Antenna

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Cover Picture: *Episyrphus balteatus* - Hoverfly homing in by Zach Haynes.

Editorial

There is something of a conservation theme running through this issue of *Antenna*. V.P. Uniyal and Vandana Mehrwar relate how they were able to engage their university campus in India in a collaborative pollinator project, focusing on the often-overlooked solitary bees. Conservation of a different kind is recounted in the article on the earliest entomology books held in the Old Library at Cambridge, and Rose Pearson reviews some of the RES's own collection of books.

We have two letters from our President in this issue. Our outgoing President, Jane Hill OBE, has contributed much to the success of the Society during her tenure, and our incoming President is Professor Jane Stott, whose account of her work in insect conservation in Ireland is of great interest. This is an area in which the RES as a society has played a significant role, for example having established Invertebrate Link (Joint Committee for Conservation of British Invertebrates: please see https://www.royensoc.co.uk/invertebrate-link/ for details).

Stuart Reynolds contributes another excellent article in the 'Research Spotlight' series, this time on the longstanding (as in, millions of years') war between moths and bats. Peter Smithers' Honorary Fellow Interview victim is Rebecca Kilner, a Professor of Evolutionary Biology at Cambridge and a Director of the Cambridge Museum of Natural History. Rebecca delivered both the Verrall and Young Verrall lectures this year and is no stranger to being interviewed, having recently been the subject of the BBC Radio programme *The Life Scientific*. Peter has conducted more Honorary Fellow interviews than some of us have had hot mealworm dinners, and we are very grateful to him for his substantial and enduring contributions to *Antenna*. While this is Peter's final interview in the series there remain Hon. Fellows on the loose, so this is a good time to remind readers that we would now welcome someone to take over the baton.

The Society's outreach activities include providing awards to deserving entomologists, including scholarships to promising MSc students. The stories of this year's recipients (one of whom only heard of entomology relatively recently!) are revealed on pages 144 and 145, and make interesting reading. Meanwhile, Diptera, Hymenoptera, Lepidoptera and Odonata, as well as riverflies, silverfish and long-dead lacewings, are among the winning entries in the 2023 RES annual photography competition; they can be seen on pages 146 to 155. To borrow a contemporary idiom, people who enjoyed these images may also enjoy those depicted on the website https://www.insectweek.org/art-and-photography, where previous years' winning entries, going back to 2016, may be found.

Dafydd Lewis

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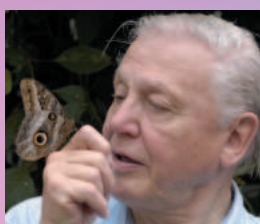
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Submissions are made by email to antenna@royensoc.co.uk and reviewed by *Antenna's* editorial team. There are no page charges for publication in *Antenna*, where we encourage use of full colour figures and photographs to accompany text. Standard articles are normally 1,000–3,000 words in length and submitted with four to eight images (file should be original size of image taken and not reduced in size nor cropped heavily).

Letter from the outgoing President

It's been a great honour to be the RES President over the past two years. Time has flown by! I'm proud to have supported the Society in making such excellent progress in addressing its strategic aims. There is more to be done of course, but it's great to have been involved with a Society that is forward-looking and ambitious.

I have seen the Society go from strength to strength, increasing our membership (we now have more members than we have ever had), increasing the number of papers we publish in our journals, and arranging more great ways for members to network and talk about insect science. It's been a privilege to work with the RES staff team – you are fabulous! Many members may not be aware of what a great team they are, working hard to make the Society, and everything we do, better for everyone. And of course, a huge thank you to all our members who volunteer for the Society, and who lie at the heart of our successful Society and its activities. If you are not doing so already, I encourage you to get more involved with the Society – there are lots of ways of doing this - have a look at the Society's webpages to find out more.

If I had to choose, the 'Presidential' highlights for me over the past two years have been the RHS Chelsea Flower Show (what an amazing opportunity to talk with people about the wonders of insects, and bringing insects into our gardens), visiting Daneway Banks (a joint RES event with the Botanical Society of the British Isles, on a glorious sunny June day when the Large Blues were flying), and working with Helen Roy (Past President), Allan Watt (trustee) and Emilie Aimé (Director of Publishing) to produce the book on 'Insects' with DK publishers. I think DK were surprised when we said we would go out to our members for content – and what an amazing response from members! Thank you to the 90 members who got involved and shared your amazing knowledge and enthusiasm for insects - I hope you are all proud of what we have achieved.

I was fortunate to learn from the wise advice and leadership experience of the previous President, Prof. Helen Roy, and it's now a privilege to hand over to Prof. Jane Stout, knowing that the Society is in safe hands (and for the first time we have a President based outside the UK). There are huge concerns about insect declines, especially declines of pollinators, and tackling this important issue is a key part of Jane's research, helping to improve environmental policy and practice. Good luck Jane, and I hope you enjoy being President as much as I have!

Jane Hill OBE
President
Royal Entomological Society

Thank you to everyone who contributed to the book.

Letter from the incoming President

It's a real pleasure to be writing this as RES President. I am extremely honoured to be in this position, and very fortunate to be following in the footsteps of our wonderful outgoing President, Jane Hill, from whom I am already learning an enormous amount. I am grateful for all the work that Jane has put in as RES President, and that the RES has instigated a system of keeping the Past President on speed dial, as I try and learn the ropes.

It has been wonderful getting to know the RES staff and trustees over the past year – there is a fantastic team spirit, great optimism and genuine commitment from everyone I have met. I look forward to working with all of them, and all of you, the members, over the coming years. It's been great to watch from the sidelines as the 'Insects' book has been finalised, and I was thrilled to be able to contribute, along with so many of you.

I have been a Fellow of the RES since hosting the 2015 Annual Meeting in Trinity College Dublin, Ireland. It was a real pleasure to host Ento15, and I'm excited to be able to build on that experience now. I note that I am the first non-UK-based President and hope that I can bring a more international perspective to the Society's work too.

Although I started my entomological career in England, doing my PhD at the University of Southampton with Dave Goulson, on bee foraging ecology, I have been based in Ireland since 2001. I have continued to work on bees – on their ecology and conservation, as well as the benefits they bring to human society, its health and economy. I have been able to go beyond bees to insects more broadly, and the value of biodiversity and its restoration in general.

