of lepidopteran species that reduce their risk of being attacked by bats, emphasizing moths’ ears, auditory-evoked evasive flight and defensive sounds. We also review auditory-based defences in other insect groups. Lastly, we discuss the evolutionary refinement of bat echolocation and related adaptations that have allowed bats to better exploit insects at night, including, but not limited to, moths with bat-detecting ears. In

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Glossary

Aerial hawking

The capture of airborne prey on the wing. Considered to be the predominant means of prey capture in most bats.

Chordotonal organs

Sensory structures specific to insects and crustaceans that contain stretch receptors and are dispersed throughout the body. Most chordotonal organs are proprioceptors, meaning that they detect and encode information about the position or movement of the animal's own body parts.

Feeding buzz

After laryngeal-echolocating bats detect airborne prey, they increase their echolocation call rate dramatically over the course of their attack, culminating in a feeding buzz (>90 calls s^{-1}).

Phonotaxis

The act of moving in response to sound. Positive phonotaxis refers to movement towards sound, such as when female crickets walk towards a singing male, whereas negative phonotaxis refers to movement away from sound, such as when a flying cricket flies away from an echolocating bat.

Stridulatory organ

A structure on an animal that is used to produce sound by rubbing one part against another. Often these consist of a series of ridges, called the file, and a single protrusion that is scraped against the file to produce sound.

Substrate gleaning

The capture of prey from terrestrial surfaces, e.g. vegetation or the ground. Although long known to be a means by which bats take prey, its prevalence has been underestimated.

Tymbal

A thin area of insect cuticle buckled by muscular action to produce sound. In tiger moths, tymbals are located on the ventral surface of the thorax and can be unstriated (producing two clicks per muscular contraction and relaxation cycle) or striated (producing multiple clicks per cycle).

Tympanum

A very thin region of insect cuticle forming a membrane that oscillates in response to sound waves. The tympanum is usually backed up by air sacs and is innervated either directly or indirectly by a chordotonal organ that transduces the movement of the tympanum into neural activity.

summary, we feel the relationship between bats, moths and other night-flying insects continues to represent an ideal system to improve our understanding of the sensory ecology and neuroethology of predator–prey interactions.

Anti-predator adaptations

The evolutionary origins of bat-detecting ears

The evolution of echolocation in bats set the stage for the vast diversity of ultrasound (>20 kHz) sensitive ears found in modern insects. As an active sensing system using high-energy acoustic signals, echolocation provides potential information to would-be prey. High-frequency-sensitive ears and auditory-evoked avoidance behaviours have evolved in at least six orders of insects (Yack and Dawson, 2008): Orthoptera (crickets, katydids and locusts), Diptera (some tachinid flies), Dictyoptera (mantids), Coleoptera (some tiger and scarab beetles), Neuroptera (green lacewings) and Lepidoptera (moths and butterflies) (Fig. 2A, Table 1). Within the Lepidoptera alone, ears have evolved independently at least six times (Fig. 2A, Table 1).

In insects with bat-detecting ears, auditory organs apparently evolved from chordotonal organs, which are sensory organs specific to insects and crustaceans that contain neurons sensitive to body movements (Kavlie and Albert, 2013). Chordotonal organs are dispersed throughout the body, explaining why ears are found in many different locations in insects (Fullard and Yack, 1993; Yack

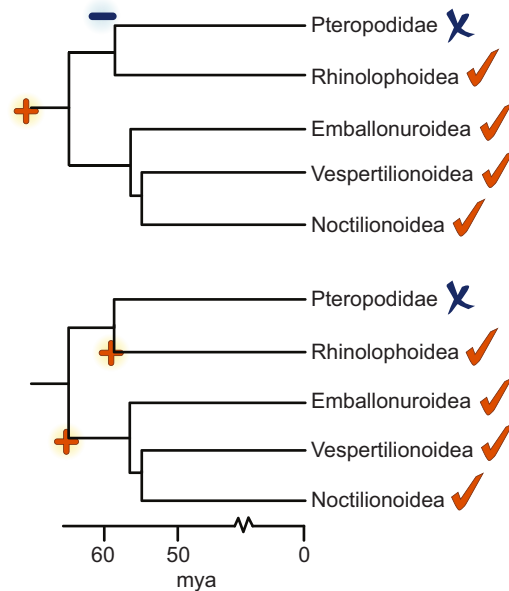


Fig. 1. Two equally parsimonious scenarios for the evolution of laryngeal echolocation in bats.

(A) Laryngeal echolocation is presumed to be the ancestral state of bats and to have evolved once (+) with subsequent loss (–) in the family Pteropodidae. (B) Laryngeal echolocation is presumed to have evolved twice (+), once in the lineage leading to the Yangochiroptera, which includes the superfamilies Emballonuroidea, Vespertilionoidea and Noctilionoidea, and again in the lineage leading to the Rhinolophoidea, a superfamily within the suborder Yinpterochiroptera, which includes the Pteropodidae. Ticks indicate superfamilies in which all species are laryngeal echolocators, crosses indicate a lack of laryngeal echolocation. Adapted from Teeling (2009), Fenton and Ratcliffe (2010) and Fenton et al. (2012). mya, million years ago.

and Dawson, 2008; Fig. 2A). Insect ears that evolved from chordotonal organs consist of a tympanum (a membrane that vibrates in response to sound) and auditory receptor cells activated by sound-induced tympanal vibrations (Fig. 2B,C). Given the intense sounds produced by echolocating bats (Waters and Jones, 1995; Holderied and von Helversen, 2003; Holderied et al., 2005; Surlykke and Kalko, 2008), and thus the ability of these sounds to vibrate cuticle, it is easy to imagine an evolutionary progression from a chordotonal organ measuring the movements of particularly thin areas of the exoskeleton to the ears of modern insects (Yack, 2004; Yack and Dawson, 2008). Although some insects have non-tympanal ears, none of these ears are known to function in bat detection because they are insensitive to high-frequency sounds (Yack and Dawson, 2008). The ears of noctuid moths are the best studied among the numerous families of moths with ears.

Despite the common use of ears for bat detection among the groups listed above, the original selection pressure for hearing varies. Fossil evidence shows that hearing evolved in orthopterans for intraspecific communication before the appearance of bats (Plotnick and Smith, 2012). Tachinid flies that listen for the calling songs of their cricket hosts also had ears before bats evolved (Rosen et al., 2009). For both of these groups, hearing was co-opted for bat detection in addition to still performing its original function. The original selection pressure for ears in some beetles is unclear: the ear is well suited for bat detection and ultrasound triggers evasive flight, but many species also produce sounds themselves, possibly for intraspecific communication (Yager and Spangler, 1995, 1997).

