



SYMPOSIUM

What Does an Insect Hear? Reassessing the Role of Hearing in Predator Avoidance with Insights from Vertebrate Prey

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Synopsis Insects have a diversity of hearing organs known to function in a variety of contexts, including reproduction, locating food, and defense. While the role of hearing in predator avoidance has been extensively researched over the past several decades, this research has focused on the detection of one type of predator—echolocating bats. Here we reassess the role of hearing in antipredator defense by considering how insects use their ears to detect and avoid the wide range of predators that consume them. To identify the types of sounds that could be relevant to insect prey, we first review the topic of hearing-mediated predator avoidance in vertebrates. Sounds used by vertebrate prey to assess predation risk include incidental sound cues (e.g., flight sounds, rustling vegetation, and splashing) produced by an approaching predator or another escaping prey, as well as communication signals produced by a predator (e.g., echolocation calls, songs) or nonpredator (e.g., alarm calls). We then review what is known, and what is not known, about such sounds made by the main predators and parasitoids of insects (i.e., birds, bats, terrestrial vertebrates, and invertebrates) and how insects respond to them. Three key insights emerged from our review. First, there is a lack of information on how both vertebrate and insect prey use passive sound cues produced by predators to avoid being captured. Second, while there are numerous examples of vertebrate prey eavesdropping on the calls and songs of predators and nonpredators to assess risk, there are currently no such examples for eared insect prey. Third, the hearing sensitivity of many insects, including those with ears considered to be dedicated to detecting bats or mates, overlaps with both sound cues and signals generated by nonbat predators. Sounds of particular relevance to insect prey include the flight sounds and calls of insectivorous birds, the flight sounds of insect predators and parasitoids, and rustling vegetation sounds of birds and terrestrial predators. We conclude that research on the role of insect hearing in predator avoidance has been disproportionately focused on bat-detection, and that acoustically-mediated responses to other predators may have been overlooked because the responses of prey may be subtle (e.g., ceasing activity, increasing vigilance). We recommend that researchers expand their testing of hearing-mediated risk assessment in insects by considering the wide range of sounds generated by predators, and the varied responses exhibited by prey to these sounds.

Introduction

Hearing is well developed in many insects. Ears have evolved multiple times and are morphologically and physiologically diverse (Yager 1999; Greenfield 2002; Yack 2004; Hedwig 2014; Strauß and Stumpner 2015; Pollack et al. 2016). This diversity reflects a wide range of functions, which can be divided into five non-mutually exclusive categories: (1) Reproduction (e.g., locating mates, species

recognition, courtship, competition, and pair maintenance); (2) Aggression (e.g., territoriality, competition for resources); (3) Host location (e.g., parasitoid flies locating hosts); (4) Social interactions (e.g., group formation and organization); and (5) Predator detection (e.g., bat detection). With respect to predator detection, the vast majority of studies focus on the detection of echolocating bats (reviewed in Hoy 1992; Miller and Surlykke 2001; Conner and

Corcoran 2012; Yager 2012; Pollack 2015, 2016). While there is no question that echolocating bats have imposed significant selection pressures on the evolution of hearing in night flying insects, bats are not the only predators of insects, and night flying insects are not the only insects with ears. Conceivably, insects also use their hearing to detect their many non-bat predators and enemies, including birds, terrestrial vertebrates, and invertebrate predators and parasitoids.

The main objective of this article is to consider how insects use their hearing to assess predation risk, with a focus on predators other than echolocating bats. The incentive for this line of investigation was prompted by the following: First, while there are few examples of insects using their hearing to detect nonbat predators, this is not the case for vertebrates. In fact, vertebrate prey rely heavily on a diversity of sounds to assess risk. In addition to detecting the echolocation calls of hunting bats and aquatic mammals, they eavesdrop on calls and songs of predators, attend to alarm calls of both conspecifics and heterospecifics, and respond to incidental sound cues generated by predator movements. If vertebrate prey use these sounds to assess risk, then it is reasonable to assume that insects do also. Second, there is a growing number of examples of insects that have ears, or ear tuning, with no identified function. These examples include hearing in diurnally active, noncalling insects such as butterflies (e.g., Lane et al. 2008; Lucas et al. 2009; Sun et al. 2018), noncalling grasshoppers (e.g., Riede 1987; Lehmann et al. 2010; Lehmann 2012), praying mantids with low frequency tuning (e.g., Yager 1996), and insects with hearing sensitivity that is mismatched to the species' calling songs (e.g., Mason 1991; Yack et al. 2000). In these cases, hearing must function for purposes other than bat-detection and conspecific communication, and has been proposed to function in detecting nonbat predators. Third, even those insects with ears deemed to be dedicated "bat detectors," which includes the ears of most moths, may have broadband tuning extending to sound frequencies that are lower than ultrasonic bat echolocation calls (i.e., >20 kHz), or have retained hearing once released from the selection pressures of echolocating bats (e.g., Surlykke 1986; Fullard 1994; Surlykke et al. 1998; Muma and Fullard 2004; Jacobs et al. 2008). Again, these results have led scientists to propose that hearing may function to detect predators other than bats. Similarly, other insects such as crickets, katydids, and cicadas, often presumed to have ears that are "dedicated" to reproductive behaviors, may also use their hearing to

detect predators. It is reasonable to assume that, like for most vertebrates, insect ears function in more than one context. There are examples of insects using their hearing for dual purposes (see Pollack 2016). Based on these arguments, and the suggestions by several scientists that insect ears may function in nonbat predator avoidance (e.g., Mason 1991; Ribarič and Gogala 1996; Yack et al. 2000; Jacobs et al. 2008; Lehmann 2012; Fournier et al. 2013; Strauß and Stumpner 2015; Mikhail et al. 2018), we decided that it was time to reassess the role of insect hearing in predator detection.

We have three primary goals. First, we consider how vertebrate prey use their hearing in predator avoidance. By identifying the different types of sounds that vertebrate prey attend to, and how they respond to these sounds, we "set the stage" for posing and testing hypotheses on hearing-mediated predator avoidance in insects. Second, we will consider the question, "What does an insect hear?" by discussing the different types of hearing organs in insects, the breadth of their hearing capabilities, and the known functions (or lack thereof) of hearing in different species. Third, we consider the main enemies of insects, including bats, birds, terrestrial vertebrates, and invertebrates. We assess what sounds these enemies generate, and review evidence supporting the hypothesis that insect prey can hear or respond to these sounds. We also consider whether insects listen to nonpredator sounds such as conspecific or heterospecific alarm calls to assess predation risk. Note that we have restricted our focus to "hearing" airborne sounds, and do not review the many interesting examples of prey (both vertebrate and invertebrate) using solid-borne vibrations in the context of predator avoidance (for reviews see Hill 2008; Warkentin 2011; Virant-Doberlet et al. 2019). We emphasize that this is not intended to be a comprehensive review of all examples of hearing-mediated risk assessment in either vertebrate or insect prey. The main objectives are to identify gaps in our knowledge of hearing-mediated predator detection and avoidance in insects, and to develop hypotheses for future research.

Vertebrate prey: How do they use hearing to avoid predators?