I co-founded the All-Ireland Pollinator Plan with Una FitzPatrick, who won the RES Award for Insect Conservation in 2022, and it has been wonderful to watch the Pollinator Plan, and people's fondness and fascination for pollinators, grow beyond all expectations. Every Local Authority on the island of Ireland has now signed up to the Plan, agreeing to manage public land in a pollinator-friendly way. In addition, several hundred businesses are taking actions for pollinators, along with countless community groups, sports clubs, schools and other organisations. Of course, actions that benefit pollinators often benefit other insects too, which given the biodiversity and climate crises we are currently experiencing has never been more important. I also co-founded Natural Capital Ireland, a not-for-profit organisation that promotes the value of nature, and works to support greater understanding of our dependencies and impacts on nature.

In my current role in Trinity, I am Vice President for Biodiversity and Climate Action, and lead the development and implementation of our Sustainability Strategy. One of the learnings has been the importance of partnership and effective communication. No-one has all the answers, but by taking an evidence-based approach, educating ourselves and others to increase understanding, sharing challenges and learnings, working together, and investing strategically in resources, we can make progress. These things align very closely with the strategic priorities of the RES, and I look forward to working on the next iteration of the RES's Strategy.

So, a massive thank you to Jane Hill for everything, and I look forward to my term as RES President, and to kicking it off by seeing many of you at Ento24 in Liverpool!

Prof. Jane Stout
RES President Elect

RESEARCH SPOTLIGHT

The noisy, deceptive ultrasonic world of moths and bats

Bats are a menace to night-flying moths

This Research Spotlight focuses on how moths defend themselves from predatory bats, not only by avoiding flying when bats are active, but adopting stealth body coverings, 'listening in' to bat calls, and even actively interfering with the predator's echolocation system. Astonishingly, some moths even send threatening messages to the predators using the bats' own ultrasonic hearing channel. Müllerian mimicry explains why many of these

moths not only look alike but sound alike too. Fascinatingly, some moth species dishonestly parasitise the same communication system by emitting fake warning calls through Batesian mimicry. Welcome to the complicated and noisy adversarial world of bats and moths!

Bats and moths

If you were a moth, you would be worried about bats, most of which are predators of nocturnal flying insects, many being moth specialists; more than 70% of insects consumed by the bat *Miniopterus schreibersii* are lepidopterans, with noctuid moths the most frequently consumed prey (Aihartza *et al.,* 2023). Individual bats can eat as much as 85% of their own body mass in insects every day (Kurta *et al.,* 1989). At peak hunting times,

individual hawking bats may attack a moth as frequently as once every 4–5 s, with a success rate of 30–40% (Kalko, 1995). All of this shows that bats are a menace to night-flying moths.

Bats hunt in the dark; living in a sensory world that is dominated by hearing, they orient their flight, detect obstacles, and most importantly locate their insect prey by repeatedly emitting pulses ('clicks') of loud (~125 dB) ultrasonic sounds from their larynx, detecting reflected soundwaves using ears tuned to the frequencies of their own calls (Jones *et al.,* 2007). Ultrasonic echolocation for navigation and predation has proved a remarkably successful predatory strategy. It was probably already in use by the first bats, which appeared around 64 MY ago (Thiagavel *et al.,* 2018; Hand *et al.,* 2023); since then, bats have

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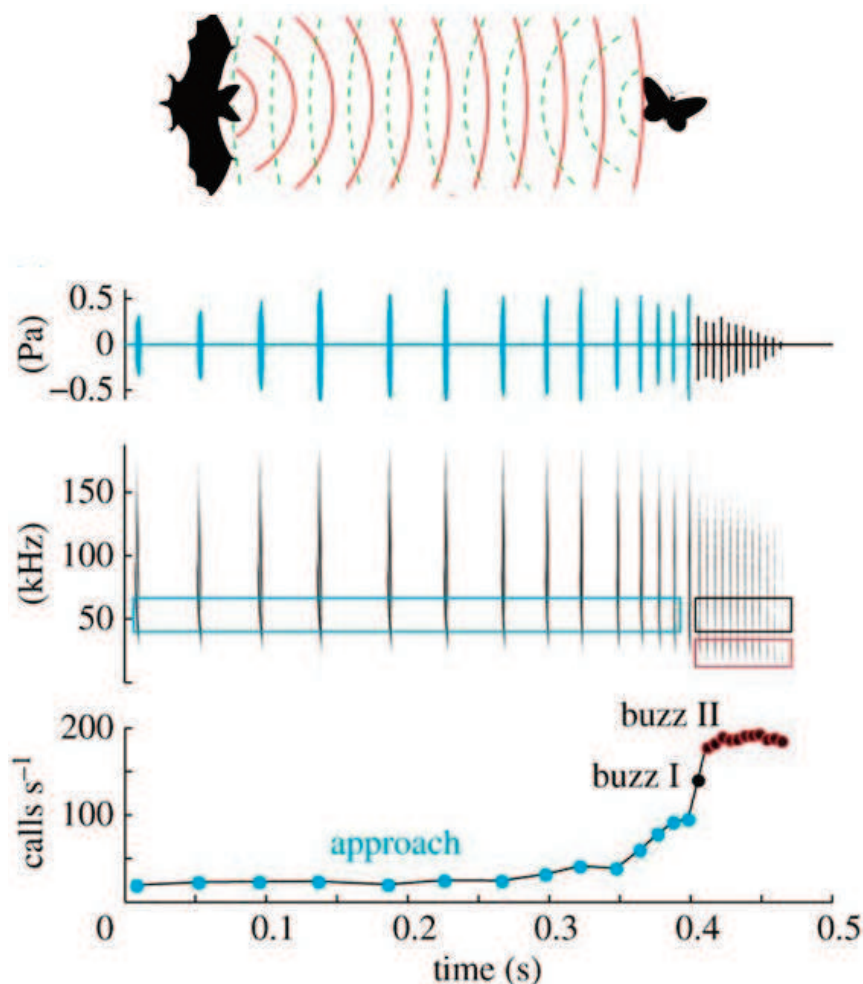(s.e.reynolds@bath.ac.uk)

Fig. 1. Echolocation calls as a bat approaches and prepares to seize a moth. From top, cartoon of echolocation principle (red, bat-emitted calls; green, reflected sound from target); sound pressure oscillogram of emitted call; frequency distribution spectrogram; pulse frequency. Data for *Myotis daubentonii* from Ratcliffe *et al.* (2013), reproduced with permission.

proliferated so greatly that there are now more than 1,400 species, representing about 20% of all mammals (Hao *et al.*, 2023).