For mantids, green lacewings and moths, it had been assumed that hearing evolved in response to echolocating bats, because bat

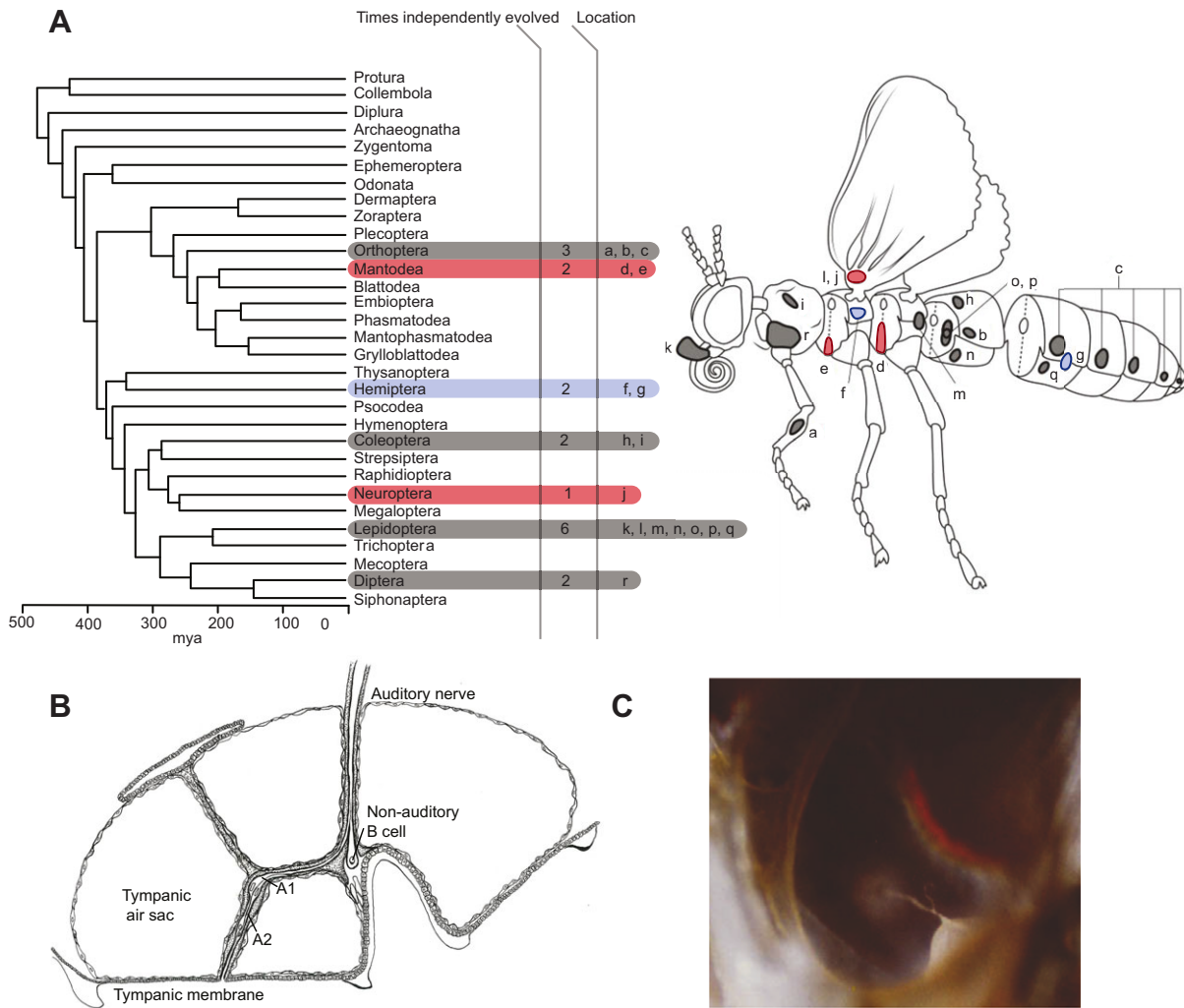


Fig. 2. Distribution of ears across insects and moth ear structure. (A) A generalized insect and an insect phylogeny indicating where ears, if present, are located on the body in different orders and how many times ears have evolved independently in each of these orders. Shading indicates the known functions of ears: red, bat detection only; blue, functions other than bat detection; grey, bat detection plus other functions. Other functions include communication and eavesdropping on host signals. See Table 1 for references. Adapted from Yack and Dawson (2008); phylogeny redrawn from Misof et al. (2014). (B) Structural diagram of a noctuid moth ear, illustrating the presence of air sacs behind the tympanum and the attachment of the two auditory receptor cells, A1 and A2, to the tympanum (adapted from Roeder and Treat, 1957). The axon of the non-auditory B-cell, which monitors the movement of the moth’s wings (Yack and Fullard, 1993), is also present in the auditory nerve. (C) Photograph of the inner surface of a noctuid moth tympanum showing the site of attachment of the receptor cells to the tympanic membrane (white fibres attaching to pale patch on dark tympanic membrane). Photo credit: M. B. Fenton (reproduced with permission).

detection is the primary and often sole function of these ears today (Yack and Dawson, 2008). A recent paper using molecular methods, however, suggests that mantids had ears before bats evolved (Yager and Svenson, 2008). Mantid hearing may have first functioned in detecting other types of danger-indicating acoustic stimuli, and might then have been co-opted to detect bat echolocation calls. Although the evidence that bats drove the evolution of hearing in moths is strong, these surprising results from mantids make it clear that further molecular studies are needed to confirm whether the original function of moth and lacewing ears was indeed bat detection.

What is the evidence that moth ears evolved in response to echolocating bats? First, bat avoidance is the sole function of ears in most moth species (Fullard, 1988), and sound-triggered evasive flight provides a survival advantage for moths under attack by bats (Roeder and Treat, 1962; Acharya and Fenton, 1999; Fullard, 2001). Other uses, such as detecting insect-eating birds or intraspecific communication, are likely to be derived (Conner, 1999; Jacobs et al., 2008; Fournier et al., 2013). That said, ever more moth species

are being reported to use sound for communication, and this function might be much more common than previously realized (Nakano et al., 2009). Second, the relative insensitivity of moth ears suggests that they are adapted to detecting high-intensity ultrasound sources, such as bat calls (Waters and Jones, 1995; Holderied and von Helversen, 2003; Holderied et al., 2005; Surlykke and Kalko, 2008), rather than faint ambient sounds like crackling vegetation (Fullard, 1988). Third, moth ears are typically tuned to the frequencies of echolocation calls used by their sympatric bat community and not to other environmental sources of sound (Fullard, 1988, 1998). The auditory receptors also quickly exhibit sensory adaptation to constant sound, but remain sensitive to pulsed sounds like bat calls (Fullard et al., 2008a). Fourth, there is a strong correlation between the sensitivity of moths’ ears and their expected exposure to bats (ter Hofstede et al., 2008a).

Moth ears consist of a tympanum (see Glossary) that vibrates in response to sound and 1–4 auditory receptor neurons (depending on the species) that are activated by this movement (Fig. 2B,C; Box 1).

Table 1. Comparative anatomical, physiological and behavioural traits of insect groups with ultrasound-sensitive ears

Order	Superfamily	Family	Location of ear	Original function of ear	No. of auditory afferents	Neural threshold (dB SPL)	Best frequency (neural, kHz)	Evasive responses to ultrasound? (Y/N/U)	Graded evasive response? (Y/S/U)	References	
Lepidoptera	Bombycoidea	Sphingidae	Mouth	B	1	50–60	20–40	Y	Y	1–5	
		Noctuoidea	Noctuidae,	Thorax	B	2	20–55	15–45	Y	Y	6–8
	Geometroidea	Nolidae, Erebiidae	Oesandridae	Thorax	B	2	50	20–40	U	U	9
			Notodontidae	Thorax	B	1	45–55	35–50	Y	Y	10, 11
			Geometridae	Abdomen	B	4	35–50	20–30	Y	Y	12–15
			Uraniidae	Abdomen	B	2	30	20–25	U	U	16
		Drepanoidea	Drepanidae	Abdomen	B	2	50	30–50	U	U	17
		Pyraloidea	Pyrilidae	Abdomen	B	4	40–50	30–70	Y	Y	18–22
	Crambidae		Abdomen	B	4	U	U	U	U	16	
	Papilionoidea	Hedyliidae	Wings	B	U (15–45?)	60	40–80	Y	U	23, 24	
		Nymphalidae	Wings	U	U	U	U	Y	U	25	
	Diptera	Oestroidea	Tachinidae	Thorax	O	60–150	45–60	10–40	Y	Y	26–29
Coleoptera	Scarabaeoidea	Scarabidae	Thorax	B	3–8	55–65	40–50	Y	Y	30, 31	
		Cicindelidae	Abdomen	B or C	4–20	50–55	20–35	Y	Y	32–34	
Neuroptera	Chrysopoidea	Chrysopidae	Wings	B	28	60	40–50	Y	Y	35–37	
Dictyoptera	Mantodea	Mantidae	Thorax	U	32	55–60	25–50	Y	Y	38–42	
Orthoptera	Acridoidea	Acrididae	Abdomen	O	60–100	40	10–20	Y	Y	43–45	
	Grylloidea	Gryllidae	Legs	C	60–80	35–55	14–16	Y	Y	43, 46–49	
	Tettigonoidea	Tettigoniidae	Legs	C	20–60	30–45	10–30	Y	S	43, 50–55	

