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# Predator–prey interactions between gleaning bats and katydids

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## Abstract

Bats are voracious predators of insects, and many insects have ears sensitive to the high-frequency echolocation calls of bats. Eared insects show a variety of defences when they detect bat echolocation calls. Professor Brock Fenton was an early contributor to the field of bat–insect interactions, inspiring many students to pursue investigations that have advanced our understanding of the relationship between predators and prey. Reflecting on the integrative nature of Dr. Fenton’s research, this review highlights research on the evolutionary arms race between gleaning insectivorous bats and katydid prey. Studies on this system have enhanced the field of sensory ecology by illuminating how animal auditory systems can encode and distinguish between signals that overlap in their acoustic properties but have very different consequences for the listener (sex or death). These studies also inform us about the ecological and evolutionary selection pressures on signalers and receivers that can shape mate attraction and predator avoidance behaviour. In particular, many Neotropical katydids rely on preventative instead of reactive defences against gleaning bats, likely due to the regular presence of echolocation calls from non-gleaning bats that reduce the information content of predator cues. We conclude with suggestions for future research on these fascinating animals.

**Key words:** biosonar, Chiroptera, echolocation, evolutionary arms race, hearing, sensory ecology, Tettigoniidae

## Introduction

Research on the interactions between bats and insects has a long history of integrating neurophysiological, behavioural, and ecological approaches (ter Hofstede and Ratcliffe 2016). The studies of Professor M. Brock Fenton have been instrumental in advancing, and inspiring others to advance, this field of study. Early in Dr. Fenton’s career, discoveries by insect electrophysiologist Kenneth Roeder with assistance from entomologist Asher Treat had demonstrated that many moth species have tympanal hearing organs (i.e., ears) to detect bat echolocation calls. Most bats orient in the dark using echolocation, which involves producing high-frequency calls and listening for the echoes that return from surrounding objects (Griffin 1958). Echolocation calls are typically ultrasonic (>20 kHz), meaning higher than the average human range of hearing (audio sound: 0.02–20 kHz). When stimulated with ultrasound, free-flying moths performed evasive flight manoeuvres that enabled them to avoid being captured and eaten by bats. It was also known that some arctiin moths had evolved tymbal organs capable of producing ultrasonic click trains when stimulated with bursts of ultrasound, with the possibility that the clicks served as a warning signal to bats that their prey was distasteful.

Two of Fenton’s early contributions to the field of bat–insect predator–prey interactions were both with Roeder. First, they reported on the auditory sensitivity of herald moths (*Scoliopteryx libatrix* Linnaeus, 1758) found hibernating at the entrances to caves and mines that were bat hibernacula. The ears of hibernating moths remained highly sensitive to ultrasound, yet during stationary flight in the lab most did not react or display a turning tendency when stimulated with ultrasound (Roeder and Fenton 1973). They also described variation in the anatomy of the sound-producing tymbals of several arctiin moths (Fenton and Roeder 1974). James Fullard, an early graduate student of Fenton’s, was fascinated with arctiin moth sound production in response to tactile and acoustic stimulation and the use of clicks as a possible defense against echolocating bats (Fullard 1977a, 1977b; Fullard and Fenton 1977; Fullard et al. 1979). Fullard subsequently learned electrophysiology to study hearing in Lepidoptera as an adaptation for detecting echolocation calls of sympatrically foraging bats and mediating escape behaviour (Fullard 1987). Together, Fullard and Fenton greatly advanced the understanding of bat–moth predator–prey interactions (Fenton and Fullard 1979, 1981) and later became invaluable mentors, colleagues, and friends to both authors.