Many vertebrates that are vulnerable to predation use their hearing to avoid predators (see examples in Table 1). In fact, the detection of both predators and prey are considered to be the most fundamental functions of hearing in vertebrates (Fay and Popper 2000). Sounds of importance to prey can be

Table 1 Examples of sounds used by vertebrate prey to detect and avoid predators

Predator as Sound Producer		Prey (focal recipient)						
Sound Category	Source/type	Species/taxon		Species/taxon				
		Species name	Common name	Order	Species name	Common name	Response (behavioral)	Reference
Cues								
Incidental ^a sound	Bat wing beats	<i>T. cirrhous</i>	Frog-eating bat	Anura	<i>P. pustulosus</i>	Túngara frogs	Males decreased mate calling	Bernal et al. (2007)
Incidental sound	Predator walking on leaf litter	<i>Strepera graculina</i>	Pied currawong	Passeriformes	<i>Sericornis frontalis</i>	White-browed scrubwren	Nestlings stopped calling	Haff and Magrath (2010)
Incidental sound	(Proposed) flight	<i>Tyto alba</i>	Barn owl	Rodentia	<i>A. cahirinus</i>	Spiny mice	Flee, freeze	Ilany and Eilam (2008)
Incidental movement through vegetation	Rustling leaves	Not specified	Terrestrial predators	Rodentia	<i>T. striatus</i>	Eastern chipmunk	Increased vigilance	Wearly and Kramer (1995)
Signals								
Echolocation	Calls of mammal-eating whales	<i>O. orca</i>	Killer whale	Carnivora	<i>P. vitulina</i>	Harbor seal	Avoidance behavior	Deecke et al. (2002)
Echolocation	Calls of dolphins and porpoises	<i>T. truncatus</i> ; <i>P. phocoena</i>	Bottlenose dolphin; Harbour porpoise	Clupeiformes	<i>A. sapidissima</i>	American shad	Evasive responses, swimming away, group formation, group division	Plachta and Popper (2003)
Echolocation	Odontocete-type calls	<i>Odontocete cetaceans</i>	Toothed whale	Clupeiformes	<i>Clupea pallasii</i>	Pacific herring	Stopped eating, dropped in water column, grouped, increased swim speed	Wilson and Dill (2002)
Calling/song ^b	Roar	<i>Panthera leo</i>	Lion	Artiodactyla	<i>Alcelaphus buselaphus caama</i>	Red hartebeest	Increased vigilance	Makin et al. (2019)
Calling/song	Howl	<i>Canis lupus</i>	Wolf	Artiodactyla	<i>Cervus elaphus</i>	Elk	Increased vigilance	Berger (2007)
Calling/song	Conspecific calls	<i>Panthera tigris</i>	Tiger	Artiodactyla	<i>Cervus elaphus</i>	Elk	Increased vigilance	Berger (2007)
Calling/song	Lion roars and hyena whoops	<i>Panthera leo</i> ; <i>Crocuta Crocuta</i>	Lion, Spotted hyena	Carnivora	<i>Acinonyx jubatus</i>	Cheetah	Increased vigilance; inspecting; less likely to hunt	Durant (2000)
Calling/song	Low frequency "pops"	<i>T. truncatus</i>	Bottlenose dolphin	Batrachoidiformes	<i>Opsanus beta</i>	Gulf toadfish	Reduced calling rates	Remage-Healey et al. (2006)
Calling/song	Whistles	<i>T. truncatus</i>	Bottlenose dolphin	Perciformes	<i>Bairdiella chrysoura</i>	Silver perch	Stopped chorusing, decrease in loudness of calling to conspecifics	Luczkovich et al. (2000)
Calling/song	Shrieks	<i>S. coronatus</i>	Crowned eagles	Coraciiformes	<i>C. elata</i>	Yellow-casqued hornbills	Inspection of sound source	Rainey et al. (2004)

(continued)

Table 1 Continued

Predator as Sound Producer		Prey (focal recipient)						
Sound Category	Source/type	Species/taxon			Species/taxon			
		Species name	Common name	Order	Species name	Common name	Response (behavioral)	
Calling/song	Vocalizations	<i>B. jamaicensis</i>	Red-tailed hawk	Columbiformes	<i>Z. aurita</i>	Zenaida doves	Produced wing whistles as alarm call, reduced foraging	Barrera et al. (2011)
Calling/song	Female territorial call	<i>Tyto novaehollandiae castanops</i>	Masked owl	Dasyuromorpha	<i>Dasyurus viverrinus</i>	Tasmanian eastern quoll	Moved less, increased vigilance, freezing, escape responses	Jones et al. (2004)
Calling/song	Conspecific calls	<i>Bubo virginianus</i>	Great horned owl	Passeriformes	<i>Corvus brachyrhynchos hesperis</i>	American crow	Mobbing	Hauser and Caffrey (1994)
Calling/song	Predator vocalizations	<i>Cracticus torquatus</i>	Grey butcherbird	Passeriformes	<i>Malurus lamberti</i>	Variiegated Fairy-wren	Proposed alarm call, mobbing call, pursuit deterrent signal	Greig et al. (2010)
Calling/song	Roar	<i>Panthera leo</i>	Lion	Perissodactyla	<i>Equus quagga</i>	Zebra	Increased vigilance	Makin et al. (2019)
Calling/song	Pant hoots, drumming	<i>Pan troglodytes</i>	Chimpanzees	Primates	<i>Procolobus badius</i>	Tai colobus monkey	Stopped calling, moved higher up in trees	Bshary and Noë (1997)
Calling/song	Vocalizations	<i>C. ferus</i>	Fossa	Primate	<i>Propithecus verreauxi</i>	White sifakas	Vocalization (growls), looked down	Fichtel and Kappeler (2002)
Calling/song	Vocalizations	<i>P. radiatus</i>	Harrier hawk	Primates	<i>Propithecus verreauxi</i>	White sifakas	Vocalization, escape response, look up/ scanned sky, moved down from exposed positions	Fichtel and Kappeler (2002)
Calling/song	Vocalizations	<i>C. familiaris</i>	Stray dogs	Primates	<i>Propithecus verreauxi</i>	White sifakas	Vocalization (growls), look down	Fichtel and Kappeler (2002)
Calling/song	Vocalizations	<i>C. ferus</i>	Fossa	Primates	<i>Eulemur fulvus rufus</i>	Redfronted lemurs	Vocalizations (woofs), escape response, look down	Fichtel and Kappeler (2002)
Calling/song	Call	<i>Falco peregrinus</i>	Peregrine falcon	Psittaciformes	<i>Platycercus elegans</i>	Crimson rosellas	Increased number of looks/vigilance; fly to nearest cover	Adams et al. (2006)
Calling/Song	Territorial calls	<i>S. aluco</i>	Tawny owl	Rodentia	<i>Microtus socialis</i>	Vole	Crouching, reduced movement, increased time in burrows	Hendrie et al. (1998)

Calling/Song		S. aluco	Tawny owl	Rodentia	<i>Jaculus jaculus</i>	Jerboas	Hendrie et al. (1998)	
Calling/Song	Territorial calls	S. aluco	Tawny owl	Rodentia	<i>Jaculus jaculus</i>	Jerboas	Decreased movement, rearing and sniffing, crouching, freezing	
Calling/Song	Territorial calls	S. aluco	Tawny owl	Rodentia	<i>Eliomys melanurus</i>	Dormice	Increased time in/around burrows, decreased movement	
Calling/Song	Calls	<i>F. sparverius</i>	Kestrel	Squamata	<i>A. sagrei</i>	Brown anole (male)	Increased vigilance in the form of head tilting	
Calling/Song	Calls	<i>B. jamaicensis</i>	Red-tailed hawk	Squamata	<i>A. sagrei</i>	Brown anole (male)	Increased vigilance in the form of head tilting	
Calling/Song	Calls	<i>F. sparverius</i>	Kestrels	Squamata	<i>Anolis cristaeillus</i>	Crested anole	Decrease display rates, tonic immobility	
Calling/Song	Hunting call	<i>Harpia harpyja</i>	Harpy eagle	Primates	<i>A. palliata</i>	Howler monkey	Initiate escape response	
Calling/Song	Human voices (perceived as hunters)	<i>Homo sapiens</i>	Human	Proboscidea	<i>Loxodonta Africana</i>	African elephant	Defensive bunching; investigative smelling; decreased calling	
Non-predator as sound producer								
Sound		Species/taxon						
Category		Latin name		Order (superfamily)		Common name		
Sound Source		Common name		Latin name		Response (Behavioral)		
References								
Incidental flight sound	"alarmed" wing whistles	<i>O. lophotes</i>	Crested pigeon	Columbiformes	<i>O. lophotes</i>	Crested pigeon	Escape flight	
Incidental flight sound	"startled" wing whistle	<i>Z. macroura</i>	Mourning dove	Columbiformes	<i>Z. macroura</i> ; <i>C. cardinalis</i> ; <i>P. domesticus</i>	Mourning dove; Northern cardinal; House sparrow	Increased vigilance, startle responses	
Conspecific alarm call	Alarm calls	<i>T. striatus</i>	Eastern chipmunk	Rodentia	<i>Tamias striatus</i>	Eastern chipmunk	Alert posture, flee	
Conspecific alarm call	Long-distance alarm call of males	<i>C. diana diana</i> (male)	Diana monkey	Primates	<i>C. diana diana</i>	Diana monkey	Moved to lower position in tree canopy, approach playback speaker, vocalized at higher rates	
Conspecific alarm call	High frequency alarm calls	<i>P. montanus</i>	Willow tit	Passeriformes	<i>P. montanus</i>	Willow tit	Freezing, move to center of tree	