Original function of ear (hypothesized): B, bat detection; C, communication; O, other (detection of prey or other predatory sounds); U, unknown. Neural threshold: lowest sound level to elicit sensory neural activity. Best frequency: frequency of best threshold (kHz). Neural thresholds vary in terms of criteria for thresholds and whether neural thresholds were recorded from auditory afferents or interneurons. Evasive responses to ultrasound: Y, yes; N, no; U, unknown. Graded evasive response: form or intensity of the response changes with increasing sound amplitude (Y, yes; U, unknown; S, some species and not others).

¹Göpfert and Wasserthal, 1999a; ²Göpfert and Wasserthal, 1999b; ³Göpfert et al., 2002; ⁴Roeder, 1975; ⁵Roeder et al., 1968; ⁶Fullard et al., 2008b; ⁷Surlykke et al., 1999; ⁸ter Hofstede et al., 2013; ⁹Fullard, 2006; ¹⁰Surlykke, 1984; ¹¹ter Hofstede et al., 2008a; ¹²Fenton and Fullard, 1979; ¹³Rydell et al., 1997; ¹⁴Surlykke and Filskov, 1997; ¹⁵Svensson et al., 1999; ¹⁶Minet and Surlykke, 2003; ¹⁷Surlykke et al., 2003; ¹⁸Pérez and Zhantiev, 1976; ¹⁹Skals and Surlykke, 2000; ²⁰Rodríguez and Greenfield, 2004; ²¹Takanashi et al., 2010; ²²Heller and Krahe, 1994; ²³Yack and Fullard, 2000; ²⁴Yack et al., 2007; ²⁵Rydell et al., 2003; ²⁶Robert et al., 1996; ²⁷Robert et al., 1992; ²⁸Stumpner and Lakes-Harlan, 1996; ²⁹Rosen et al., 2009; ³⁰Forrest et al., 1995; ³¹Forrest et al., 1997; ³²Spangler, 1988; ³³Yager and Spangler, 1995; ³⁴Yager and Spangler, 1997; ³⁵Miller, 1970; ³⁶Miller, 1971; ³⁷Miller and Olesen, 1979; ³⁸Yager and Hoy, 1987; ³⁹Yager and Hoy, 1989; ⁴⁰Yager and Svenson, 2008; ⁴¹Tribblehorn and Yager, 2001; ⁴²Yager et al., 1990; ⁴³Yack, 2004; ⁴⁴Robert, 1989; ⁴⁵Römer et al., 1988; ⁴⁶Nolen and Hoy, 1986; ⁴⁷Schildberger, 1984; ⁴⁸Boyd et al., 1984; ⁴⁹Fullard et al., 2010; ⁵⁰Faure and Hoy, 2000; ⁵¹ter Hofstede and Fullard, 2008; ⁵²ter Hofstede et al., 2008b; ⁵³ter Hofstede et al., 2010; ⁵⁴Schulze and Schul, 2001; ⁵⁵Libersat and Hoy, 1991.

Regardless of the number of auditory afferents in different moth taxa, each afferent has the same frequency tuning as the others, meaning that moths are not capable of frequency discrimination (Fullard, 1988, 1998). Each afferent, however, has different sound level thresholds (Fig. 3A; Roeder, 1967). The difference between the most sensitive receptor and the next most sensitive receptor is ~2–6 dB in pyralids (Skals and Surlykke, 2000), 15 dB in geometrids (Roeder, 1974a; Surlykke and Filskov, 1997) and 15–20 dB in noctuids (ter Hofstede et al., 2013). These differences in threshold between afferents increase the range of amplitudes to which the ear can respond by allowing the less sensitive afferent to continue encoding increasing sound amplitude once the most sensitive afferent has reached its maximum firing capability. This allows for a very large dynamic range for intensity discrimination of 40–60 dB (Roeder, 1967; Coro and Perez, 1993), which should provide valuable information about the relative distance of an approaching bat.

Despite the convergence of form and function in moth ears, there are differences between moth species and taxonomic families that could provide insight into the evolutionary history between bats and moths. For example, the lowest threshold of the most sensitive receptor can range from 20 to 60 dB across different species of noctuids and notodontids (Surlykke, 1984; Surlykke et al., 1999; Fullard et al., 2008b; ter Hofstede et al., 2008a). By comparison,

bats have much more sensitive ears, with hearing thresholds similar to those of humans, at 2–20 dB sound pressure level (SPL; Moss and Schnitzler, 1995). The enormous 40 dB range in hearing thresholds across moth species has important behavioural and ecological consequences: sensitivity determines the distance at which moths can detect an oncoming bat, and thus the time available for escape. Below, we consider the selection pressures that could have contributed to, or resulted from, variation in moths' hearing ranges and sensitivity.

Moth auditory sensitivity: cause and effect

Determining cause and effect in relationships between moth auditory sensitivity and behavioural ecology is difficult. Here, we present these relationships with no assumptions about which came first, variation in auditory sensitivity or variation in life history. Regardless, we must consider the costs that select against ever more sensitive high-frequency hearing. For a moth, reacting to non-threatening environmental sources of ultrasound, like crackling vegetation (Fullard, 1988) or bats that are too far away to be a viable threat, could result in missed mating or feeding opportunities, or even more dire consequences, such as being exposed to non-aerial predators as a result of evasive diving (Guignion and Fullard, 2004). In addition to such costs, species size, nocturnal activity level, phenology and aspects of the sympatric bat community are all