## The bat–insect arms race: diverse problems and solutions

Most insectivorous bats hunt insects in flight using echolocation (Griffin 1958; Grinnell et al. 2016). Many flying insects have ultrasound-sensitive ears that allow them to hear bat echolocation calls and then deploy evasive manoeuvres to avoid predation (Yager 2012; Conner and Corcoran 2012; ter Hofstede and Ratcliffe 2016), known more generally as an acoustic startle response (Hoy 1992). In-flight evasion can include negative phonotaxis (i.e., directional flight away from the sound source; Roeder 1962), diving or looping flight that is difficult for bats to follow (Yager et al. 1990; Ghose et al. 2009; Corcoran and Conner 2016), or a combination of the two (Corcoran and Conner 2012). Evasive manoeuvres statistically increase the probability of an insect escaping a bat attack (Acharya and Fenton 1999; Corcoran and Conner 2016). For example, eared moths that detect and attempt to evade a bat increase their chances for survival by 40% (Roeder 1967). In turn, some bat species produce echolocation calls with acoustic properties that reduce their conspicuousness to eared prey. For example, some bats call at frequencies that are above or below insects' typical range of best hearing (Fenton and Fullard 1979; Faure et al. 1990; Jacobs and Bastian 2016) or produce quiet echolocation signals that allow bats to sneak up on their prey (Goerlitz et al. 2010; Corcoran and Conner 2017). Red bats (*Lasiurus borealis* Müller, 1776) are known to intercept moths when they show evasive flight in response to another bat's calls, and some bats even re-attack the same moth when it is in this vulnerable state (Reddy and Fenton 2003).

A variety of non-evasive defences have also been documented in insects. Before resorting to evasion, some eared moths produce ultrasonic clicks in response to bat echolocation calls (Fullard and Fenton 1977; Barber et al. 2022), and these sounds might serve to startle the bat (Bates and Fenton 1990), warn the bat of its toxicity (Acharya and Fenton 1992; Hristov and Conner 2005), or even jam its echolocation (Corcoran et al. 2009). Some insects that lack ears continuously produce these clicks in flight to ward off bats (O'Reilly et al. 2019; Krivoruchko et al. 2021), have scales on their wings that reduce the reflection of ultrasound (Neil et al. 2020), or have wings with conspicuous but disposable appendages that act as decoys for bat attacks (Rubin et al. 2018). The prevalence and diversity of insect defences is a testament to the significant evolutionary selective predation pressure exerted by insect-eating bats in flight.

Not all bats, however, catch their prey in the air. Gleaning bats capture prey from surfaces, such as plants or the ground (Fiedler 1979; Arlettaz 1996). To locate prey, some gleaning bats use echolocation (Fenton et al. 1983; Schumm et al. 1991; Geipel et al. 2013), whereas many others use passive listening to localize prey-generated sounds (Bell 1982; Ryan and Tuttle 1987). Prey-generated sounds can include incidental noises, such as rustling sounds generated by animals moving through (Fullard 1988; Goerlitz et al. 2008) and (or) fluttering on vegetation (Faure and Barclay 1992). Other prey-generated sounds include communication signals, such as the calling songs of Orthoptera (e.g., crickets and katydids; Walker 1964).

When studying gleaning bats earlier in our careers, both of us were curious if a diverse suite of defences exists among insects that are at risk from gleaning bat predation, as seen for insects in flight. For example, some perched tympanate moths respond to loud pulses of ultrasound by ceasing movement and tucking their body and wings closer to the substrate, behaviours that could render the moth less conspicuous to substrate-gleaning bats (Werner 1981).

In the anti-bat defenses described above, we see examples of both reactive defenses (i.e., those requiring the ability to detect the predator and respond to its cues) and preventative defenses (i.e., those that function at all times and without the need to detect a predator). We were curious whether insects show both reactive and preventative defences against substrate gleaning bats, and more generally, which selective pressures favour the use of reactive versus preventative defences in animals. We studied katydids (Orthoptera: Tettigoniidae) because (1) males produce loud and repetitive calling songs in many parts of the world (see chapters in Bailey and Rentz 1990), putting them at risk of predation by eavesdropping gleaning bats (Belwood and Morris 1987), and (2) evidence of potential reactive (Sales and Pye 1974; Spangler 1984) and preventative (Belwood 1990) defenses had been reported from a variety of katydid species. These earlier publications were inspirational to our work on katydids and their interactions with gleaning bats.