(continued)

Table 1 Continued

Non-predator as sound producer		Prey (focal recipient)						
Sound	Species/taxon	Species/taxon						
		Latin name	Common name	Order (superfamily)	Latin name			
Category	Sound Source	Latin name	Common name	Order (superfamily)	Common name			
Conspecific alarm call	Chatter (terrestrial predators), whistle (avian predators)	<i>Spermophilus beecheyi</i>	California ground squirrel	Rodentia	<i>Spermophilus beecheyi</i>	California ground squirrel	Less time foraging, more time in covered areas	Hanson and Coss (2001)
Heterospecific alarm call	Alarm call	<i>M. flaviventris</i>	Yellow-bellied marmot	Cetartiodactyla	<i>O. hemionus</i>	Mule deer	Increased vigilance, oriented toward sound	Carrasco and Blumstein (2011)
Heterospecific alarm call	Alarm calls	<i>P. atricapillus</i>	Black-capped chickadee	Passeriformes	<i>S. canadensis</i>	Red-breasted nuthatch	Initiated mobbing, moved closer to sound	Templeton and Greene (2007)
Heterospecific alarm call	Alarm calls	<i>Ceropithecus diana</i>	Diana monkey	Bucerotiformes	<i>C. elata</i>	Yellow-casqued hornbill	Moved closer to sound source to inspect	Rainey et al. (2004)
Heterospecific alarm call	Alarm calls	<i>Corythaixoides leucogaster</i>	White-bellied go-away bird	Artiodactyla	<i>Madoqua guentheri</i>	Gunther's dik-dik	Increased alertness, decreased foraging, inspection	Lea et al. (2008)
Heterospecific alarm call	High-risk alarm calls ("seet calls") and mobbing calls	<i>Baeolophus bicolor</i>	Eastern tufted titmouse	Rodentia	<i>T. striatus</i>	Eastern chipmunk	Decreased foraging	Schmidt et al. (2008)
Heterospecific alarm call	Alarm call	<i>Cynomys ludovicianus</i>	Black-tailed prairie dog	Strigiformes	<i>Athene cunicularia hypugaea</i>	Western burrowing owl	Increased alert behaviors	Bryan and Wunder (2014)
Heterospecific alarm call	Galápagos mockingbird alarm call	<i>N. parvulus</i>	Galápagos mockingbird	Squamata	<i>A. cristatus</i>	Galápagos marine iguana	Increased vigilance	Vitousek et al. (2007)

^aIncidental sounds are produced by movements or activities, either directly (e.g., aerodynamic sounds from flight), or indirectly (e.g., rustling sounds when moving through leaf litter).

^bCalling/song sounds are deliberately produced by the predator while communicating to/with conspecifics.

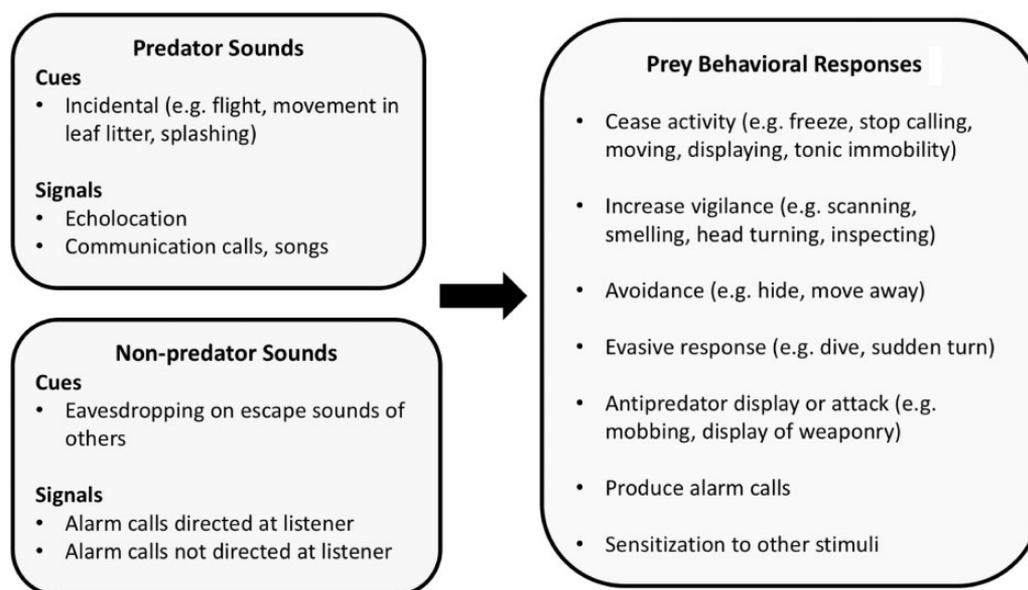


Fig. 1 An overview of different types of sounds that prey use to avoid predation, and how they respond to these sounds.

generated by the predator (e.g., echolocation calls, communication songs, and calls), or by another individual or group (e.g., conspecific or heterospecific alarm calls). Sounds from these sources can be categorized as (passive) cues or (active) signals. By cues, we are referring to sounds that have not evolved to alter the behavior of a recipient, including incidental sounds generated as a consequence of movement (e.g., flying, walking, and digging). Signals, in contrast, have evolved in the context of conveying a message to an intended receiver (Maynard-Smith and Harper 2003), which could be oneself (e.g., echolocation) or another recipient (e.g., alarm or mating call). Prey respond to sounds that alert them to predators in a number of different ways. We identified seven non-mutually exclusive behavioral responses: (1) Ceasing activity (e.g., stop calling or moving, tonic immobility); (2) Increased vigilance (e.g., scanning, smelling, and inspecting); (3) Avoidance (e.g., seeking shelter, moving away); (4) Evasive response (e.g., sudden turns, dives); (5) Antipredator display or attack (mobbing, display of weaponry); (6) Alarm calls (e.g., warning others of danger); (7) Increased sensitization to other stimuli that indicate a threat. The types of sounds used by vertebrate prey, and their behavioral responses, are illustrated in Fig. 1. Table 1 provides a list of selected examples that highlight the variety of sounds used by prey representing different taxa, and their respective behavioral responses.

Sounds made by predators

Sound cues used, or allegedly used, by vertebrate prey to detect predators include those generated

directly by a predator's movements (e.g., aerodynamic or mechanical sounds produced by wing movements) or indirectly by a predator's movements (e.g., crackling branches, rustling leaves, and splashing). Such incidental sound cues tend to be broadband with significant ultrasonic components, and with dominant frequencies typically <20 kHz (e.g., sounds associated with flight (Bernal et al. 2007; Fournier et al. 2013; Clark et al. 2020) and moving through vegetation (Fullard 1988; Bernal et al. 2007; Goerlitz et al. 2008; Jacobs et al. 2008; Haff and Magrath 2010)). These sound frequencies overlap with the hearing of many vertebrate prey. Most birds, amphibians, and reptiles have best hearing sensitivities >10 kHz, most fish are sensitive between 40 Hz and 1 kHz, and mammals are sensitive to sonic (<20 kHz) and ultrasonic (>20 kHz) frequencies (reviewed in Fay and Popper 2000; Köppl et al. 2014; Clark et al. 2020). While it is often assumed that vertebrate prey use their hearing to detect incidental sounds of approaching predators, there is surprisingly little empirical evidence for this (see Table 1). Nestlings of the white-browed scrubwren (*Sericornis frontalis*) stopped calling following playbacks of a predator walking on leaf litter (Haff and Magrath 2010), and male túngara frogs (*Physalaemus pustulosus*) decreased their calling rate when exposed to sounds of the beating wings of frog-eating bats (*Trachops cirrhous*) (Bernal et al. 2007). Eastern chipmunks (*Tamias striatus*) spent more time being alert when the sounds of rustling leaf litter were played in conjunction with alarm calls (Weary and Kramer 1995). While there has been much research