Box 1. Adaptive simplicity in bat detection

With only 1–4 sensory cells per ear, depending on the family or superfamily (Table 1), moth ears are among the simplest sensory organs in nature, which could be adaptive for predator detection (Forrest et al., 1997; Yack et al., 1999; Surlykke et al., 2003). Sensory system complexity is advantageous if it provides more information for improved decision making and subsequent adaptive behaviours (Dangles et al., 2005). For rapid, reflex-like responses to predators, however, just a few cells with an appropriate threshold could provide an ideal rate of information transfer (Yack et al., 1999). Indeed, when we consider the number of auditory afferents across bat-detecting insects (Table 1), those that use their ears solely to detect bats have fewer afferents (1–32) than those that also use their ears for other purposes (60–150). The number of afferents is even greater for insects that only use their ears for communication, such as cicadas (~1500; Wohlers et al., 1979) and bladder grasshoppers (~2000; Van Staaden et al., 2003). In addition to rapid information processing, evolutionary history and physical and energetic constraints probably contributed to the simplicity of bat-detecting ears (Hasenfuss, 1997; Dusenbury, 2001; Smith and Lewicki, 2006; Niven and Laughlin, 2008). In most moth superfamilies, the number of auditory receptors in adult moths is the same as the number of sensory cells in the homologous chordotonal organ of the larva or closely related atympanate species (Hasenfuss, 1997; Yack et al., 1999). The complexity of the sense organ does not increase during the transition from chordotonal organ to ear, as it does in insects that also use their ears for communication (Yack et al., 1999). In the Noctuoidea, there is a reduction to one (Notodontidae) or two (other noctuid families) auditory receptors from an original three sensory cells in the homologous larval structure (Hasenfuss, 1997). It is unclear whether Notodontidae is basal to the other noctuid families, and lost two cells in one event (Zahiri et al., 2011), or whether this group is nested within the other noctuid families (Regier et al., 2009, 2013) and independently lost these cells twice. In the adult ear of the Drepanidae, moths maintain the four sensory units found in the homologous larval structure, but only two function as auditory receptors (Surlykke et al., 2003). Thus, conserving just a few afferents, or even losing afferents, is common for moth ears and suggests a constraint on complex ears, or a benefit for simple ears, in this group.

correlated with moth auditory sensitivity – each of these aspects of life history is considered below.

Moth species size

Bats can detect larger moths at greater distances than they can detect smaller moths. Larger moths, however, have more sensitive ears (Surlykke et al., 1999) and detect bats at greater distances than do smaller moths, essentially compensating for their increased conspicuousness. This relationship between size and sensitivity is strongest for frequencies that are used by a large number of sympatric bats for echolocation (ter Hofstede et al., 2013). Forrest et al. (1995) suggest that this pattern of size and sensitivity may apply across all insects with bat-detecting ears. Römer et al. (2008), however, show that there is no relationship between size and high-frequency sensitivity in phaneropterine katydids, which produce high-frequency communication signals.

Nocturnal activity level

Moth species can vary in the sensitivity or tuning of their hearing depending on their exposure to bats, either temporally or geographically. Where there is sexual dimorphism in flight ability (flightless females, flight-capable males), males are at greater risk of bat predation, and females have less sensitive ears than males (Cardone and Fullard, 1988; Rydell et al., 1997). Interestingly, this relationship is also found in mantids (Yager, 1990). At a finer-grained level, for moth species in which both sexes fly, males might

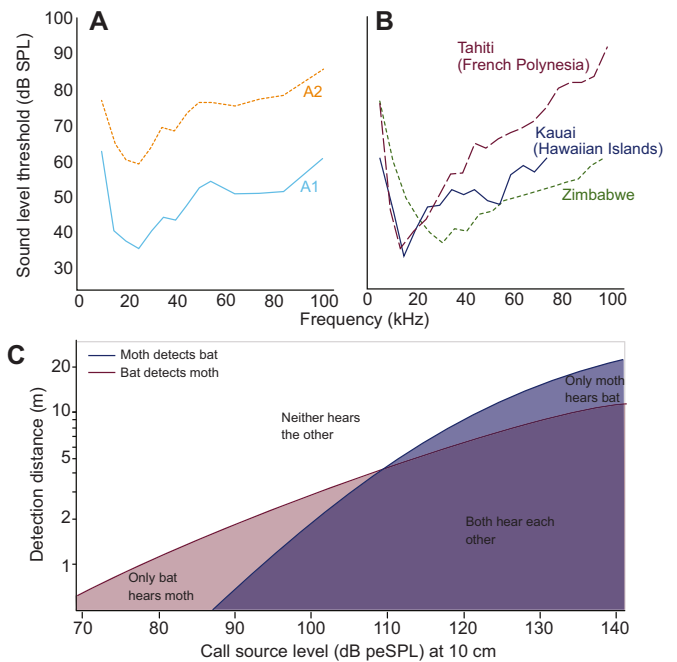


Fig. 3. Moth auditory tuning curves and distance model for bat–moth detection. (A) Threshold tuning curves for A1 and A2 of the noctuid moth *Noctua pronuba* (adapted from Madsen and Miller, 1987), showing the lowest sound level to elicit neural activity (lower values indicate more sensitive hearing). The two neurons have similarly shaped tuning curves – with greatest sensitivity to the ultrasonic frequencies typical of bat echolocation calls – but differ in sensitivity, with A2 thresholds ~20 dB greater (less sensitive) than A1 thresholds. SPL, sound pressure level. (B) Variation in the sensitivity and shape of auditory tuning curves for noctuid moths living in the bat-free habitat of Tahiti (French Polynesia), the single bat species community of Kauai (Hawaiian Islands) and the bat-rich community of Zimbabwe (adapted from Fullard, 1998; Fullard et al., 2007). (C) Model depicting detection distances based on moth threshold tuning curves. The blue line shows the distance at which one moth species can hear the calls of one bat species, and the red line shows the distance at which the bat can hear the echo from the moth. For bat echolocation calls at low call source levels, bats hear moth echoes over greater distances than moths hear bat calls, and the opposite is true at high source levels. peSPL, peak equivalent sound pressure level, the sound level of a pure tone of the same frequency and peak-to-peak amplitude as the bat call. Adapted from Goerlitz et al. (2010).

still be at greater risk of bat predation if they fly more at night in search of perched pheromone-releasing females. Although male-biased moth predation by bats has been observed around streetlights (Acharya, 1995), a male-biased flight-to-light response also exists in some moths (Altermatt et al., 2009). In general, for moth species in which both males and females fly, there is no evidence for differences in sensitivity between male and female moths (Surlykke and Gogala, 1986; Surlykke and Treat, 1995; Skals and Surlykke, 1999, 2000; Fullard, 2006). Sex and size aside, moth species with less sensitive ears fly less at night (ter Hofstede et al., 2008a). Thus, although less sensitive moths experience greater risks in terms of their proximity to bats before initiating evasive flight, they compensate for this cost by reducing their exposure to bats (ter Hofstede et al., 2008a).

Diurnal moth species either do not have ears or have less sensitive ears than nocturnal moths (Fullard et al., 1997, 2000; Surlykke et al., 1998; Muma and Fullard, 2004). Similarly, in butterflies, ultrasound-sensitive ears are only found among nocturnal species (Yack and Fullard, 2000), whereas some diurnal butterflies have ears that are sensitive to low-frequency sounds for communication

or hearing avian predators (Yack et al., 2000; Lane et al., 2008; Lucas et al., 2009). Actograms of flight activity have revealed that many moths that were considered diurnal are also active at night, explaining the maintenance of sensitive ears in these species (Fullard and Dawson, 1999; Fullard and Napoleone, 2001). Moths that are active during the day often have greater sensitivity to sonic (<20 kHz) frequencies (Fullard et al., 1997; Surlykke et al., 1998), perhaps as a derived defence to detect the rustling sounds of birds (Jacobs et al., 2008).

Moth phenology

Seasonal differences in moth activity also correlate with ultrasound sensitivity. Moths that emerge in early spring before bats are active have higher hearing thresholds (Fullard, 1977; Fullard and Barclay, 1980). Yager et al. (2000) show a similar seasonal pattern for hearing in beetles. Winter moths also have higher thresholds, but only if they are effectively isolated from bats (Surlykke and Treat, 1995; Svensson et al., 1999; Rydell et al., 1997). Defensive sound production in tiger moths (see ‘Sound production in moths: defence, courtship and sexual antagonism’, below) follows the same pattern: species emerging in spring, when bat activity is low, have lost the ability to produce sound, whereas those emerging in summer, when bat activity is high, have not (Fullard, 1977; Fullard and Barclay, 1980; Ratcliffe and Nydam, 2008).