## Reactive defences by katydids against gleaning bats

Male katydids produce a loud mate-calling song to attract females by rubbing together specialized sound-producing structures on their forewings. Many katydid species produce high-frequency or ultrasonic calls (Heller et al. 2015; ter Hofstede et al. 2020; Tan et al. 2023), so it is not surprising that they can also hear ultrasonic frequencies (Schul and Patterson 2003; Römer et al. 2008). Katydids possess a pair of tympanal hearing organs on their forelegs. The tympanal membranes of each ear vibrate in response to airborne sound. Tympanal movement is transduced by receptor cells into action potentials (i.e., spikes), which are physiological signals that travel through neurons, allowing them to communicate with each other and target tissues. The auditory nerve of katydids, containing axons of the receptor cells, runs through the front legs, and the receptor cells communicate with interneurons within the central nervous system. Interestingly, many katydids possess extensions of the cuticle (cuticular pinnae) that form air-filled cavities around the ear. New research on the function of these cuticular pinnae suggests that they evolved to enhance detection of bat echolocation calls (Pulver et al. 2022).

Experiments on individuals of several katydid species have demonstrated that they can hear bat echolocation calls when bats are ~13–30 m away (Schul et al. 2000) and exhibit evasive flight manoeuvres in response to pulses of ultrasound or simulated bat echolocation calls (Libersat and Hoy 1991; Schulze and Schul 2001). Early field recordings showed that some katydids also pause singing when bats fly overhead (Sales and

Pye 1974; Spangler 1984), and Spangler (1984) confirmed that this was a reaction to ultrasound using playback experiments in the field. Is song cessation in katydids also a reactive defence against gleaning bats? Could it be the in-flight response expressed in another context? To address these questions, we studied the North American katydid, *Neoconocephalus ensiger* (Harris, 1841). This species is particularly interesting because its calling song is broadband, containing both audio (<20 kHz) and ultrasonic ( $\geq 20$  kHz) frequencies, hence ambiguity exists in the biological significance of ultrasound (i.e., is the sound from a mate or predator; for a discussion on stimulus ambiguity and decision-making in a predator-prey context, see Leavell and Bernal 2019). A previous study showed that in response to ultrasound pulses, flying *N. ensiger* fold their wings over their back, which would cause the insect to lose altitude (i.e., dive) when in flight (Libersat and Hoy 1991). Flight cessation was temporary, with an average duration of 260 ms and a range of 50–500 ms (Libersat and Hoy 1991). Faure and Hoy (2000a, 2000b, 2000c, 2000d) conducted a series of experiments to assess whether singing male *N. ensiger* would show song cessation to acoustic stimulation and the possible sensory basis for this startle response.

The mate-calling song of *N. ensiger* consists of a 30 ms syllable (pulse of sound) repeated every 70 ms (Faure and Hoy 2000a). The syllable period (i.e., time from the start of one syllable to the start of the next) of *N. ensiger*'s song is highly stereotyped (coefficient of variation  $\sim 2.5\%$ ), hence period deviations are easy to detect. Faure and Hoy (2000a) reported that singing males did not startle when presented with a train of pulsed audio sound but reliably did so to pulsed ultrasound with either cessation of singing or song pausing (i.e., a lengthening of the syllable period immediately following stimulation). Song pausing and cessation occurred only when the arriving ultrasonic stimulus did not overlap in time with the production of a stridulatory syllable, with a startle reaction time of ca. 20–50 ms. The functional significance of these behaviours is straightforward: in response to ultrasound, male *N. ensiger* either stop singing so that they no longer emit a signal that could be localized by an acoustically orienting predator, or they insert a brief (<1 s) gap in their calling song so that they can listen and monitor their environment. Cessation of singing was defined as an interruption in mate-calling lasting  $\geq 1$  s, but clearly this behaviour falls along the same continuum as song pausing.