on the acoustically “cryptic” flight of owls and other predatory birds (see [Clark et al. 2020](#)), there are in fact few examples showing that vertebrate prey detect flight sounds of predatory birds. One study provided indirect evidence for this. [Ilany and Eilam \(2008\)](#) monitored behavioral reactions of common spiny mice (*Acomys cahirinus*) during an attack by a tawny owl (*Strix aluco*). The mice responded to attacks by fleeing either immediately after the owl was noticed or by freezing and fleeing when the owl was in closer proximity. The authors stated that it was unclear what aspect(s) of the owl attack—visual, acoustic, or both—the mice responded to. However, sound detection was assumed to be involved because the owl was reportedly in flight when noticed by the mice. Sound cues that aquatic prey such as fish could use to detect predators include water splashing, tail slaps, and breaching (e.g., [Finneran et al. 2000](#); [Van Opzeeland et al. 2005](#)). There is also a lack of information on how vertebrates use their hearing to detect harmful flying insects such as biting flies and mosquitoes that have potential to carry harmful diseases or cause considerable blood loss. There is evidence that vertebrates react to flying insects. For example, ungulates have been shown to repel flies by muscle twitching, ear twitching, head-tossing, leg stomping, and biting, and small rodents have been observed to repel mosquitos by shaking their head, flipping their ears, shifting their feet, and rubbing their face ([Edman et al. 1974](#); [Hart and Hart 2018](#)). Elephants were observed to repel flies by using branches to swat them away from more inaccessible areas of their body ([Hart and Hart 1994](#)). Despite the evidence that vertebrates detect and respond to flying insect enemies, the sensory cues used by vertebrates to detect flying insects are not mentioned in these studies. Flying insects, including several species of Diptera and Hymenoptera, produce low frequency sounds with fundamental frequencies <1 kHz and harmonics reaching 5 kHz (e.g., [Offenhauser and Khan 1949](#); [Sotavalta 1963](#); [Raman et al. 2007](#); [Rashed et al. 2009](#); [Potamitis and Rigakis 2016](#)); therefore, these sounds are potentially important cues for vertebrates. How vertebrate prey use incidental sound cues to assess risk is clearly a topic of interest for further research.

There are numerous examples of vertebrate prey responding to acoustic communication signals produced by predators ([Table 1](#)). These sounds include calls and songs that predators use to communicate with conspecifics for different functions (e.g., attraction, courtship, warning, and cohesion). Because these sounds have evolved as communication signals, they tend to be more specialized, and in many cases,

prey have evolved specialized hearing capabilities to detect and distinguish between different sound characteristics. A wide range of vertebrate prey, including mammals, birds, fish, amphibians, and reptiles, attend to predator communication signals ([Table 1](#)) and they typically respond by freezing, moving away, or releasing an alarm call (reviewed by [Hettena et al. 2014](#)). For example, Zenaida doves (*Zenaida aurita*) reduced foraging and produced alarm signals when exposed to red-tailed hawk (*Buteo jamaicensis*) vocalizations ([Barrera et al. 2011](#)). Silver perch respond to playbacks of bottlenose dolphin (*Tursiops truncatus*) whistles by ceasing or lowering the volume of their chorusing activity ([Luczkovich et al. 2000](#)). Being able to recognize and react to these sounds is considered to be highly adaptive, as continued chorusing may attract unwanted attention from predatory dolphins. Anoles lizards detect and respond to calls of predatory birds. [Huang et al. \(2011\)](#) found that female crested anoles (*Anolis cristaeillus*) decreased their display rates and freeze when exposed to kestrel (*Falco sparverius*) calls. [Cantwell and Forrest \(2013\)](#) tested the responses of brown anoles (*Anolis sagrei*) to predatory bird calls and found similar results. The auditory systems of anoles are well developed, which is interesting because they are nonvocal animals. Their hearing sensitivity (1–7 kHz) ([Brittan-Powell et al. 2010](#)) overlaps with the calling frequency of most birds ([Dooling et al. 2000](#)). It is likely that a key role of hearing in anoles is to detect avian predators, as anoles constitute a large portion of the diet of predatory birds. Howler monkeys (*Alouatta palliata*) responded to hunting calls of the predatory harpy eagle (*Harpia harpyja*) ([Gil-da-Costa et al. 2003](#)). Upon hearing the eagle calls, female monkeys gathered their offspring and moved into more densely covered parts of the forest, while males produced alarm calls. Some prey can even discriminate between calls of different predators and respond appropriately. [Fichtel and Kappeler \(2002\)](#) presented the vocalization sounds of three different predators to two different prey, redfronted lemurs (*Eulemur fulvus rufus*) and white sifakas (*Propithecus verreauxi verreauxi*). The predator vocalizations were those of two terrestrial predators, a fossa (*Cryptoprocta ferox*) and stray dog (*Canis familiaris*), and one aerial predator, the harrier hawk (*Polyboroides radiatus*). Both the redfronted lemurs and white sifakas responded to vocalizations of the terrestrial predators by looking down at the ground and producing vocalizations of their own. Both prey species also showed very similar reactions when responding to vocalizations of the aerial predator, including looking up and scanning

the sky as well as moving lower in the tree canopy (Fichtel and Kappeler 2002).

Echolocation is a signal that predators use to communicate with themselves, by sending a sound pulse and receiving the echo to assess the location and characteristics of their prey. The primary echolocating predators are odontocete cetaceans (e.g., killer whales, dolphins, and porpoises), and bats. While many vertebrate prey, including frogs, birds, fish, and seals are hunted by echolocating predators, there are few examples of these prey responding to echolocation calls (Table 1). Most examples of vertebrate prey responding to echolocating predators are fish responding to odontocete cetaceans. For example, American shad (*Alosa sapidissima*) are preyed upon by bottlenose dolphins (*Tursiops truncatus*) and harbor seals (*Phocoena phocoena*), both of which use sonar clicks to forage (Plachta and Popper 2003). American shad have hearing sensitivity between 200 Hz and 180 kHz (Mann et al. 1998), which overlaps with the echolocation clicks of harbor porpoises (120–140 kHz) and bottlenose dolphins (70–130 kHz) (Plachta and Popper 2003). Three types of prey responses were reported, depending on the loudness and sound frequencies of the echolocation calls. Harbor seals (*Phoca vitulina*) are preyed upon by killer whales (*Orcinus orca*). The seals respond to the echolocation calls of killer whales by moving farther away from the surface of the water to lessen their chances of being detected (Deecke et al. 2002). Not only were the seals able to recognize and respond to killer whale echolocation calls, but they could also discriminate between different populations of killer whales. The seals did not respond to the calls of local killer whales known to only eat fish, thus not being a threat to the seals, but did respond to the calls of killer whales known to prey on mammals (Deecke et al. 2002).

Sounds made by nonpredators

Vertebrate prey also attend to sounds of nonpredators to assess predation risk. Such sounds can also be categorized as cues or signals (Table 1). Cues made by nonpredators include the incidental sounds produced by another animal escaping a predator. For example, crested pigeons (*Ocyphaps lophotes*) produce a whistling sound when taking off in an alarmed state. Playbacks of these “alarmed” take off whistles elicited alarm responses in conspecifics (Hingee and Magrath 2009). The authors state that these wing sounds could either be a cue, if the sounds provided information about danger but did not evolve in that context, or an alarm signal, if the

sounds evolved to convey information to others. In another study, Coleman (2008) played acoustic “startle wing whistles” of mourning doves (*Zenaidura macroura*) to other potential flock-mates, including other mourning doves, northern cardinals (*Cardinalis cardinalis*), and house sparrows (*Passer domesticus*). All species responded to startle wing whistles with increased vigilance and startling behavior. The authors state that it cannot be concluded whether these sounds of escaping prey constitute cues or signals.