Key features of bat echolocation calls are illustrated in Fig. 1. A notable feature in almost all bats is the gradual increase in the calling frequency during the pursuit of a flying insect, culminating in a terminal 'buzz' during the final approach, when the frequency of ultrasonic pulses rises sharply to 100–200 calls s^{-1} (Ratcliffe *et al.*, 2013). This enables an observer with ultrasonic hearing to follow the progress and possible success of a bat's pursuit of a moth. Such observers include not only scientists, but also other

bats, and (as we shall see) the moths themselves.

Defensive strategies: time of flight

The majority (~80%) of moths are nocturnal; the remaining ~20% of species have evolved to fly in the day, mitigating the nighttime predation pressure exerted by bats. Phylogenetic analysis indicates that although the earliest lepidopterans were probably diurnal, there was an early (250 MY bp) transition to nocturnality in the ancestor of all heteroneuran families (the vast majority of today's Lepidoptera). This switch was successful because it took place when there

were no echolocating bats and enabled avoidance of daytime predators (lizards or dinosaurs, presumably - too early for birds), but with the advent of echolocating bats, nighttime risk increased sharply. Since then, more than 40 separate reversions to daytime activity have occurred, probably to allow moths to escape bats (Kawahara *et al.*, 2017). The best-known diurnal Lepidoptera are of course butterflies (Papilionoidea), but many other moths fly during the day. Even so, life in the light is not completely safe. Specialist avian predators of flying insects include swallows and martins (Hirundinidae), swifts (Apodidae), and Old World and New World flycatchers (respectively Muscicapidae and Tyrannidae), not to mention aerial predatory insects such as dragonflies (Odonata), robber flies (Asilidae), and hornets (Vespinae).

Acoustic invisibility

Since most moths remained active only at night, new strategies to avoid bats must have been needed by night-flying moths. One partial solution was to become less visible to bat echolocation calls by absorbing incoming ultrasonic sound, effectively reducing the distance from which moths can be 'seen'. This soundproofing relies on a unique asset of lepidoptera, the overlapping array of scales that covers the body and wings.

Lepidopteran scales have long been known to provide thermal insulation (Grodnitsky *et al.*, 1991) as well as visual camouflage or conspicuous display (Mouchet *et al.*, 2018); moreover, the easy detachability of scales makes moths slippery and hard to catch (Eisner *et al.*, 1964). We now know that moth scales also constitute a 'stealth' coating of soundproofing metamaterial, which strongly absorbs incident sound energy (average 67%) over a wide range (20–160 kHz) of ultrasonic frequencies (Neil *et al.,* 2020a). The ultrathin moth scales are

The moths that are most at risk of being predated by bats are also those best equipped to hear the calls of their enemies

individually tuned (Shen *et al.*, 2018) and broadband sound absorption is achieved by using a wide variety of scale architectures. Thoracic scales are more diverse in size and shape than wing scales and soak up ultrasound even more efficiently (Neil *et al.*, 2020b), directing attention away from the moth's vulnerable thorax and abdomen, towards the wings. Scale-mediated anti-bat soundproofing is more strongly absorbent in larger moths, which would otherwise be more easily detected by bat sonar (Simon *et al.*, 2023).

Ultrasonic sound absorption by scales is now known to be widespread in night-flying species right across the Lepidoptera (Simon *et al.*, 2023), but interestingly, the wing scales of butterflies (not under selection pressure from bats) are much less efficient absorbers of sound than those of nocturnal moths (Neil *et al.*, 2020a).

The ears of bats

A defensive strategy against bats used by many moths is to monitor the bats' own echolocation system. Almost 150 years ago, White (1877) speculated that some moths had anatomical structures that looked like ears, whose function was to detect bats. Early attempts to confirm this (e.g., Turner *et al.*, 1914) were frustrated by the fact that moths do not readily react to sound frequencies audible to humans. The key to progress was the realisation by Griffin *et al.* (1941) that bat clicks utilise short pulses in which almost all the acoustic energy is ultrasonic, i.e., they use sound frequencies higher than those that can be heard by humans (Fig. 1). Fifteen years later, Haskell *et al.* (1956) discovered that some moths have specialised ears (tympanal organs) that detect ultrasonic sound. They have a very simple structure with a small number of sensory neurons (derived from ordinary stretch receptors) embedded in a tightly stretched membrane over an air-filled cavity (Neil *et al.*, 2021); the range of frequencies of sound that stimulate these sense organs is similar to that used by echolocating bats (Fig. 2).

Today, we know that all the most diverse families of
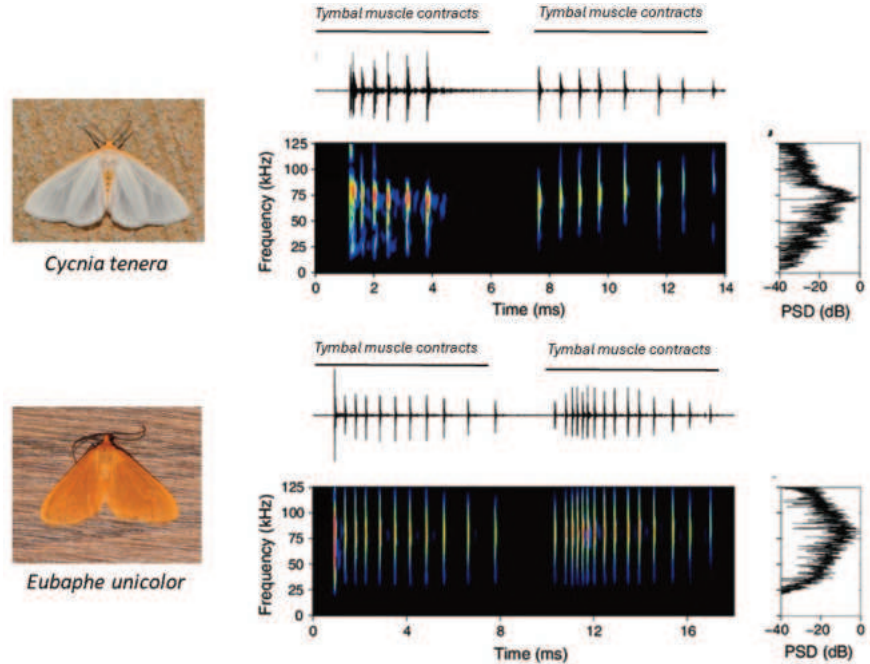
Fig. 2. Moth defensive sounds. *Top*, the Dogbane Tiger, *Cycnia tenera* (Arctiinae) emits aposematic clicks that convey an honest warning signal of its distastefuness. Below, the Orange Beggar, *Eubaphe unicolor* (Geometridae) produces a similar pattern of clicks that are Batesian mimics of those of *C. tenera* and other chemically defended arctiids, thus sending a dishonest warning signal. For each species, the figure shows (middle top) sound intensity oscillogram of the on- and off-phases of the tymbal sounds; (middle below) spectral composition; (right) power spectral density. Images: *C. tenera* by Andy Reago & Chrissy McClarren, CC BY 2.0; *E. unicolor* by Laura Gaudette, CC BY-SA 4.0.