The sympatric bat community

Geographic variation in moth auditory sensitivity often corresponds with the number of bat species in an area (Fig. 3B). The approach of comparing auditory tuning in moths to the relevant ‘echolocation assemblage’ in which they live has been reviewed previously (Fullard, 1988, 1998). Moth species in areas with bat echolocation assemblages covering a wide frequency range have more sensitive ears that are more broadly tuned than those in areas of low bat diversity (Fullard, 1982a; Fullard et al., 1983). In the Neotropics, where there are many fruit-eating bats, the tuning of moth ears shows better congruence with the insect-eating bat echolocation assemblage than with the bat community as a whole (Fullard, 1988). In addition, moths with extremely sensitive ears tend to be found in areas of high bat predation pressure (Fullard, 1982a; Fullard et al., 2008b). In some cases, particular bat species seem to have an impact on the tuning of local moth ears. For example, the ears of Hawaiian moths have a much narrower tuning curve than those of moths found elsewhere, and they are closely tuned to the echolocation frequency of the one bat species in Hawaii, *Lasiurus cinereus semotus* (Fullard, 1984a). Horseshoe bats, if present, usually have the highest frequency echolocation calls in a community, and their presence appears to select for improved higher frequency hearing in local moth populations (Jacobs et al., 2008; ter Hofstede et al., 2013) and several Old World mantis species (Triblehorn and Yager, 2001).

Studies have found some evidence of neural regression in moth species that live where bats do not. Moths endemic to bat-free French Polynesia are less sensitive to sounds >25 kHz compared with more recent immigrants (Fullard, 1994; Fullard et al., 2007). This high-frequency deafness might reflect neural regression (Fullard et al., 2007) or thickening of the tympana (Ratcliffe, 2009). The behavioural response to ultrasound is also lost in most of these endemic species (Fullard et al., 2004; Fig. 3B). However, this pattern was not found for bat-free arctic locations, possibly because these moth populations are not isolated from gene flow from southern populations or have not been isolated for long enough for changes to occur (Surlykke, 1986; Rydell et al., 2000).

Bat-avoidance behaviour in moths and other insects

Given the well-supported hypothesis that the original and primary purpose of moths’ ears is to detect predatory bats, we should expect to see adaptive behavioural responses to ultrasonic sounds in moths with ultrasound-sensitive ears. Many studies have shown evasive behaviours by moths in response to bat-like sounds (Table 1). These evasive responses are usually graded, meaning that the responses change in a quantitative or qualitative manner with increasing sound amplitude. Almost all other insects with bat-evasive behaviours also show this pattern of graded response, changing from small alterations in flight direction or speed to drastic, last-ditch behaviours as sound amplitude at their ears increases (green lacewings: Miller and Olesen, 1979; crickets: Nolen and Hoy, 1986; mantids: Yager et al., 1990; beetles: Forrest et al., 1995; some katydids: Schulze and Schul, 2001; tachinid flies: Rosen et al., 2009). This is a highly adaptive pattern for bat avoidance. Many insects can detect bats before the bats can detect the echoes reflected from the insect (Surlykke, 1988; Surlykke et al., 1999; Goerlitz et al., 2010; Fig. 3C), and under these circumstances, directional flight or small changes in flight trajectory should allow the insect to get out of the path of the approaching bat before it is detected (Surlykke, 1988; Surlykke et al., 1999; Goerlitz et al., 2010). Insects with two ears might use differences in the sound arrival time or intensity at each ear as information about the direction of the sound source (Payne et al., 1966). Most of these studies have investigated responses to ultrasound in tethered animals, and it is not entirely clear whether or how some of these graded behaviours translate into differences in behaviour in free flight.

If a bat makes a sudden change in flight direction, a flying insect might find itself confronted by a hunting bat ready to attack. Similarly, some bats will continue to track evasively flying insects, rather than give up. In such situations, the insect may take advantage of its greater manoeuvrability compared with that of the larger bat (Ghose et al., 2009), and behaviours such as loops, dives, zig-zigs and spirals can allow the insect to drop out of the bat’s sonar beam. Directional flight away from low-amplitude ultrasonic pulses and last-ditch manoeuvres in response to high-amplitude ultrasonic pulses have been observed in noctuids, geometrids and notodontids (Roeder, 1962, 1964; Agee, 1967, 1969; Surlykke, 1984; Rydell et al., 1997; Svensson et al., 1999). Pyralids (Table 1) probably have a graded response as well; they dive in response to loud ultrasound, but flight responses to low-amplitude ultrasound have been difficult to classify (Skals and Surlykke, 2000; Rodríguez and Greenfield, 2004). Graded responses have also been observed for insects that lack directional hearing (e.g. mantids and sphingids), with low-amplitude ultrasound eliciting turning and higher amplitudes eliciting flight cessation (Yager et al., 1990; Göpfert and Wasserthal, 1999a).

The behavioural responses of moths to bat calls are known to occur at lower sound amplitudes when sound pulses are broadcast at biologically relevant repetition rates, i.e. those used by bats during their search for and approach to prey, rather than isolated sound pulses (noctuids: Agee, 1969; Roeder, 1964; arctiids: Fullard, 1984b; pyralids: Skals and Surlykke, 2000). This pattern also holds for other insect groups with bat-detecting ears (lacewings: Miller and Olesen, 1979; crickets: Nolen and Hoy, 1986; mantids: Triblehorn and Yager, 2005). In addition, moths with ears will fly less at night when subjected to the playbacks of bat calls than they do under silent conditions (Fullard et al., 2003; Ratcliffe et al., 2008). Together, these studies show that insect responses to ultrasound are fine-tuned to the predatory cues of bats.

Erratic flight is a pervasive strategy for predator avoidance for many flying insects, providing defence against birds (Jacobs et al., 2008; Fournier et al., 2013) and bats (Roeder, 1967; Acharya and Fenton, 1999) alike. Compared with eared moths, earless moths rely more on passive defences, such as flying less at night (Morrill and Fullard, 1992; Fullard and Napoleone, 2001; Soutar and Fullard, 2004), closer to vegetation (Lewis et al., 1993; Rydell, 1998), more erratically (Lewis et al., 1993; Rydell and Lancaster, 2000) or at times when bats are not active (Yack, 1988; Morrill and Fullard, 1992; Lewis et al., 1993). *Hepialis humuli* is an earless moth that performs short visual flight displays at dusk, thereby reducing its exposure to birds and bats (Andersson et al., 1998). Although these moths exhibit this and all the other passive defences listed above for earless moths (Rydell, 1998; Rydell and Lancaster, 2000), the bat *Eptesicus nilssonii* can apparently overcome these defences by emerging early in the evening and using vision to locate these large white moths (Eklöf et al., 2002).

With the appearance of bats, different moth species took parallel paths to bat avoidance: reactionary auditory-evoked evasive flight in eared moths and preventative continuous erratic flight in earless moths. The evolution of ears might have released some moths from the necessity of inefficient erratic flight, allowing for a more efficient straight flight path, only interrupted by erratic flight in the presence of bats.