Many vertebrate prey respond to acoustic alarm signals. Alarm sounds detected by a focal prey could be directed at the focal prey, such as in the case of an alarm call produced by conspecifics, or they could be directed at another individual, such as when the focal prey eavesdrops on the alarm calls of another species. Responses by vertebrate prey to alarm calls typically include hiding, freezing, or coordinating a defensive response (Table 1 and Fig. 1). Examples of prey responding to alarm calls that are directed at the focal prey include the following. Eastern chipmunks (*T. striatus*) responded to conspecific alarm calls by either fleeing or stopping and assuming an alert position (Weary and Kramer 1995). Male diana monkeys (*Cercopithecus diana diana*) elicit alarm calls in response to predators whose hunting style relies on the element of surprise, such as leopards and crowned hawk eagles (Zuberbühler et al. 1997). Females and juveniles showed a variety of responses to playbacks of these alarm calls, including lowering themselves in the canopy and inspecting the location of the sound source. Willow tits (*Parus montanus*) produce high-frequency alarm calls when they detect a predator (Rajala et al. 2003). In response to an alarm call that was produced in the presence of a stuffed pigmy owl, tits froze, and moved toward safety. Prey may also eavesdrop on alarm calls intended for another recipient (see Carrasco and Blumstein 2012; Magrath et al. 2015). For example, mule deer (*Odocoileus hemionus*) respond to yellow-bellied marmot (*Marmota flaviventris*) alarm calls by looking around, orienting their body toward the sound with ears faced forward, and erecting their neck (Carrasco and Blumstein 2012). African savannah herbivores responded to heterospecific alarm calls, particularly if they shared similar predators with the caller (Meise et al. 2018). The Galápagos marine iguana (*Amblyrhynchus cristatus*) eavesdrops on the alarm call of the Galápagos mockingbird (*Nesomimus parvulus*) in response to a shared predator, the Galápagos hawk (*Buteo galapagoensis*) (Vitousek et al. 2007). The iguana’s response to playbacks of the mockingbird alarm calls was to increase

vigilance. In some cases, prey have been shown to discriminate between different alarm calls of heterospecifics. For example, red-breasted nuthatches (*Sitta canadensis*) could discriminate between three distinct alarm calls of black-capped chickadees (*Poecile atricapillus*) that were indicative of different predators (Templeton and Greene 2007). In a study by Rainey et al. (2004), yellow-casqued hornbills (*Ceratogymna elata*) were shown to distinguish between the alarm calls produced by another prey species, diana monkeys (*C. diana*). Diana monkeys produce distinct alarm calls for each of two predators, the crowned eagle (*Stephanoaetus coronatus*) and the leopard (*Panthera pardus*). Of these two predators, only the eagle is a threat to the yellow-casqued hornbill. When diana monkey eagle alarm calls were played, the yellow-casqued hornbills responded by moving closer to the playback site in attempt to spot the predator. This same response was observed following playbacks of the diana monkey leopard alarm call, but significantly less so.

In summary, our review of hearing-mediated predator avoidance in vertebrate prey shows that prey attend to a variety of sounds to assess risk of attack. Behavioral responses by prey are also varied, ranging from freezing to coordinating group attacks against the predator. The vast majority of studies report on prey eavesdropping on the communication songs and calls of their predators. There are also numerous examples of prey attending to alarm calls produced by conspecifics or heterospecifics. Less research has focused on prey attending to sound cues (e.g., flight sounds, leaves rustling, branches breaking, and splashing) that predators produce when hunting, or that other prey produce when escaping. Likewise, there are few examples of prey detecting and responding to echolocation sounds of odontocete cetaceans. The types of sounds relevant to prey, and the prey's responses, are summarized in Fig. 1. We will now use this information to consider if and how insects detect and respond to such sounds.

Insect prey: How do they use hearing to avoid predators?

Many insects have ears, but our understanding of how they use hearing to avoid predators other than echolocating bats, is not well documented. In the previous section, we identified a variety of sound cues and signals that vertebrate prey use to avoid predation (Fig. 1 and Table 1). We will now explore how insects might use hearing for predator detection in similar ways. First, we provide a brief overview of the hearing capabilities of insects. Second, we review the main

enemies of insects, including predators and parasitoids, the sounds that they produce, and how insect prey might respond to these sounds. We also discuss whether insects attend to sounds of nonpredators.

What does an insect hear?

Insects have two types of hearing organs, often referred to as “near-field” and “far-field” receptors, that respond to the particle displacement and pressure components of air-borne vibrations, respectively (Ewing 1989; Yack 2004; Windmill and Jackson 2016). Near-field sound receptors in insects are light-weight structures that are displaced by the movement of air molecules. Examples include long hair-like structures called trichoid sensilla in caterpillars (Fig. 2A) (e.g., Tautz and Markl 1978; Taylor and Yack 2019) and the plumose antennae of mosquitoes (e.g., Göpfert et al. 1999; Menda et al. 2019). Near-field receptors typically are sensitive to low frequency sounds (<1 kHz) arising from sound sources close to the receiver, although there is recent evidence that such types of sensors can detect higher sound frequencies at farther distances (e.g., Zhou and Miles 2017; Menda et al. 2019). Near-field sound receptors are not well studied, but are thought to be widespread, and could play an important role in detecting aerial insect predators or parasitoids. Far-field sound receptors detect the pressure component of sound, which can travel long distances from a sound source. Insects detect pressure waves with tympanal ears (Fig. 2B and C) that comprise a tympanal membrane associated with an air sac that allows the membrane to vibrate in response to sound pressure (Yager 1999, 2004; Greenfield 2002; Windmill and Jackson 2016). Tympanal ears vary widely in their morphological and physiological characteristics, and many are capable of detecting and discriminating a broad range of sound frequencies, amplitudes, and temporal patterns. In contrast to near-field sound receptors, a great deal is known about tympanal ears, including their neurophysiological responses to different sound characteristics, and the behaviors associated with hearing (see Yager 1999, 2004; Greenfield 2002; Hedwig 2014; Pollack et al. 2016). The functions of tympanal hearing have focused primarily on behaviors associated with reproduction and bat detection in adults. Here we consider how hearing in insects may function to detect not only bats, but also other predators.

Bat predators: Sounds made and insect responses

Bats are a major predator of both flying and non-flying insects (Neuweiler 1989; Vaughan 1997;