Cessation of singing and cessation of flight are two types of ultrasound-mediated acoustic startle responses in katydids that presumably enhance survival in the individuals performing the behaviours. While cessation of singing can last much longer than cessation of flight (Libersat and Hoy 1991; Schulze and Schul 2001), sound production and flight involve many of the same muscles, motor neurons, and neural networks that control katydid wing movements (Josephson and Halverson 1971; Elder 1971). A shared physiological basis for these two startle behaviours suggests that behavioural context allows katydids to categorize and respond to sound stimuli appropriately. Interestingly, cessation of singing and cessation of flight have comparable intensity thresholds and similar frequency tuning curves (Faure and Hoy 2000a). This close correspondence between behavioural tuning curves

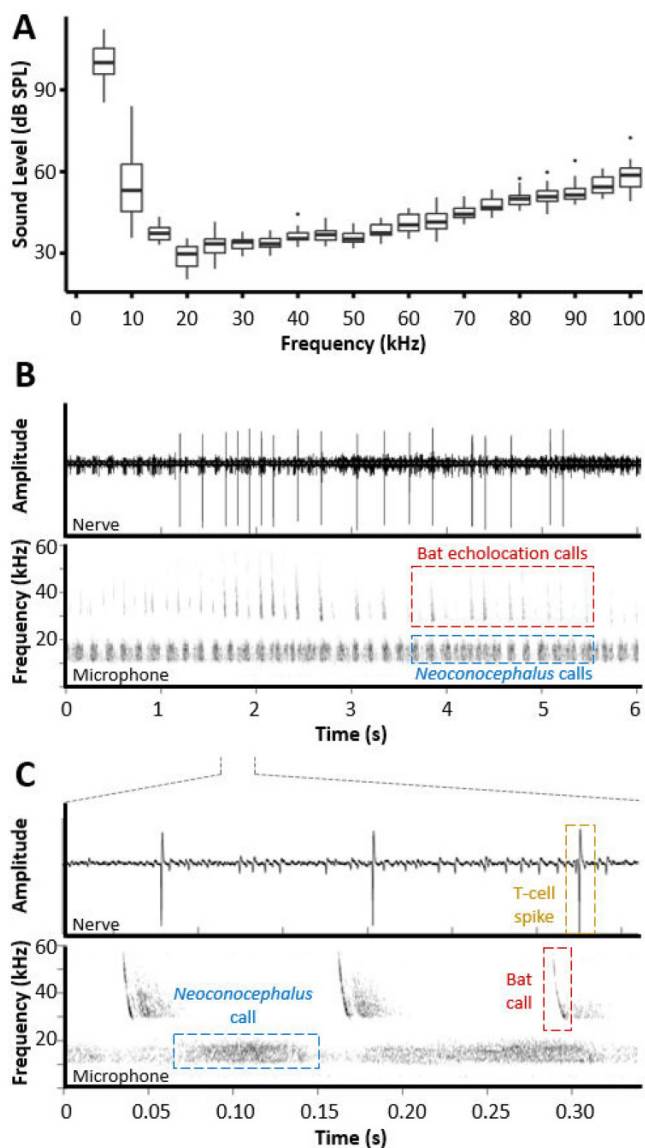
suggests that a similar mechanism may be common to both types of startle behaviour.

Flying and singing *N. ensiger* rarely startle when listening to conspecifics but consistently do so when presented with bat-like ultrasound (Schul 1997; Schul and Schulze 2001; Faure and Hoy 2004). This raises an important question: how does the central nervous system of *N. ensiger* distinguish conspecific song, which contains ultrasonic frequencies, from bat ultrasound so that the appropriate behaviours of mate attraction and predator avoidance are correctly performed? To understand this ability, a series of neurophysiological studies recording from a large auditory interneuron called the T-cell (TN-1 neuron) were conducted. Faure and Hoy (2000b, 2000c, 2000d) measured T-cell thresholds across frequencies and T-cell activity in male and female *N. ensiger* in response to pure tones, conspecific song, and bat-like echolocation sounds at behaviourally relevant durations and rates. As summarized below, these, and parallel studies on katydid species in Europe (Schul 1997; Schul and Schulze 2001), found that the responses of the T-cell likely play a major role in distinguishing conspecific song from predatory bat ultrasound, as well as in mediating the acoustic startle responses of flying and singing katydids (Faure and Hoy 2004).