Sound production in moths: defence, courtship and sexual antagonism

Until now, we have considered only passive bat avoidance behaviours in earless insects (e.g. meandering flight) and two forms of active bat avoidance in eared moths: auditory-evoked negative phonotaxis (i.e. moving away from a sound source; see Glossary), which occurs in response to distant bats, and erratic flight behaviours, which occur in response to nearby bats. Tiger moths and their allies (family Erebiidae, subfamily Arctiinae) are closely related to the noctuids and Lymantriids, and, as expected based on their phylogenetic position, possess a pair of ears with two auditory afferents (the A1 and A2 cells found in noctuids; Box 2, Figs 2B, 3A). Chemical defence, by way of compounds produced *de novo* or sequestered from plants during the caterpillar stage, and high-frequency, high-energy sound production are thought to be ancestral characteristics of this clade (Weller et al., 1999; Nishida, 2002). Tiger moth species that produce sound do so using two tymbals (see Glossary) found on opposite sides of the thorax. These produce a train of clicks as they buckle in and out. Tiger moths produce these sounds in response to tactile stimulation, bat echolocation calls or both. The timing of the clicks varies within and between species, but most sound-producing species appear to time their clicks to the echolocation pulses of nearby bats in the approach phase of attack (Fullard, 1984b; Ratcliffe and Fullard, 2005; Barber and Conner, 2006).

Sound production in tiger moths has long been recognized to have a defensive function against bats, deterring experienced bats from completing their aerial hawking attacks (see Glossary) in both the field and flight room (Acharya and Fenton, 1992; Dunning et al., 1992; Hristov and Conner, 2005; Ratcliffe and Fullard, 2005). Three hypotheses have sought to explain how tiger moth clicks deter bats: (i) by startling naive bats, (ii) by jamming bat echolocation and (iii) by acting as warning signals, reminding experienced bats of the moths' chemical defences (Hristov and Conner, 2005; Ratcliffe and Fullard, 2005; Ratcliffe, 2009; Corcoran et al., 2010). We argue that startle and jamming should be considered together as auditory interference, where startle effects of the tiger moth clicks diminish

Box 2. Neural basis for evasive flight in moths

Moth auditory neurophysiology has been best studied in noctuids. The noctuid auditory nerve is composed of two auditory receptor cells (A1 and A2) and a non-auditory B-cell (see Fig. 2B). The axons of these cells enter the pterothoracic ganglion located in the thorax (Surlykke and Miller, 1982), where they synapse with auditory interneurons (Boyan and Fullard, 1986). The A1 and B-cells have projections that either terminate in the pterothoracic ganglion or extend up to the suboesophageal ganglion, whereas A2 projections are limited to the pterothoracic ganglion (Agee and Orona, 1988; Zhemchuzhnikov et al., 2014). The exact circuitry involved in processing auditory inputs is unknown in moths, although models have been proposed (Boyan and Fullard, 1986; Boyan et al., 1990). Numerous interneurons, which either repeat or filter/process the input of the auditory receptors, have been identified in the pterothoracic ganglion, and many are believed to have axons extending to the brain (Boyan et al., 1990). The influence of the brain on evasive flight has been studied by observing the behavioural responses of decapitated moths to pulsed ultrasound, with mixed results depending on moth family (Treat, 1955; Agee, 1985; Fullard, 1982b; Dawson and Fullard, 1995; Skals and Surlykke, 2000). Therefore, the role of the brain in bat evasion appears to differ between these groups. The context of bat detection can also influence decision-making processes in some moths. For example, the detection of pheromones reduces anti-bat behaviour in male moths (Svensson et al., 2004; Skals et al., 2005). A frequently cited but untested hypothesis for the neural basis of evasive flight in noctuid moths is that the more sensitive receptor (A1) triggers directional flight, whereas the less sensitive receptor (A2) triggers last-ditch behaviour (Roeder, 1974b). This hypothesis implies that A1 and A2 encode different types of information about predation risk: potentially 'I am not yet detected by the bat' and 'I am now detectable by the bat' (ter Hofstede et al., 2013). Other authors (Surlykke, 1984; Ratcliffe et al., 2009) have suggested that A2 might only increase the dynamic range of the ear, i.e. simply the number of receptor spikes in a given time from A1 or both A1 and A2 would determine the type of behavioural response. Whether moths with more than two receptors display more than two types of evasive behaviour has also never been tested. Further work on the relationship between neural activity and behaviour is needed to address the adaptive significance of hearing for anti-predator defences in moths.

with bats' experience, and, regardless of experience, tiger moth species able to produce greater numbers of clicks per unit time are better able to interfere with the ranging abilities of attacking bats (in other words, 'jamming' bat echolocation).

Moths of the palatable species *Bertholdia trigona* are at the extreme of this tymbal click rate continuum, producing so many clicks that they inarguably must interfere with an attacking bat's target ranging capabilities. *Cynia tenera* and *Euchaetes egle*, conversely, produce roughly the same number of clicks per unit time and far fewer clicks than *B. trigona*, and, as follows, these clicks are less likely to fall within the 2 ms window at the bat's ear when it is expecting target echoes (<20% of the time for *C. tenera*; Ratcliffe and Fullard, 2005). Supporting this contention, behavioural data from naive bats suggest that clicks, in and of themselves, deter bats ~20% of the time in palatable *E. egle* and >90% of the time in *B. trigona* (Hristov and Conner, 2005; Corcoran et al., 2009). Further, when the clicks of chemically defended *C. tenera* fall within this 2 ms window, they do interfere with echolocation in experienced bats (Ratcliffe and Fullard, 2005). Sound production is not limited to tiger moths, and new evidence suggests that some sphinx moths also deter bats by producing many clicks per unit time with a stridulatory organ (see Glossary; Barber and Kawahara, 2013; Kawahara and Barber, 2015).

During aerial hawking attacks, tiger moth clicks can act as warning signals for experienced bats. We have suggested previously

that this third hypothesized mechanism of bat deterrence (‘acoustic aposematism’) may be related to the effectiveness of the clicks as interference signals (Ratcliffe and Fullard, 2005). Specifically, we suggest that the more high-frequency clicks produced per unit time, the more negative and salient the warning signal. To illustrate, with respect to food flavours, the more negative and salient the signal (e.g. bitter or sour), the more readily the signal is associated with a negative consequence (e.g. gastrointestinal malaise; reviewed in Ratcliffe et al., 2003). If this is also the case in the auditory domain, tiger moths producing more clicks per unit time may be more effective at training individual bats to avoid them in the future (Ratcliffe and Fullard, 2005). At present, the inter- and intra-specific relationships, if any, between palatability and signal complexity are unknown, and these relationships are complicated by mimics – sympatric sound-producing tiger moths that are more palatable than their putative models (Barber and Conner, 2007).

As seen in noctuid moths, the context in which tiger moths detect bats can influence decision making in these species. In the dogbane tiger moth, *C. tenera*, anti-bat sounds are initially produced in equal numbers to bat-like sounds representing a searching bat (low risk) or an attacking bat (high risk). Over time, however, the moths habituate more (i.e. produce fewer sounds) to the sounds of a low-risk searching bat than to those of an attacking bat, reflecting an adaptive response to different levels of risk. These changes in behaviour are not due to sensory adaptation or muscle fatigue, and thus are the result of changes at the central nervous system level (Ratcliffe et al., 2011a).