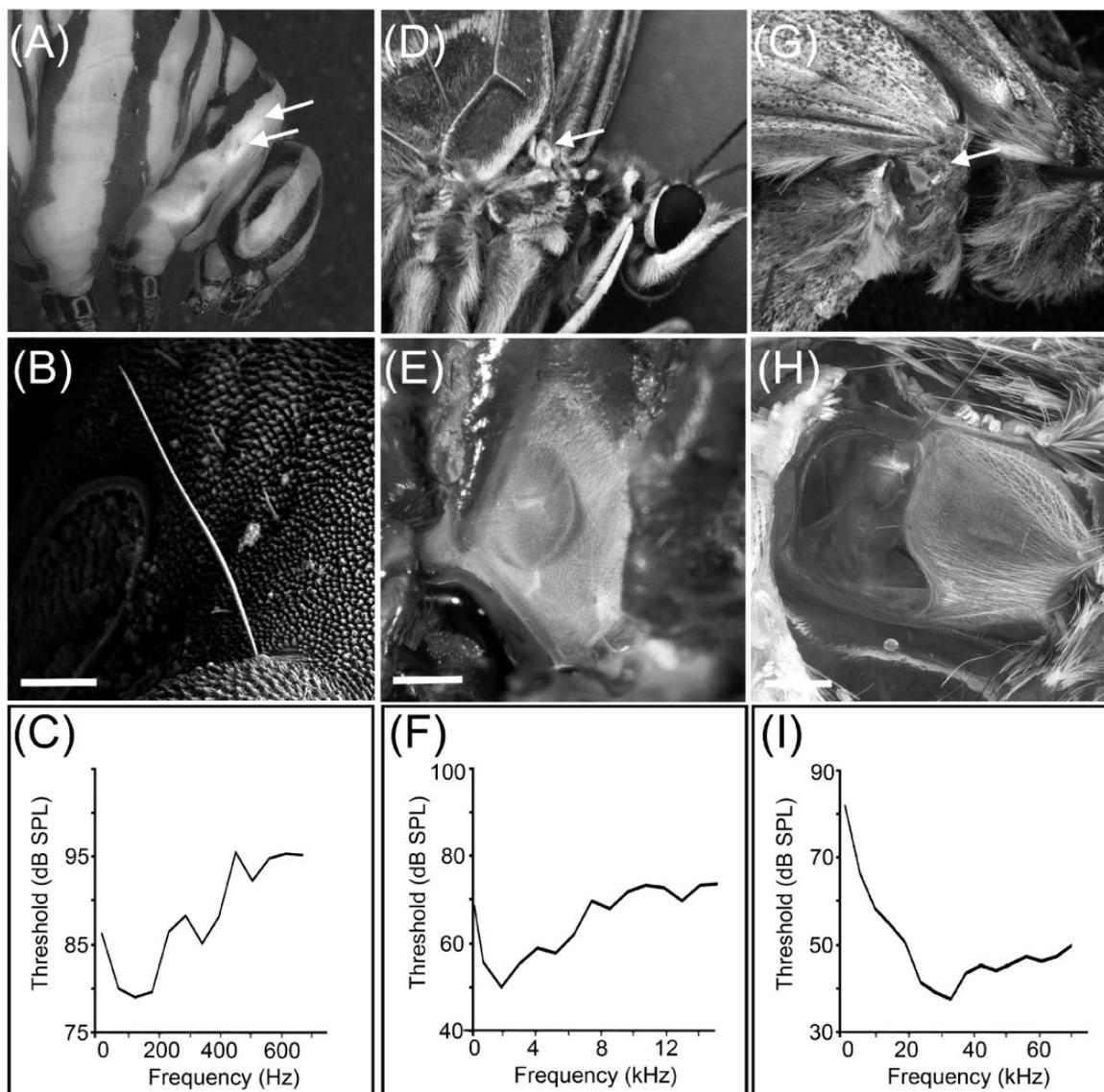


Fig. 2 Hearing organs in insects, showing different receptor types (near-field and far-field) and their respective sensitivity ranges. (A) Monarch butterfly caterpillar (*Danaus plexippus*) showing the location (arrows) of trichoid sensilla (a near field sound receptor) on the prothorax. (B) A single trichoid sensillum. Scale bar: 100 μ m. (C) Behavioral tuning curve showing the best sensitivity to sounds <500 Hz. (D) Morpho butterfly (*M. peleides*) showing the location (arrow) of a tympanal ear (far field sound receptor) at the base of the forewing. (E) Close up of the tympanal membrane. Scale bar: 350 μ m. (F) Tuning curve of the auditory nerve showing broad tuning with best sensitivity to frequencies between 1 and 8 kHz. (G) Noctuidae moth (*Trichoplusia ni*) showing the location (arrow) of a tympanal ear on the metathorax. (H) Close up of the tympanal ear. Scale bar: 300 μ m. (I) Tuning curve of the auditory nerve showing broad tuning with best sensitivity to frequencies >18 kHz. All photos and audiograms are from the Yack lab.

Bayefsky-Anand 2005; Jones and Rydell 2005; Lacki et al. 2007). Many bats feed on nocturnally flying insects and hunt using ultrasonic echolocation calls (Norberg and Rayner 1987; Schnitzler and Kalko 2001). Other bats consume insects by gleaning from the foliage, whereby they flutter above the insect prey, and may or may not use echolocation calls (Bell 1982; Swift and Racey 2002; Geipel et al. 2013). As such, in addition to detecting bat echolocation calls (see below), eared insects could potentially detect bats by passive sound cues generated by their

flight, or their echolocation calls. There are few examples of sounds produced by bat flight (Gould 1988; Bernal et al. 2007; Boonman et al. 2014). These sounds are low frequency and broadband with dominant frequencies <20 kHz. These frequencies overlap with the hearing of many insects (see Fig. 2), but there are no examples to the best of our knowledge that insects detect bats by their incidental flight cues. We recommend further investigations into the flight sounds made by insectivorous bats while they are hunting insects.

The role of insect ears in detecting bat echolocation calls has been extensively researched and the topic has been reviewed by many, including Spangler (1988a), Hoy (1989, 1992), Fullard (1998), Miller and Surlykke (2001), Waters (2003), Conner and Corcoran (2012), Yager (2012), Pollack (2015, 2016), and Ter Hofstede and Ratcliffe (2016). In some insects, hearing is thought to function exclusively to detect bat echolocation calls. These insects include nocturnally flying Lepidoptera (moths and nocturnal butterflies), lacewings, mantids, and beetles (Greenfield 2016; Pollack 2016). In other insects, ears have been proposed or demonstrated to function as bat detectors but also serve other functions associated with mating or host location (Greenfield 2016; Pollack 2016). Three general behavioral responses to bat echolocation calls have been described for eared insects (see examples in Table 2). First, flying insects exhibit evasive flight responses including negative phonotaxis, dropping to the ground, or erratic maneuvers (sometimes called acoustic startle responses). Ultrasound-evoked evasive maneuvers have been demonstrated in Lepidoptera (e.g., Roeder 1967; Yack et al. 2007), Coleoptera (e.g., Forrest et al. 1995; Spangler 1988b), Orthoptera (e.g., Schulze and Schul 2001; Dawson et al. 2004), Mantodea (Triblehorn et al. 2008; Yager 2012) and Neuroptera (e.g., Miller and Olesen 1979; Holderied et al. 2018). Second, insects that are not flying may cease their activities or remain motionless in the presence of bat calls. For example, moths reduced their mate seeking behavior in the presence of echolocation calls (Acharya and McNeil 1998; Svensson et al. 2003; Skals et al. 2005), and katydids and moths paused their calling in response to ultrasound (Spangler 1984; Faure and Hoy 2000; Greenfield and Baker 2003). Third, some insects respond to ultrasound by producing defense sounds. These insects include tiger moths (Corcoran et al. 2010), hawk-moths (Barber and Kawahara 2013), and tiger beetles (Yager and Spangler 1997). Ultrasound-evoked sound production may have different specific anti-predator functions, including aposematism or warning, mimicry, startle, and jamming bat sonar (Corcoran et al. 2009; Conner 2014). Responses of insects to bat echolocation sounds are not necessarily simplistic or predictable (Pollack 2015). Insects may respond differentially to sound features that indicate different degrees of threat (e.g., close or distant predator), they may need to distinguish between the sounds of a predator and a mate, or make decisions on how to respond to a predator's sound when there are conflicting demands, such as following a pheromone or singing to a mate.

While bat echolocation has undoubtedly imposed significant selection pressures on the evolution and tuning of ears in nocturnally flying insects, it is arguable that all insects with ultrasonic sensitivity do not necessarily use their hearing exclusively for bat detection. First, many insect ears considered to function as dedicated “bat detectors” are broadly tuned with sensitivity spanning both sonic and ultrasonic frequencies [e.g., moths (Ter Hofstede et al. 2013); mantids (Yager 1996); beetles (Yager and Spangler 1997); lacewings (Miller 1971)]. Such ears may also be capable of detecting incidental sounds of foraging birds and terrestrial vertebrates that produce broadband sounds associated with flight and rustling vegetation (e.g., Jacobs et al. 2008; Fournier et al. 2013) (see also discussion below under bird predators) (Figs. 2 and 3). Second, some insects with ultrasound sensitive ears retain their hearing, or have shifted their hearing to lower sound frequencies once released from the selection pressure of bats (e.g., Fullard 1994; Fullard et al. 1997; Surlykke et al. 1998; Muma and Fullard 2004). Third, the assumption that moth hearing evolved in response to echolocating bats has come under scrutiny. A recent study suggests that hearing organs in Lepidoptera appeared multiple times and millions of years prior to the evolution of bat echolocation (Kawahara et al. 2019). These results led the authors to question the hypothesis that moth ears evolved in direct response to echolocating bats, and to propose that hearing in many moths and butterflies may have evolved to detect other predators, such as the walking or wing-beat sounds of other predators such as birds. We recommend that hearing in insects with ultrasound sensitivity be further tested by assessing behavioral responses to broadband sounds such as those produced by other predators (see below). Moreover, these tests should assess not only escape responses, but also immobility and vigilance (see Fig. 1).

Bird predators: Sounds made and insect responses

Many insects are consumed by insectivorous birds (Chai 1986; Pinheiro 1996; Gibbs 1998; Yard et al. 2004; Orłowski and Karg 2013; Nyffeler et al. 2018), but do birds produce sounds that are detectable by insect prey? Sounds produced by avian predators that could be of importance to insect prey include incidental cues produced by foraging, or, communication signals and calls. We look at these sounds and discuss evidence for insects detecting and/or responding to these sounds.