Fig. 3. The Lucerne Moth, *Nomophila nearctica* (Crambidae). Image by Eugene Zelenko. CC BY-SA 4.0.

macromoths are able to hear. Moths equipped with ultrasonic ears have been shown to take evasive action (e.g., to fly erratically, or cease flying altogether) when they hear the predator's ultrasonic clicks. A nice example is the Lucerne Moth, *Nomophila nearctica* (Crambidae) (Fig. 3), which detects and avoids the calls of a hawking bat long before it is close enough to be targeted (Nakano *et al.*, 2018).

Being able to hear a bat echolocation call makes it possible for a moth to react evasively to bat calls, either by getting out of the way, or if not already airborne, staying on the ground (Nakano, 2015b). Both males and females of *Pseudaletia unipuncta* (Noctuidae) and *Ostrinia nubilalis* (Pyralidae) terminate mate-seeking behaviour when alerted to bat ultrasound (Acharya *et al.*, 1998).

Multiple independent origins of

Fig. 4. *Melese laodamia* (Arctiinae), image by Stephen Easley, CC BY–NC.

lepidopteran tympanal ears are suggested by their various different locations on moth bodies. DNA-based phylogeny of Lepidoptera (Kawahara *et al.,* 2019) confirms this, indicating that ultrasonic ears have evolved on at least 9 separate occasions, all in the most derived clades. Surprisingly, however, Lepidopteran ears apparently first arose 77.6-91.6 MY ago, a period at least tens of millions of years before the first echolocating bats. This indicates that the immediate prompt for the evolution of moth ears was not (as previously assumed) selection pressure from bat predation, but to satisfy some other need, possibly avoiding non-bat animal predators (perhaps birds), or intraspecific sexual communication, which may have involved ultrasonic signals (see below). Clearly, however, once ultrasonic ears had been invented, they would have been strongly selected by bat predation.

Naturally, evolution has ensured that those moths most at risk from bats are also the best equipped to hear the calls of their enemies. Segura-Trujillo *et al.* (2024) used DNA methods to survey moths caught by 17 species of bat in Mexico; they note that the families of moths most often eaten by bats all possess ultrasonic ears. That bats eat mostly eared moths is not because they are more vulnerable (as we shall see, they are actually less at risk), but simply because these are the species that fly in the dark. Moths without ears are not only less diverse, but they are also more diurnal, presumably being excluded from the nighttime environment by the threat from bats.

Passive defensive sounds of moths

Many moths go beyond mere avoidance and reply to the predators' calls by emitting their own ultrasonic signals. That some arctiid moths emit audible clicks when disturbed was first noticed by Carpenter (1938), the sound being produced by paired abdominal air-filled cavities underlying a region of thin surface cuticle, subsequently termed 'tymbal organs' by Hinton (1955). It was then discovered by Blest *et al.* (1963) that in the Central American arctiid, *Melese laodamia* (Fig. 4)*,* the clicks produced by the moth's tymbal organ are bursts of 1-20 sound pulses of substantial ultrasonic content, with most energy content being at 30-90 kHz. Although the best studied examples are tiger moths (Arctiinae), the production of ultrasonic calls by night-flying lepidopterans is widespread across the order. Moths from other families, e.g., Geometridae (Corcoran *et al.*, 2014a) and Sphingidae (Barber *et al.*, 2013) also have tymbal organs and use them to make similar sounds with a proven defensive role, and it has recently been estimated that as many as 20% of Macroheterocera (higher moths) emit ultrasonic sounds (Barber *et al.*, 2022); this would represent more than 30,000 species of moth.

What is the function of these bat-evoked clicks? Many insects produce defensive sounds in the presence of predators (Low *et al.*, 2021). The evoked noises (not necessarily ultrasonic) are startling to the predator and may potentially cause it to miss its target. They are effective as anti-predator devices simply because they are unexpected, loud and distracting. The visual equivalent of such sounds is usually called a 'startle display' or deimatic behaviour (Drinkwater *et al.*, 2022), in which a previously concealed bright colour is suddenly revealed on disturbance; such displays occur in many phasmids, mantids and grasshoppers, as well as notably in lepidopterans such as eyed hawk-moths that display brightly coloured areas of their cuticle (Umbers *et al.*, 2015a).

It is an attractive idea to suppose that the ultrasonic defensive sounds of moths may have first evolved as deimatic deterrents to predation by bats. Surprised by the sudden noise, we may suppose that the startled bat would be distracted and allow the insect to escape. But Corcoran *et al.* (2014) were sceptical that startle is ever a primary defensive mechanism against bats. They reported that startle responses are observed when first introducing arctiid moths to bats during experimental training regimes, but the predators learn quickly not to be fooled in this way. Only 1-3 trials are required for the bats to habituate to recorded clicks (Bates *et al.,* 1990) and a single trial is enough when the ultrasonic clicks come from a real moth (Barber *et al.,* 2007).