In addition to this defensive function, some tiger moths and noctuids use sounds during courtship. Although we will not describe this additional function of sound production in detail, we mention it here because we believe it is an interesting extension of the bat–moth story. For example, males of the pyralid moth *Ostrinia furnacalis* produce sounds to elicit an anti-bat response (freezing) so they can forcibly mate with perched females, whereas females of the arctiid moth *Eilema japonica* can distinguish between bat and male calls and only take defensive action to bat calls (Nakano et al., 2013). Producing sounds for mating purposes also comes at the potential cost of attracting eavesdropping bats, as is seen in the pyralid moth *Achroia grisella* (Alem et al., 2011). Generally considered rare in moths, acoustic communication for mating has been discovered in more and more moth species in recent years, suggesting that it is far more common than previously appreciated, but was previously overlooked in some species because of the low intensity of the signals (Nakano et al., 2008, 2009). For reviews of intraspecific acoustic communication in moths, see Conner (1999) and Nakano et al. (2015).

Evolution of hunting strategies in bats: better ways to catch insects, eared or otherwise

The evolutionary origins of echolocation in bats

The case for bats having evolved counter-measures against eared prey is not nearly as strong as the evidence supporting bat predation as the selection pressure for hearing in many insect groups. The adaptive radiation of bats into the ~20 families and >1300 species seen today occurred ~50 mya, after laryngeal echolocation had evolved in the ancestral bat (Teeling et al., 2005; Teeling, 2009; Fenton and Ratcliffe, 2010). More than 1000 extant bat species are laryngeal echolocators (Ratcliffe et al., 2013). This diversification was due to the success of bats in exploiting the unoccupied foraging niche of night-flying insects (Griffin, 1958). Although the first bats might not have echolocated (Simmons et al., 2008; Veselka et al.,

2010), they most likely ate insects, using passive listening to detect prey on the vegetation and the ground (Simmons and Geisler, 1998). As powered flight further developed, so too, we expect, did echolocation and the ability to track airborne prey (Ratcliffe et al., 2011b, 2013). Emerging hundreds of millions of years after the appearance of insects (Bininda-Emonds et al., 2007; Misof et al., 2014) and ~100 million years after the origin of the Lepidoptera (Bininda-Emonds et al., 2007; Misof et al., 2014), the first echolocating bats would have encountered many night-flying insects that were defenceless against aerial attacks. Presumably, these insects would, at first, have been easy prey compared with modern night-flying insects.

Aerial hawking was and remains the primary selective pressure for the evolution and maintenance of bat detection and defence in insects (Ratcliffe and Fullard, 2005; Ratcliffe, 2009). Although many bat species take prey from water and terrestrial surfaces, most of these species also capture prey in flight (Ratcliffe et al., 2006; Ratcliffe, 2009). Over time, airborne insects, through the evolution of bat-detecting ears and auditory-evoked defensive flight behaviours and passive anti-bat behaviours (both discussed above), would in general have become more difficult to track and capture, providing selective pressure for bat biosonar systems to better track would-be prey.

Here, we review the evidence for adaptive counter-strategies in bats against eared moths. We propose two criteria for assessing whether a given bat species or clade evolved adaptations specifically to circumvent bat-detecting ears in insects. The first criterion is met if the bat species eats a significantly larger proportion of eared insects than is available in the environment. This is frequently estimated using the proportion of moths in the diet (Box 3). This level of evidence can be considered as a ‘low bar’ that represents only weak support for the existence of counter-adaptation, given that eared moths fly relatively slowly, are soft-bodied and thus should be especially attractive to bats as compared with hard-shelled beetles, fast-flying sphinx moths, measly flies (e.g. mosquitos) and miniscule chironomids. The second ‘high bar’ criterion, which provides a higher level of support for bat counter-adaptation, requires that the putative bat counter-measure against insect hearing has no plausible alternative explanation for its origination and maintenance.

The allotonic frequency hypothesis

The majority of eared insects are most sensitive to sounds within the range of most bat echolocation signals, between 20 and 50 kHz (Fullard, 1998; Ratcliffe, 2009). Therefore, one potential counter-strategy for bats against insect hearing, referred to as the allotonic frequency hypothesis, would be to produce either very high- or very low-frequency echolocation calls outside the best hearing range of most insects. A handful of species, including several molossid and at least one vespertilionid – the spotted bat, *Euderma maculatum* – are known to produce exceptionally low-frequency echolocation calls (Fullard and Dawson, 1997). *Euderma maculatum* is a small- to medium-sized bat. Based on the relationship between size and echolocation call frequency that is well established among vespertilionid species (Jones, 1999), *E. maculatum* would be expected to use echolocation calls with maximum energy around or above 30 kHz. Instead, they produce narrowband calls with peak frequencies of ~10 kHz, outside the sensitivity range of sympatric eared moth species (Fullard and Dawson, 1997). Genetic diet analyses have not been conducted, but faecal analysis suggests that these bats consume many more moths than would be predicted from moth abundance alone (Painter et al., 2009).

Box 3. What is a moth specialist?

Frequently, the proportion of moths in the diets of bats is used as a measure of the proficiency of a bat species at overcoming the auditory defences of insect prey. Moths, however, make up a substantial proportion of the large flying insects that are active at night, and, not surprisingly, constitute a large proportion of the diet of many bat species (Ratcliffe, 2009; Clare et al., 2009; Bohmann et al., 2011). Thus, an actual preference for moths in a given bat species dictates that the proportion of moths consumed must be significantly larger than the proportion of moths making up the community of insect species flying at night. That is, for a bat to be a 'moth specialist', its moth encounter rate must be lower than its moth consumption rate. Furthermore, the preference of a given bat species for a specific size range of flying insect prey should also be taken into consideration: a general preference for moth-sized insects in a moth-rich environment should not be taken as unequivocal evidence of dietary preference. For example, the eastern red bat, *Lasiurus borealis*, was until recently considered to be a moth specialist. These fast-flying, open-space aerial hawkers often hunt moths around streetlights, using two remarkable behaviours. First, these bats use the longest feeding buzzes recorded, at times exceeding 3 s (Acharya and Fenton, 1999). Most bats produce ~200 ms buzzes in the field, and shorter ones in a flight room (Simmons et al., 1979; Surlykke and Moss, 2000; Schnitzler and Kalko, 2001; Moss et al., 2006; Ratcliffe et al., 2013). By combining the high-update rates of the buzz with a lower-frequency, broader sonar beam, red bats should be able to track unpredictably flying insects for much longer than other bats. Second, eared moths, when they do escape the attack of one bat, are often taken by a second opportunistic red bat as the moth dives to the ground (Reddy and Fenton, 2003). Although anecdotal evidence once suggested that red bats were moth specialists, recent genetic diet analyses show that red bats are dietary generalists, taking no greater percentage of moths than expected based on their availability (Clare et al., 2009). These putative moth specialists are thus similar to the majority of insect-eating bat species; they are opportunists, foraging to maximize energy intake versus time and energy output.

Although *E. maculatum* and some of the molossids with low-frequency calls (e.g. *Eumops* spp.) satisfy our criterion for the low bar, they do not unequivocally cross our high bar for evidence of counter-adaptation. This is because the use of very low-frequency echolocation calls has other advantages for the species that produce them. All of these species are fast-flying, open-space aerial hawkers. Low frequencies attenuate less rapidly in air (Griffin, 1971; Lawrence and Simmons, 1982) and, all else being equal, these bats should enjoy the advantage of greater detection ranges (reviewed in Ratcliffe, 2009).

At the other extreme of the echolocation call frequency spectrum is the little-studied African hipposiderid, *Cleotis pervalis*, which produces echolocation calls with maximum energy at a frequency higher than any animal ever recorded (~212 kHz; Fenton and Bell, 1981); these signals are almost certainly inaudible to even the most sensitive moth species throughout the entire pursuit (Fullard, 1998; Ratcliffe, 2009). Owing to the extreme atmospheric attenuation of such frequencies, however, the detection range of *C. pervalis* will be very short, imposing a cost for orientation and prey detection, and suggesting that this extreme frequency might have evolved to circumvent auditory detection by insects. However, using high-frequency calls can also provide the benefit of more-detailed information about one's immediate surroundings, and therefore only fulfils the low bar criterion as a counter-adaptation to insect hearing.