Table 2 Examples of sounds used by insect prey to detect and avoid predators

Sound	Predator as sound producer						Prey (focal recipient)					
	Species/taxon			Species/taxon			Species/taxon			Species/taxon		
Category	Source/type ^a	Species name	Common name	Order (family)	Species name	Common name	Developmental stage	Response (Behavioral)	Reference			
Cues												
Incidental flight sound	Buzzing of flying bumble bees and wasps	<i>Bombus spp.</i> , <i>Vespa germanica</i> , <i>Encarsia formosa</i>	Bumble bees German wasp	Lepidoptera (Nymphalidae)	<i>Danaus plexippus</i>	Monarch butterfly	“fully grown” larvae	Ducking, twitching, agitation of tubercles, proposed release of volatiles	Rothschild and Bergström (1997)			
Incidental flight sound	Tones of 175–180 Hz and 330–360 Hz	<i>Cotesia sp.</i>	Parasitoid wasp	Lepidoptera (Notodontidae)	<i>Cerura borealis</i>	Northern cerura	Second to fifth instar larvae	Moving tentacles, extending flagella, rearing head	White et al. (1983)			
Incidental flight sound	Tones of 100–160 Hz	<i>Dolichovespula media</i>	Median wasp	Lepidoptera (Noctuidae)	<i>Barathra brassicae</i> (now <i>Mamestra brassicae</i>)	Cabbage moth	Fourth to sixth instar larvae	Stopping movement, squirming, dropping	Tautz and Markl (1978)			
Incidental flight sound	Tones 50–900 Hz	proposed <i>Diptera</i> and Hymenoptera	N/A	Lepidoptera (Nymphalidae)	<i>Danaus plexippus</i>	Monarch butterfly	Fourth, fifth instar larvae	Freezing, contraction of body, flicking	Taylor and Yack (2019)			
Incidental flight sound	Flying wasp (potential near field sounds)	<i>Liris niger</i>	Digger wasp	Orthoptera (Gryllidae)	<i>Acheta domestica</i>	House cricket	Adults and immatures	Head stand, stilt stand, kick escape	Gnatzy and Heußlein (1986)			
Rustling leaf sounds	Rustling sounds and tossed stones	<i>P. capensis</i>	Cape Bulbul bird	Lepidoptera (Noctuidae)	<i>H. armigera</i>	N/A	Adult	Escape flight	Jacobs et al. (2008)			
Signals												
Echolocation	Pulsed ultrasound 20–100 kHz	N/A	N/A	Orthoptera (Tettigoniidae)	<i>Neocoenophalrus ensiger</i>	Eastern sword-bearing conehead	Adult males	Stopped or paused songs	Faure and Hoy (2000)			
Echolocation	Ultrasound (24 kHz)	Bat like sounds presented in a cricket chirp pattern	N/A	Diptera (Tachinidae)	<i>Omia ochracea</i>	Parasitoid fly	Adult females	(In flight) negative phototaxis or landing	Rosen et al. (2009)			
Echolocation	Echolocating bats and artificial ultrasound (23–250 kHz)	N/A	N/A	Orthoptera (Tettigoniidae) and Lepidoptera (Pyralidae)	<i>Insara covilleae</i> and <i>Achroia grisella</i>	Bush katydid and Lesser wax moth	Adult males	Stopped calling	Spangler (1984)			
Echolocation	Pulsed ultrasound (40 kHz)	N/A	N/A	Lepidoptera (Pyralidae)	<i>Achroia grisella</i>	Lesser wax moth	Adult males	Stopped calling, startle response	Greenfield and Baker (2003)			

(continued)

Table 2 Continued

Predator as sound producer	Prey (focal recipient)								
	Species/taxon			Species/taxon					
Sound	Source/type ^a	Species name	Common name	Order (family)	Species name	Common name	Developmental stage	Response (Behavioral)	Reference
Echolocation	Pulsed ultrasound 30 kHz	Resembling aerially hawking and gleaning bats	N/A	Lepidoptera (Noctuidae and Pyralidae)	<i>Pseudaletia unipuncta</i> and <i>Ostrinia nubilalis</i>	True armywormEuropean corn borer	Adults males and females	Male moths aborted flight in a pheromone plume, and females stopped releasing pheromone	Acharya and McNeil (1998)
Echolocation	Pulse train of 30 kHz	Representing bat search call	N/A	Lepidoptera (Noctuidae)	<i>Spodoptera littoralis</i>	N/A	Adult males	Males ceased walking or froze	Skals et al. (2005)
Echolocation	Echolocation calls	<i>Eptesicus fuscus</i>	Big brown bat	Mantodea (Mantidae)	<i>Parasphendale agrionina</i>	Budwing mantis	Adult males	Power dive	Triblehorn et al. (2008)
Echolocation	20–100 kHz pulses	Representing bat search call	N/A	Neuroptera (Myrmeleontidae)	<i>Myrmeleon hyalinus</i> and <i>M. formicarius</i> and <i>Scotoleon carrizonus</i>	Antlions	Adult	Flight cessation, flexed abdomen	Holderied et al. (2018)
Echolocation	40 kHz pulses	Representing echolocation pulses	N/A	Coleoptera (Scarabaeidae)	<i>Euethola humilis</i>	N/A	Adult	Evasive flight	Forrest et al. (1995)
Calling, Song	125 Hz to 16 kHz	Possibly represent bird vocalizations	N/A	Lepidoptera (Satyridae)	<i>Erebia manto</i> and <i>E. euryale</i>	Yellow-spotted ringlet and Large ringlet butterflies	Adult	Twitching, opening and closing of wings, fluttering, escape	Ribaric and Gogala (1996)

^aSounds are either playbacks of natural sounds or simulations of proposed natural sounds. N/A, not applicable.

Do birds produce incidental sound cues while foraging on insects? The enormous diversity of bird species, the habitats they live in, and the insect prey available results in a wide variety of insect capturing methods (see Remsen and Robinson 1990). Foraging strategies of different species feeding on invertebrates include, but are not limited to, pulling prey from the soil, picking from plants or under bark, and various flight capture methods such as aerial hawking, sallying, and aerial gleaning. While all of these foraging tactics likely produce incidental sound cues, there are very few studies that have recorded the sounds generated by foraging insectivorous birds. Fournier et al. (2013) recorded flight sounds from eastern phoebes (*Sayornis phoebe*) while attacking tethered insects, and from chickadees (*P. atricapillus*) when gleaning insects (Fig. 3A). Foraging birds produced broadband sounds with dominant frequencies <20 kHz but with significant energy extending into the ultrasound (>20 kHz). Flight sounds of a bird approaching an insect had distinct repetitive elements (18–20 Hz) that corresponded to the upward and downward strokes of wings during flight. These sounds increased in loudness and frequency bandwidth as they approached the insect. Similar sound characteristics were recorded from other flying birds, although in these cases the birds were not actively foraging on insects (e.g., Mahony 2006; Hall 2014; Clark et al. 2020). Foraging birds also produce sounds by landing on or moving through plant substrates (Jacobs et al. 2008). The sounds of breaking twigs, rustling leaf litter, and crackling underbrush (through various grasses) are broadband sounds with dominant frequencies <20 kHz, but again, with significant energy in the ultrasound (Fullard 1988).