But I think that we should not abandon the idea that the first-evolved moth defences against bats may originally have been deimatic in nature; trained bat experiments of the type just described may not be a realistic model of natural bat behaviour. The missing feature is the presence of other bats. In real life, hawking bats are almost always within hearing range of others, not necessarily conspecifics, and competition for prey may be fierce. In the dark, the best evidence that an insect is nearby is the accelerating pulse train of another bat as it closes in on its intended prey. Bats are known to listen actively to the calls of their rivals, competing to be first to seize the hapless insect (Lewanzik, *et al.,* 2019). Under these more challenging conditions, the evoked moth ultrasonic calls may be more distracting than when only one bat is present at a time. Nevertheless, however the first bat-evoked ultrasonic clicks of moths arose, it is certain that early in their evolution they acquired additional features that enabled them to outwit questing bats.

Aggressively defensive sounds

Another effective way for moths to ward off bat attacks is actively to interfere with the predator's echolocation system, by flooding the bat's auditory input of reflected ultrasonic sounds with the moth's own defensive calls. Because the bat's echolocation system relies on the estimation of distance from target by measuring the duration of the gap between the time at which a sound pulse is emitted and the time of its return as a reflected echo, the moth can 'jam' the system by emitting a loud sound of the right frequency to be heard by the bat during this brief 'empty' return phase (generally 1-2 ms) in-between the repeated pulses of the bat's echolocation calls. The theoretical possibility of 'jamming' interference of this kind was first postulated by Fullard *et al.* (1979) and was only much later shown to actually occur in Grote's tiger moth, *Bertholdia trigona* (Arctiinae) (Fig. 5), whose defensive clicks are effective in jamming the echolocation system of the Big Brown Bat, *Eptesicus fuscus* (Corcoran *et al.*, 2009). Because of the need to measure the return echo time, the echolocation calls of most bats are made up mostly of periods of silence that are briefly interrupted by pulses of ultrasonic noise, even during the accelerating final 'buzz' [i.e., these calls have a 'light duty cycle' (LDC), in which <20% of the signal's cycle is occupied by ultrasound]. Unlike the pursuing bat, however, the insect has no need to leave empty sound space, and some moths have evolved to produce 'high duty cycle' (HDC, >20%) calls, in which ultrasonic pulses are both longer and separated by relatively little 'empty' time. Moth calls of this type are very frequently made only as the bat approaches closely and are accompanied by evasive action.

In another study (Fernández *et al.*, 2022), recorded *B. trigona* defensive calls were experimentally altered by progressively increasing the length of ultrasonic pulses to leave shorter gaps, thus increasing the duty cycle from 0% to 100%. When these synthetic clicks were played back to bats during a tethered capture protocol, the ability of the bats to catch moths declined steadily as

Fig. 5. Grote's Bertholdia, *Bertholdia trigona* (Arctiinae). Image by Christian Schwartz, CC BY-NC.

the % duty cycle increased; there appeared to be no threshold value for jamming. Interestingly, as pulse width increased, the duration of the terminal buzz also increased, as though the bats were finding it more difficult to determine the location of the moth.

The jamming story as told so far is almost certainly more complicated than this. Some bats, like horseshoe bats, *Rhinolophus* spp., always use HDC echolocating pulses in which the pulses are longer, with shorter intervening gaps, than are used by LDC bat species. The reason for this is not known, but it looks as though an HDC echolocation system is harder for the moth to evade or interfere with, and two species of crambid moth, *Conogethes punctiferalis* and *Ostrinia furnacalis*, showed lower hearing thresholds for detecting bat sounds when the pulse duration of ultrasonic pulses was longer, meaning that they would be able to detect the presence of these bats when they are farther away.

At first sight, we might speculate that all moth anti-bat calls ought to use HDC rather than LDC clicks, but in fact most moth anti-bat

calls are of the LDC type. This isn't because HDC anti-bat calls are more expensive to make; their cost is insignificant (Corcoran *et al.*, 2014b). It may be that to use HDC calls would make the moths more detectable at a distance; it may also decrease the moth's ability to monitor the signals of the bat itself. This could be disadvantageous, especially when there are other bats nearby. Moreover, it may not be necessary for chemically-defended moths to use HDC signals; a highly distasteful arctiid (*Creatonotos transiens*), which uses only LDC ultrasonic signals, is still able to deter HDC-using horseshoe bats, presumably because it is recognised as being distasteful (Hu *et al.*, 2023).

Moth ultrasonic clicks and sex

A complication to this story is that some moths emit ultrasonic sound for the additional purpose of sexual signalling. Male moths from several families use very low amplitude ultrasonic 'whispers' to communicate with females at very close range (in the order of 1 cm), perhaps because this reduces the risk of the call being eavesdropped by a bat (Nakano *et al.*, 2009;

Fig. 6. Spindle Ermine moth, *Yponomeuta plumbella* (Yponomeutidae). Image: Hectonichus. CC BY-SA.

Takanashi *et al.*, 2010). Ermine moths, *Yponomeuta* spp. (Fig. 6) are examples of this (Mendoza Nava, *et al.*, 2024). Ultrasonic communication of this kind is produced not by tymbal organs, but by flexing specially modified areas of wing cuticle. These quiet ultrasonic sexual signals may occur much more widely than has so far been realised (Nakano *et al.* 2015b). To be useful, ultrasonic sounds have to be heard, and so perhaps these amorous 'whispers' may explain why moth ultrasonic ears evolved in the first place.

Some loud ultrasonic anti-bat sounds produced by tymbal organs in night flying macromoths also appear to have sexual significance. The HDC clicks produced by *B. trigona* males are required for successful mating, females of this species preferring to mate with males producing calls with higher duty cycles (Fernandez *et al.*, 2020). This appears to be an example of sexual selection of a costly heritable trait (ultrasonic sound production). Noisy male moths are telling choosy females that they can produce high quality bat-deterrent signals, indicating their desirability as reproductive partners. This raises the question of whether the ultrasonic acoustic signals of moths might in some cases be subject to a trade-off between mating competitiveness and the ability to deter bats.