The T-cell of *N. ensiger* is quite sensitive, with a low threshold and broad spectral tuning that overlaps with the frequency ranges of conspecific sound and the echolocation frequencies emitted by North American bat species (Fig. 1A; Faure and Hoy 2000a; ter Hofstede and Fullard 2008). The T-cell is directionally sensitive, with lower thresholds when a speaker is positioned  $90^\circ$  relative to the main body axis compared to  $0^\circ$  (Faure and Hoy 2000b). T-cell tuning in juveniles, which cannot fly, was similar to adult katydids, and such precocious ultrasound sensitivity is consistent with the notion that the neuron functions to detect terrestrial sources of ultrasound (i.e., predators). There were also several ways that the T-cell responded differently to pulses of 15 kHz, which mimics the peak frequency of conspecific song, compared to pulses of 40 kHz, which mimics the peak frequency of a bat echolocation call (Faure and Hoy 2000c). First, 40 kHz pulses elicited more spikes per pulse with increasing sound amplitude, and at shorter spike latencies (the time between the start of the pulse and the first spike), than 15 kHz pulses. Second, the T-cell responded with more spikes at 40 kHz compared to 15 kHz in response to sound pulses  $\leq 10$  ms in duration, which are typical durations for bat echolocation calls. Third, the T-cell reliably responded to each pulse of 15 kHz and 40 kHz sound at low repetition rates (e.g., 5 pulses/s), but at higher repetition rates (e.g., 20 or 30 pulses/s), typical of bat echolocation sequences, it reliably responded to each pulse at 40 kHz, but only sporadically responded, or even stopped responding, to each pulse at 15 kHz. Lastly, over long duration (3 min) playbacks of conspecific song or downward frequency modulated (FM) sweeps (80 to 30 kHz) like those of a bat, the T-cell responded more consistently to each sound pulse, with more spikes per sound pulse, and at shorter and more consistent latencies for bat-like sounds than conspecific calls, especially in male katydids (Faure and Hoy 2000d). Altogether, these neurophysiological studies reveal that T-cell responses in *N. ensiger* may be sufficient for distinguishing between



**Fig. 1.** Threshold tuning and T-cell auditory interneuron responses to bat echolocation and conspecific song in the katydid *Neoconocephalus ensiger*. (A) Neural audiogram of the T-cell showing median thresholds (i.e., the lowest sound amplitude to elicit action potentials) for frequencies between 5 and 100 kHz (box: 25th and 75th percentiles; whiskers: 0 and 100th percentiles; dots: outlier data points). Data from [ter Hofstede and Fullard \(2008\)](#). (B) Extracellular recording from the cervical connective of *N. ensiger* in the field showing large T-cell action potentials (top panel) in response to environmental sounds (bottom panel: spectrogram of field microphone recording). Note how the large T-cell spikes (yellow box) occur only in response to the short-duration downward (60 to 30 kHz) FM sweeps of an echolocating bat flying overhead (red box). Sounds between 10 and 20 kHz, which are the calls of other singing male *N. ensiger* recorded in the field (blue box), do not evoke T-cell spikes. Unpublished data from HMT. (C) Time expanded section of panel (B) showing close correspondence between bat echolocation calls (red box) and large T-cell spikes. Also visible are the small spikes of an unidentified auditory neuron that appears to respond to *N. ensiger* song (blue box).



important classes of biological sounds associated with mate attraction and bat avoidance ([Faure and Hoy 2004](#)).