Among aerially hawking laryngeal-echolocating bats, there are those that produce short-duration, often frequency-modulated calls and separate call and echo in time to estimate the position of prey

and other objects, and those that produce longer-duration calls of constant frequency and separate call from echo using frequency differences generated by Doppler shifts (Neuweiler, 1990; Fenton et al., 2012). Bats from the first group, called frequency-modulating or low duty cycle (LDC) bats, are found in both suborders and have a worldwide distribution. Bats in the second group, called constant-frequency or high duty cycle (HDC) bats, are, with the exception of a few mormoopid species, found only in one suborder and confined to the Old World. Relative to LDC bats of the same size, HDC bats tend to use higher peak frequencies, and, as a result, have been proposed to circumvent the auditory defences of moths. Among communities of HDC bats, those that use the highest frequencies consume the most moths (Schoeman and Jacobs, 2003). However, owing to the increased sensitivity of moth ears to longer-duration sounds (Tougaard, 1996, 1998; Ratcliffe et al., 2009), any advantage conferred to HDC bats by using higher frequencies appears to be nullified by their very long duration calls (Jacobs et al., 2008). HDC bats are able to detect fluttering insect wings (through acoustic glints) and distinguish them from background echoes (e.g. those from vegetation); LDC bats cannot. For this reason, insects flying close to clutter, whether eared or earless, may be more susceptible to capture by HDC bats.

Terminal buzz phases as counter-measures against increasingly evasive flying insects

During an aerial attack, bats produce calls more rapidly as they approach prey. A feeding buzz (i.e. echolocation call rates of >100 calls s⁻¹, and ≥200 calls s⁻¹ in some species; see Glossary) has been described for almost all bats studied when taking airborne prey, a rare exception being the primarily substrate gleaning bat (see Glossary) *Megaderma lyra* from the ancient, species-poor family Megadermatidae (Schmidt et al., 2011). During the terminal sub-phase of a feeding buzz (often referred to as buzz II), species in the sister LDC bat families Vespertilionidae and Molossidae drop the peak frequency of their echolocation calls by an octave and, consequently, roughly double the breadth of their sonar beam (Jakobsen et al., 2013; Ratcliffe et al., 2013). HDC rhinolophids, through an unknown mechanism, also broaden their beam during the buzz (Matsuta et al., 2013). For all hawking species, we suggest that the buzz evolved to allow better tracking of ever more evasive prey (Elemans et al., 2011; Ratcliffe et al., 2013; Hulgard and Ratcliffe, 2016). For vespertilionids and molossids, the octave drop of buzz II might represent a further counter-adaptation to track evasively flying insects, including, but not limited to, eared moths and other insects with bat-detecting ears (Jakobsen and Surlykke, 2010; Ratcliffe et al., 2013).

Quiet calling

When flying in open space, bats are far louder than previously recognized, producing signals between 120 and 140 dB SPL when measured at 10 cm from the bat's mouth (Surlykke and Kalko, 2008). Bats therefore have much longer detection ranges than previously appreciated but are detected by eared prey at even greater distances. This occurs because, although bats' ears are more sensitive than those of insects, prey echoes returning to the bat have travelled – and attenuated – over the distance both to and from the insect, and consequently contain much less energy than the signal reaching the insect (Fig. 3C). Through substrate gleaning of prey from terrestrial surfaces, some bats might circumvent eared insects' defences. Gleaning is likely to be the ancestral condition of predatory bats, and has independently evolved many times since (Simmons and Geisler, 1998). Extant gleaning bats – and those

which both glean and hawk prey – use echolocation calls of much lower intensity than hawking bats, and are relatively inaudible to eared moths (Faure et al., 1990, 1993). The presence of gleaning bats might not select for more sensitive ears in moths if the risk of being eaten by a gleaning bat is less than the risk of never mating owing to unnecessary evasion of aerially hawking bats that are too far away to pose a threat.

There is scant evidence that gleaning bats take more eared prey than would be expected by chance, or that low-intensity echolocation calls evolved in the context of gleaning to circumvent the ears of moths or other insects. Bats use lower-intensity echolocation as they approach objects – whether to land, fly by or take prey – to prevent self-deafening from intense echoes and reduce the costs of producing high-intensity sounds when they are unnecessary to produce audible echoes (Kick and Simmons, 1984; Hartley, 1992).

The only bat thus far that meets both of our criteria for a counter-strategy to insect hearing is the hawking vespertilionid, *Barbastella barbastellus* (Goerlitz et al., 2010). When searching for prey, *B. barbastellus* produces echolocation calls of much lower intensity (~94 dB SPL) than those of the sympatric vespertilionid *Nyctalus leisleri* (~127 dB SPL). Both bat species produce calls with peak frequencies within the best hearing range of sympatric moths (*B. barbastellus*: 33 kHz; *N. leisleri*: 28 kHz). Owing to its low-intensity calls, however, *B. barbastellus* is not detected by noctuid moths until the bat is ~4 m away. Conversely, *N. leisleri* can be detected at >30 m. A stealth approach has benefits and costs; *B. barbastellus* is the only bat species known that should detect eared moths before the moths detect them (Fig. 3C). However, the prey detection range of *B. barbastellus* is only ~5 m, whereas that of *N. leisleri* is ~20 m. Molecular diet analyses of these two species reveal that ~85% of the diet of *B. barbastellus* consists of eared moths, whereas for *N. leisleri* the range is 0–56%. There is no plausible functional explanation for using echolocation calls of such low intensity in open space other than to circumvent the bat-detecting ears of insects, which is likely to explain the fact that the diet of *B. barbastellus* consists almost entirely of eared moths. This suggests that circumventing moth hearing is the selective pressure that maintains, and perhaps originally selected for, the use of low-intensity calls by *B. barbastellus*. Further phylogenetic analyses are needed to determine the ancestral state of calling amplitude in the bat lineages closely related to *B. barbastellus* to provide stronger evidence for this hypothesis.

Conclusions

Bats and their insect prey provide a fascinating study system to investigate questions related to the evolution of sensory systems and behaviour. The evolution of echolocation in bats for orientation and finding food was a major change for the entire nocturnal animal community at the time, and the number of times that bat-detecting ears have independently evolved in the insects is a testament to the intense selection pressure that bats exert on these species. Designating these relationships as co-evolutionary processes is problematic because of the very diffuse interactions between these groups, but research into potential counter-adaptations by bats to the anti-bat adaptations in insects provides exciting examples of how bat echolocation can be influenced by their prey. Several aspects of bat–insect interactions make them excellent candidates for future work on predator–prey dynamics. First, whereas most predator–prey interactions may be multimodal, and thus require many combinations of sensory stimuli for adequate behavioural tests, bats and moths present a simple, almost exclusively acoustic-based system. Second, sound is relatively

easily recorded, analysed and reproduced for experimentation. Third, recent advances in 3D microphone arrays and 3D infrared videography mean that researchers have begun to investigate these interactions in the wild (Corcoran and Conner, 2012). Fourth, using combinations of real-world interactions, naturalistic acoustic stimuli and neurophysiological recordings, researchers will soon be able to elucidate the neural underpinnings of bat–moth interactions, thus providing us with further insight into this fascinating system.

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