The aposematic warning sounds of tiger moths

The most intensively investigated acoustic defences of moths against bats are those that are produced when the moth takes the offensive, conveying to a potential predator the message "Don't eat me, or you'll be sorry". Signals like this can be described as 'warning sounds' and are the acoustic analogue of the more familiar 'warning colours' (Caro *et al.,* 2019); both are advertisements which serve to inform potential predators that the intended victim is protected by distasteful or toxic chemicals, such that any attempt to attack and eat the prey species is likely to prove an unpleasant, probably costly experience. The original idea of warning coloration, first announced in a private letter to Charles Darwin and then published anonymously, was that of Alfred Russel Wallace (1867). Warning sounds and colours are both now recognised as examples of the general class of 'aposematic signals' (Poulton, 1890), which have been studied intensively by both empirical and theoretical evolutionary ecologists (see Ruxton *et al.,* 2018). Although moths from other families also employ acoustic warning signals, aposematic sound production is particularly well-developed among tiger moths (Arctiinae) (ter Hofstede *et al.*, 2016). Many tiger moth larvae feed on toxic plants and accumulate toxic pyrrolizidine alkaloids, cardenolides and some other minor chemicals from their food. Additionally, several biogenic amines including histamine and acetylcholine are synthesised *de novo* (Weller *et al.*, 1999). As is so often the case, these chemicals are highly aversive to many animals, and as they are retained by the insect during larval, pupal and adult stages, all stages are distasteful to predators.

Potential predators are notified of the insect's nasty taste by means of aposematic warning signals. Many arctiids are protected in this way both as larvae, which are often both extremely hairy and also brightly coloured, and as adults, which are frequently conspicuously patterned and coloured. An example is the Ornate Bella Moth, *Utetheisa ornatrix* (Fig. 7). Sometimes adult warning colours are readily observed both when the moth is active and at rest, but in this species (and others) the conspicuous aposematic body colour is concealed under the wings and revealed only when the wings are spread in a deimatic display.

Because bats are not visual predators, the distastefulness of arctiid adults must be communicated to the nocturnal predator in some other way. Examples of tiger moths that emit aposematic warning sounds include the Banded Tussock, *Halysidota tessellaris* (despite its name, an arctiid) and the Isabella Tiger Moth, *Pyrrharctia isabella*. That their ultrasonic clicks protect these moths was shown by Dunning *et al.* (1965), who replayed recorded moth sounds while offering a tasty insect (a *Tenebrio* mealworm) to captive bats, which

Don't eat me or you'll be sorry

were deterred by the sounds from capturing and eating the reward. By way of a control, replaying bat clicks (or playing no sound at all) had no such deterrent effect.

These results strongly suggest that the deterrent effect of arctiid anti-bat clicks is due to aposematic communication, but don't prove it (a deimatic response, for example, is not ruled out). However, forty years later, using a different arctiid, the Milkweed Tussock Moth, *Euchaetes egle*, Hristov *et al.* (2005) used diet manipulation (i.e., not feeding on poisonous milkweed) to produce moths that were not chemically defended, as well as simple surgery to remove the tymbal organs so that no ultrasonic clicks could be produced. Naïve Big Brown Bats, *Eptesicus fuscus,* were trained to take palatable non-clicking

Fig. 7. Ornate Bella Moth, *Utetheisa ornatrix* (Arctiinae), image by Laura Gordette, CC BY–SA 4.0.
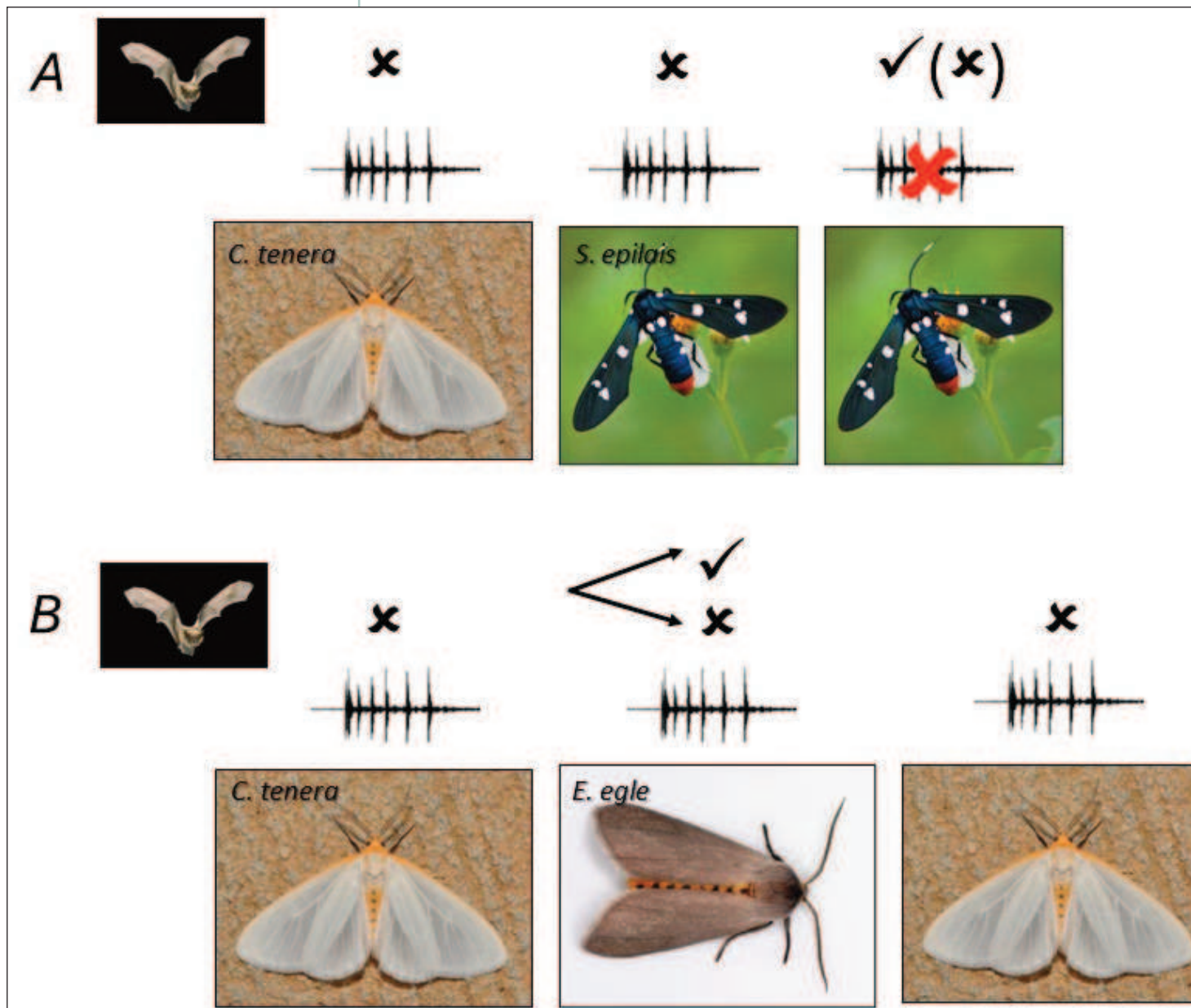
moths on the wing, and then offered experimental *E. egle* moths. The bats learned in only one or two trials to avoid intact *E. egle* moths but were unable to learn to avoid either distasteful moths that did not click, or those that clicked but did not contain unpalatable chemicals, thus establishing the link between distastefulness and warning sounds. *E. egle* produces HDC clicks capable of interfering with bat echolocation signals, so that it was theoretically possible that at least some of the deterrent effect of moth clicking could have been due to jamming. The fact that in the first day's trials, the bats initially captured and then rejected control moths (i.e., those that were chemically protected and also retained normal sound production) suggests that any jamming effect of this species is