Further studies from Johannes Schul and colleagues on *Neoconocephalus* spp. identified an additional property that makes the T-cell ideal for detecting bats in noise: it acts as a “novelty detector” ([Schul and Sheridan 2006](#); [Schul et al. 2012](#)). In response to continuous noise, such as a chorus of male katydids singing, the T-cell rapidly habituates (stops firing in response to the sound), but if a sound occurs at a different frequency, the T-cell will respond selectively to this deviant sound. The greater the difference in frequency between noise and isolated pulses of sound, the more reliably the T-cell can encode the pulses of sound in noise. Since most of the background noise in a chorus of *Neoconocephalus* katydids or a tropical forest at night is below 20 kHz, this property of the T-cell allows it to “tune out” repetitive noise and remain sensitive to the occasional ultrasonic echolocation calls of bats ([Fig. 1B, 1C](#)).

## From the laboratory back to nature

Further studies investigated whether cessation of singing and (or) song pausing in *N. ensiger* occur under natural conditions and in response to natural stimuli—the echolocation calls of an insectivorous bat *Myotis septentrionalis* (Trouessart, 1897), which is the only specialized gleaner bat species that is sympatric with *N. ensiger* in the northern part of its range ([Caceres and Barclay 2000](#); [Cigliano et al. 2023](#)). Prey-generated cues, such as the sound of fluttering moth wings, are used by *M. septentrionalis* to detect and locate prey when gleaner ([Faure et al. 1993](#); [Ratcliffe and Dawson 2003](#)). The echolocation calls produced by this bat when gleaner are significantly lower in amplitude than when flying in the open or capturing insects in flight ([Miller and Treat 1993](#)), and the tympanate ears of moths are relatively insensitive to detecting their echolocation calls ([Faure et al. 1993](#)). This raised the question of whether *N. ensiger* is even capable of hearing the calls of this bat species at natural amplitudes. To replicate natural conditions and predator cues, [ter Hofstede and Fullard \(2008\)](#) used the echolocation calls of *M. septentrionalis* recorded during a gleaner attack in acoustic playback experiments with singing *N. ensiger*. The katydids were tested in screen cages next to screen windows instead of an anechoic chamber, which allowed them to experience natural temperatures and acoustic background noise during experiments. This study confirmed that *N. ensiger* pause and cease singing in response to gleaner bat echolocation calls at natural signal amplitudes ([ter Hofstede and Fullard 2008](#)).

For song cessation to be a defence against gleaner bats, it must be shown that (1) sympatric gleaner bats use calling song as a cue to locate katydids as prey and (2) song cessation can prevent the attack of a gleaner bat. To test whether this is true, [ter Hofstede et al. \(2008\)](#) conducted playback experiments with wild-caught *M. septentrionalis* in a flight enclosure. The bats flew to singing *N. ensiger* or speakers broadcasting katydid calling song, but they ignored silent katydids. The number of bats responding to katydid calls increased over the season, suggesting a possible effect of increasing familiarity with this prey sound. If the playback of *N. ensiger* song was stopped as bats approached within 2 m of the speaker,

the bats did not land on the speaker. The results from this study confirm that song cessation can be an effective defence against gleaning bats.

## Preventative defences by katydids against gleaning bats

Although eavesdropping gleaning bats are found throughout the world (Fenton et al. 1983; Ratcliffe et al. 2005; Jones et al. 2011; Prakash et al. 2021), the Neotropics appears to have a comparatively rich and abundant community of these predators (Denzinger et al. 2018). Within the Order Chiroptera, the family Phyllostomidae, endemic to the Neotropics, is the most diverse bat group in terms of diets and feeding strategies (Leisler-Miller and Santana 2020). Many phyllostomid species glean insects from plants and many of these species can coexist in the same area of forest. For example, of the 76 bat species documented on Barro Colorado Island (BCI) in Panama, 11 (14%) are thought to use prey-generated sounds to locate prey (Denzinger et al. 2018), and at least eight of these species include katydids in their diet (Belwood 1988; Römer et al. 2010; ter Hofstede et al. 2017). Based on predator exclusion experiments in Panama and Mexico, gleaning bats eat as many or more arthropods at night as birds do during the day and contribute significantly to the reduction of herbivory in the forest (Kalka et al. 2008; Williams-Guillén et al. 2008). Experiments with captive bats demonstrate that the calling song is sufficient for many of these bat species to locate katydids (Falk et al. 2015). Together, these studies show that Neotropical gleaning bats exert strong predation pressure on katydids.