Fig 8. Bats learn not to attack distasteful moths and their mimics because of their warning sounds. **A.** Naïve bats, *Eptesicus fuscus* and *Lasiurus borealis*, quickly learn not to attack the distasteful arctiid *Cycnia tenera*, immediately transfer this avoidance skill to another warning sound-producing distasteful arctiid *Syntomeida. epilais*, but then quickly attack surgically silenced *S. epilais* from which the sound-producing tymbals have been ablated. Because *S. epilais* is still distasteful, these moths are then rejected after being attacked. **B.** As before, naïve bats quickly learn not to attack *C. tenera*, but when offered the palatable acoustic mimic *E. egle*, some bats attack but some do not; when *C. tenera* are offered again, all the bats attack it, but when surgically silenced *C. tenera* are offered, they immediately attack it (though since it is still distasteful, it is then rejected). Results are summarised and illustrated from Barber *et al.* (2007). Images: *E. fuscus*, Angell Williams, CC BY; *C. tenera* by Andy Reago and Chrissy McClarren, CC BY 2.0; *S. epilais* by Andy Blackledge, CC BY 2.0; *Euchaetes egle* by Patrick Coin, CC BY-SA 2.5.

either ineffective or perhaps has a lesser effect secondary to that of aposematic signalling.

It's all very well doing experiments on tethered moths, but do these ultrasonic defences work as well when both the bat and the moth are free to fly without restraint? Dowdy *et al.* (2016) used multiple infra-red cameras to reconstruct the flight trajectories of moths and bats in 3-D space. As expected, they found that moth ultrasonic calls were protective; two ultrasonically signalling moths, *Pygarctia roseicapitis* (Arctiini) and *Cisthene martini* (Lithosiini), were captured significantly less often by bats if they were able to produce ultrasonic clicks, as compared with those that had been surgically prevented from doing so. The bats actively avoided the moths that emitted defensive clicks. Interestingly, the calling strategies of the two moths in response to the approach of bats were different. *P. roseicapitatis,* which is less toxic, responded earlier to bat calls, and frequently paired its clicks with evasive 'diving' behaviour. By contrast, the more distasteful species, *C. martini* was more 'nonchalant', responding with clicks to bats later in the bat's pursuit sequence, and using evasion in fewer interactions.

Warning sounds and warning colours

Most moth species producing aposematic sounds are also conspicuously coloured in both sexes as adults. Why do these moths go to the trouble of advertising their distastefulness using two different communication channels at the same time? It may be that the two different signalling modalities each have their own particular benefits. Most obviously, their benefits might be partitioned between day and night, since visual warning signals are useful in the day and are directed against predators that use vision to recognise prey, while ultrasonic aposematic sounds are only useful in deterring those predators that can hear them. Even in moths that only fly during the day, warning colours may still be useful to an immobile moth in deterring non-bat predators that seek out cryptic insect prey.
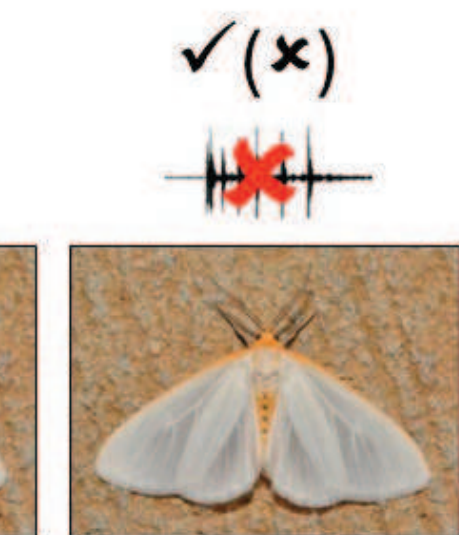
Acoustic warning signals have some advantages over other sensory modalities. These include the advantage to the prey of being audible over long distances, allowing long-range deterrence and avoiding the possible cost of being tasted and rejected. By the same token, the predator avoids the opportunity cost of wasting time on close inspection of prey. Additionally, warning sounds are transient, and thus can be directed at potential predators only when necessary (i.e., when the prey species is threatened); this reduces both the risk associated with producing the warning sound of inadvertently attracting the attention of predators not already present, and also the energetic cost of making the sound.

Mimicry: honest and dishonest warning sounds

Right from the start, much of the interest from evolutionary theorists in the topic of aposematic communication has concerned the existence of species which appear to mimic the morphological appearance of others, a topic first explored by H.W. Bates (1861) who recognised that models for mimicry are almost always actually distasteful to a wide range of predators, while those mimicking them are impostors, species that benefit from reduced predation, even though they are actually perfectly edible. This is what we call 'Batesian mimicry', in which the mimic species gains a selective free ride, not merely benefitting from a reduced rate of mortality on account of its dishonestly displayed warning coloration, but also gaining fitness through its avoidance of the expense of manufacturing or sequestering the advertised (but non-existent) toxic defences.

It was quickly recognised that the benefit to the mimic of such coloration is dependent on how quickly and completely predators learn to avoid both the model and the mimic through encounters with the distasteful species; under this condition, the persistence of mimicry in the wild must depend on the relative rarity of impostor mimics compared to the frequency with which the truly distasteful models are encountered. For an extended

Are tiger moth warning sounds honest?

review of these ideas, see Ruxton *et al.* (2018).

It is thus very satisfactory to find that just like warning colours, warning sounds appear to be highly susceptible to mimicry. An excellent example is the Orange Beggar, *Eubaphe unicolor* (Geometridae) (Corcoran *et al.*, 2014) (Fig. 8). The ultrasonic calls of this insect are very like those of arctiids, and since this moth is not chemically protected, this appears to be a case of acoustic Batesian mimicry. Appropriately, this geometrid moth even looks like an arctiid, to the extent that it was initially mistakenly identified as such by Corcoran *et al.* (2010), so that it is a visual Batesian mimic too. Because the sound-producing tymbal organ in this moth is located in the prothorax, rather than in the abdomen as in arctiids, there's no doubt at all that this moth's aposematic sounds are not homologous with those of its arctiid mimetic model.

In general, warning colours show a pronounced tendency to converge on a small number of models through both Batesian and Müllerian mimicry (Pinheiro, 2011). Is the same true of warning sounds? In principle, this is a difficult question to answer. When we say that one aposematic colour pattern is 'similar' to another, we are performing a sophisticated visual analysis using our own very complex system of colour and pattern recognition. It would be presumptuous of us humans to suppose that an animal predator would see the colour in the same way. But in the case of the ultrasonic warning sounds of moths, we can't hear them at all. Two methods are available to tackle this problem. First, we can make recordings of large numbers of sound-emitting moths and use Artificial Intelligence (AI) to assign the calls into groups. Barber *et al.* (2022) did this for a community of 33 moth species from Ecuador; they found that the sounds could be regarded as 5 different groups, which they presumed to be Müllerian and Batesian mimicry rings.

Second, and to me even more convincingly, we can ask the bats what they think about them.

Barber *et al.* (2007) trained hand-reared naïve bats using a two-part training regime in which each bat was first offered a distasteful arctiine moth, *Cycnia tenera*, which it rapidly learned to avoid. It was then offered a second unpalatable species of arctiine, the Polka Dot moth, *Syntomeida epilais*, a species that has a completely different appearance, but which utilises the same food plants and accumulates the same unpalatable chemicals as *C. tenera.* The bats immediately extended their learned avoidance behaviour from *C. tenera* to include *S. epilais* (Fig. 8A). That this was entirely explained by the ultrasonic signals emitted by these two species was shown by then offering to the same trained bats, individual *S. epilais* moths that had been surgically silenced by interfering with their tymbal organs. These moths were quickly attacked, but because they were distasteful, were then dropped. Both moths emit similar ultrasonic warning sounds and the researchers concluded that the rapid transfer of bat avoidance behaviour was due to acoustic Müllerian mimicry. But the experiment also shows that, to be maintained, such mimicry needs to be supported by the underlying chemical defences.

Barber *et al.* (2007) used the same experimental set-up to look at the transfer of learned bat avoidance behaviour from the same distasteful model species, *C. tenera*, to a different arctiid, *Euchaetes egle,* which had been fed under a regime that rendered it non-toxic and palatable. The two species both produce warning sounds, which to humans look similar on the computer screen. As in the previous experiment, when naïve bats were initially trained on *C. tenera*, they rapidly learned not to attack it. When then offered the palatable but ultrasonically similar *E. egle*, some bats quickly learned to attack and eat it, but some did not. This implies that the warning sounds of the two moths are sufficiently similar to be confused by at least some bats. When *E. egle* was again replaced in the training regime by the distasteful *C. tenera*, all the bats quickly

returned to avoiding it. Finally, when they were offered surgically silenced *C. tenera* moths, all the bats immediately returned to attacking it, even though it was distasteful and so could not be eaten (Fig. 8B). This shows that *C. tenera*'s ultrasonic warning signal can be the subject of Batesian mimicry by a 'similar' fake warning signal that is in fact empty of meaning.

Fascinatingly, tiger moth aposematic sounds can be mimicked by insects that aren't even moths. Gough *et al.* (2024) have shown that seven species of tiger beetles (Cicindelidae) that fly at night respond to playback of bat sonar calls by producing their own ultrasonic warning sounds, with multiple parameters of the calls being highly similar to those of arctiids. These beetles were readily eaten by bats in handheld feeding trials, but it isn't yet known whether the sounds would protect them from being taken in flight. By contrast, 12 cicindelid species that fly only in the day did not produce warning signals. Tiger beetles, of course, don't have moth-like tymbal organs, and produce ultrasonic clicks using their wings.

Costly aposematic signals

Evolutionary theorists have devoted much attention to aposematism, asking under what conditions warning signals can be considered to represent 'honest' signalling (Summers *et al.*, 2015). It is conventional wisdom that, under most conditions, the best indicator of a signaller's honesty is that the signal is intrinsically costly to its own fitness (Johnstone, 1995). Are tiger moth warning sounds costly, and to what extent do bats rely upon them? Again, we find that the best thing to do is to ask the bats. Although the metabolic cost of actually producing clicks seems to be negligible (Corcoran *et al.*, 2014b), arctiid warning signals are clearly costly to fitness in the sense that they inevitably make the prey more apparent to the predator. Despite emitting warning signals, tiger moths are quite likely be attacked by naïve bats that have yet to learn what the warning signal means (Barber *et al.*, 2007). Even though the

manhandled insect is subsequently dropped, there is considerable chance of harm to the moth. When Ratcliffe *et al.* (2005) experimentally prevented *C. tenera* moths from issuing warning sounds, so that they were captured but then dropped by bats, 25% of the moths were seriously damaged.

These considerations don't enable us to predict the actual cost of signalling in a real field population of intact ultrasonically active moths, but the probability of harm must surely be greater than zero. According to evolutionary signalling theory, then, bats have good reason to think that the moths are being honest when they warn the bat that it may be sorry if it eats them. But the same experiments by Barber *et al.* (2007) also show that bats learn quite quickly when a palatable moth is pretending to be distasteful. This appears to mean that bats *mostly* trust the warning signals of night-flying moths, but every now and then they check, just to be sure.

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