Inspired by studies in Costa Rica on katydid calling behaviour (Morris and Beier 1982; Rentz 1975), Belwood and Morris (1987) followed multiple lines of evidence to investigate whether Neotropical katydids use preventative defences against gleaning bats. They conducted their studies on BCI, which is a protected forest reserve within Panama. First, they showed that at least four bat species are more likely to be caught in mist nets paired with singing male katydids than those paired with silent female katydids, showing that these bats are attracted to katydid mate-calling songs. Second, remains of insects found at the feeding roosts of the bat *Micronycteris hirsuta* (Peters, 1869) showed that a large proportion (40%) of their diet was composed of katydids. Third, they recorded the calling songs of many katydid species and found that the species that live in the forest, where gleaning bats were captured, produce very short calls at long intervals compared to the species found in dense vegetation or fields, where gleaning bats were not captured. Fourth, gleaning bats tested in flight enclosures rapidly located katydids with high calling rates, but took a very long time to locate those that called less than once per minute. Finally, male katydids of many species produce spontaneous vibrational signals and females responded with vibrational signals when on the same substrate, providing these insects with an alternative mate-finding signal that is difficult for gleaning bats to detect.

Further research has supported the hypothesis that Neotropical katydid populations rely on preventative de-

fences against gleaning bats. Previous work in Panama had focused on two subfamilies of katydids—the Pseudophyllinae and Conocephalinae—in which silent females use positive phonotaxis to walk toward singing males. Many katydid species in the forest on BCI belong to the subfamily Phaneropterinae. In this subfamily, katydid species are known to “duet,” with males producing calling song, females replying with a short clicking sound after a short latency, and males walking to find females based on these short replies (Bailey 2003). Focal recordings of individuals in cages under ambient conditions showed that phaneropterine forest species also produce very short duration calls (ter Hofstede et al. 2020) at very low rates (Symes et al. 2020), resulting in less than 2 seconds of sound per night in total. Soundscape recordings from the forest found similar calling rates per species as the focal recordings (Symes et al. 2022). The duetting communication system might even facilitate the evolution of low calling rates since males quickly gain information about whether a receptive female is in range and they do not need to wait for a female to find them when signalling. In addition, many of these katydid species are more likely to call when they hear other katydids calling in the background (Symes et al. 2016). Calling at the same time as other individuals can reduce the likelihood of being the target of a bat attack due to distraction (Kernan et al. 2022) or the extra time required by the predator to locate the target (Prakash et al. 2021).

For male katydids, both the duration (Falk et al. 2015) and repetition rate (Belwood and Morris 1987) of their calls can influence the risk of predation by gleaning bats. Using phylogenetic comparative methods, Symes et al. (2021) found a strong relationship between these two signalling features in Neotropical phaneropterine katydids: katydids with long duration calls signal less frequently than those with short duration calls. Selection on male katydids to broadcast sufficient sound to probe their environment for receptive females, but not enough to greatly increase their risk of predation from gleaning bats, has likely resulted in a trade-off between how much sound males produce in a signal versus how often that signal is repeated. However, none of a katydid’s preventative defenses are foolproof. Falk et al. (2015) found that sympatric gleaning bat species exhibit sensory niche partitioning, with different species showing different preferences for the acoustic properties of katydid mating calls (Falk et al. 2015). Geipel et al. (2021) showed that this could be due to differences in sensitivity to different frequencies of sound across gleaning bat species, making subsets of prey more apparent than others to various bat species. In addition, at least one gleaning bat species does not rely on prey-generated sounds but uses echolocation to find still (Geipel et al. 2013, 2019) or moving prey (Geipel et al. 2020).

## Selection for reliance on preventative versus reactive defences

The previous paragraphs provide many examples of how Neotropical katydid communication systems have been shaped by their preventative defences against eavesdrop-

ping predators, but what about reactionary defences? Surprisingly, unlike temperate katydids, many Neotropical katydid forest species do not cease singing when they hear bat calls (Symes et al. 2018, 2020). Just like studies on *N. ensiger*, studies on Neotropical katydids show that the T-cell interneuron is sensitive to high-frequency sound and ultrasound (ter Hofstede et al. 2010) and acts as a “novelty detector” as defined previously for *Neoconocephalus* spp. (HtMH, unpublished data). An acoustic monitoring study in the forest on BCI found that although sound frequencies typical of katydids were often lower in amplitude during and after a bat passed by, the amplitude differences were very small (1–2 dB) and only statistically significant at certain heights in the forest (Symes et al. 2018). A study in which caged katydids were exposed to playbacks of gleaning bat echolocation calls showed that most Neotropical katydids do not call less when exposed to bat calls, despite neurophysiological evidence that the katydids could hear the acoustic stimuli (Symes et al. 2020).

Why would forest katydids ignore a predator cue? One possibility is that their preventative defences (short calls produced rarely) are effective enough without an additional reduction in calling. The species studied in Symes et al. (2020) were mainly phaneropterines, but one species was a pseudophylline (*Cocconotus wheeleri* Hebard, 1927) that produced significantly more sound per night than the other species (~20 s compared to <2 s) and called less during bat call playbacks than during silence or noise playback treatments. In a preliminary study, ter Hofstede et al. (2010) found that two other pseudophylline katydid species paused singing in response to bat calls. Therefore, the amount of sound produced by calling species might influence their responsiveness to predator cues. Forest recordings also show that bats fly past the monitor frequently throughout the night (~once per min), and more than 96% of the recorded echolocation sequences were from bat species that do not glean insects (i.e., they are aerial-hawking or frugivorous bat species; Symes et al. 2018). Together, these studies show that in situations where predator and non-predator cues are similar and frequent, selection likely favours preventative instead of reactive defences and that ecological context can influence the information content of predator cues and thus prey defensive behaviour.

## Conclusion

Studies on the interactions between gleaning bats and katydids have illuminated how animal auditory systems can encode signals that overlap in their acoustic properties but have very different consequences for the listener (sex or death). Likewise, studies on katydids in different areas of the world show that not all animals exhibit reactionary defences even when they can detect predator cues, and this is likely related to the information content of the cue. These studies raise additional questions about the interactions between gleaning bats and katydids:

1. How many bat species are obligate versus facultative eavesdropping gleaners? This question has implications for the predation pressure exerted on acoustically signalling animals.

2. Why do so many Neotropical gleaning bats rely on insect communication signals to find prey, whereas these sounds are often ignored by gleaning bats in other tropical forests? Are katydids outside of the Neotropics more prolific singers because of this difference in predator behaviour?
3. What neural mechanisms are used by echolocating bats to detect silent and motionless katydids and other arthropod prey?
4. How does the nervous system of Neotropical katydids differentiate the rarely occurring conspecific calls and occasional predatory bat ultrasound within high levels of background noise (re Römer 2021)?

We believe that these, and many other questions, are fruitful areas of research for future investigations in this fascinating predator–prey system.

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### Data availability

This is a review article and does not have associated primary research data.

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## Author notes

This article is part of a collection in honour of Dr. Brock Fenton for his 80th birthday

## Author contributions

Conceptualization: HMtH, PAF

Writing – original draft: HMtH, PAF

Writing – review & editing: HMtH, PAF

## Competing interests

The authors declare there are no competing interests.

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## Conflict of interest

The authors declare no conflicts of interest.

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