Can insects hear the sound cues generated by foraging birds? The hearing of many insects that are consumed by birds, including butterflies, grasshoppers, cicadas, moths, and mantids, overlaps with the above-mentioned broadband sound cues generated by foraging birds. These insects include many diurnally active, noncalling insects such as butterflies and grasshoppers that have hearing broadly tuned to sounds <20 kHz but with most sensitivity <5 kHz (see Strauß and Stumpner 2015). The adaptive function of these ears remains unknown, but they have been proposed to function in detecting foraging birds. Yet, there have been few experiments testing this hypothesis. Neurophysiological recordings from the auditory nerves of moths and butterflies show that these insects are capable of not only detecting bird flight sounds, but their sensory cells can encode the temporal and amplitude changes associated with

the wing beat sounds of an approaching bird (Fournier et al. 2013; Hall 2014; Mikhail et al. 2018). These authors propose that an insect such as a butterfly can detect a flying bird at ~2.5 m and possibly further. There is also evidence that the rustling sounds of birds landing on bushes are detectable by moth prey (Jacobs et al. 2008). Playbacks of the rustling noises of a foraging bird (*Pycnonotus capensis*) excited auditory cells in a noctuid moth (*Helicoverpa armigera*). When these rustling sounds were simulated in the field, moths responded by flying away. In another study by Dawson et al. (2004), flying locusts (*Locusta migratoria*) responded to both sonic and ultrasonic sounds equally, by negative phonotaxis; although these sounds did not simulate the incidental sounds of foraging birds, the frequencies used to overlap with such sounds. Wild caught wood-nymph butterflies (Satyrinae) responded to sound playbacks of bird flight and snapping twigs by taking flight, and *Morpho* butterflies responded to these sounds after being sensitized by tactile stimuli (Yack lab, unpublished data). Future studies should focus on recording sounds generated by predatory birds foraging on insects, and by conducting playback experiments to assess if and how insects respond behaviorally to these sounds, by flying away or ceasing activity. Also, there is the possibility that foraging birds use counter strategies to render themselves acoustically cryptic to insect prey, either by using sound-reducing feather modifications or flight maneuvers—an intriguing hypothesis worthy of further consideration.

Can insects hear the communication songs and calls of insectivorous birds, and if so, do they use these sounds to assess risk? In the previous section of this review, we saw that it is common for vertebrate prey to eavesdrop on the communication calls and songs of predators. We also discussed examples of insects that are not in flight assessing the risk of bat predation by eavesdropping on their echolocation calls. The typical responses of prey to these sounds are to remain still, increase vigilance, and cease activity. Given these observations, it is surprising that there has been little to no testing of the hypothesis that insect prey use their hearing to eavesdrop on the communication signals of insectivorous birds, although this hypothesis has been proposed (e.g., Ribarić and Gogala 1996; Mikhail et al. 2018). The frequency range of calls and songs of most insectivorous birds is between 1 and 10 kHz (e.g., Samuel 1971; Dooling et al. 2000; Martin et al. 2011), which overlaps with the hearing of many eared insects that are consumed by birds, including diurnal butterflies,

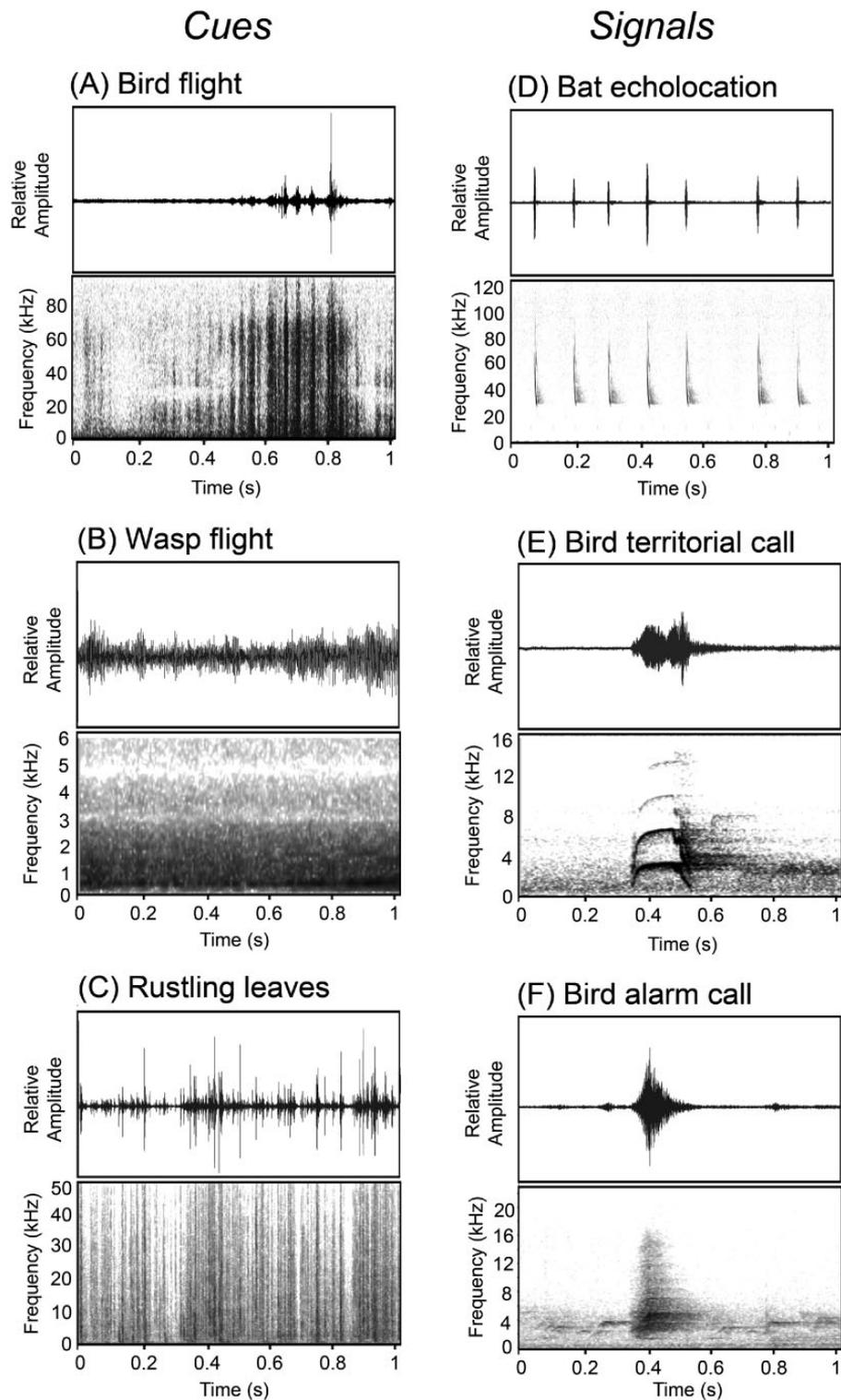


Fig. 3 Sound cues and signals that are of potential significance to insect prey in assessing risk of predation. (A–C) Incidental cues produced by predators, including (A) flight sounds of an insectivorous bird, the eastern phoebe (*S. phoebe*), attacking a tethered moth; (B) flight sounds of a predatory wasp (*Polistes* sp.); (C) rustling sounds of leaves indicating a foraging terrestrial predator. (D–F). Predator communication signals, including (D) the echolocation call of an aerial insectivorous bat, the big brown bat (*Eptesicus fuscus*); (E) a territorial call of an insectivorous bird, the rufous-tailed Jacamar (*G. ruficauda*); (F) an alarm (distress) call of an insectivorous bird, the barn swallow (*Hirundo rustica*). Sounds of the eastern phoebe, the predatory wasp, and rustling leaves were recorded by J.E.Y., the bat call was provided by J. Ratcliffe, and the jacamar and barn swallow calls were obtained from Xeno-Canto (Files: XC522878 and XC511681).

crickets, grasshoppers, cicadas, and moths (Yack 2004; Yack and Dawson 2008). Neurophysiological recordings from the auditory nerves of the blue morpho butterfly (*Morpho peleides*) showed that the ears are very sensitive to the territorial calls of one of its predators, the jacamar (*Galbula ruficauda*) (Mikhail et al. 2018) (Fig. 3E). It is possible that insects use calling songs of predators to assess risk, and that they respond to these sounds by remaining stationary, increasing alertness, or flying in the opposite direction of the sound source.

Terrestrial predators: Sounds made and insect responses

There are also many terrestrial predators of insects. These include mammals (shrews, rodents), reptiles (snakes, lizards), amphibians (frogs, toads), and other invertebrates (spiders, mantids, beetles) (Buckner 1966; Schoenly 1990; Churchfield and Rychlik 2006; Manicom and Schwarzkopt 2011). When moving through vegetation, animals generate incidental sound cues including the snapping of twigs, and the rustling of leaves and grasses (e.g., Goerlitz et al. 2008; Haff and Magrath 2010; Page and Bernal 2020). However, to the best of our knowledge, the incidental sounds of terrestrial predators have not been recorded in the context of pursuing insect prey. Also, as discussed above in the context of bird predators, there are no examples of insect prey attending to the calls and songs of terrestrial predators to the best of our knowledge. We recommend that the incidental sound cues and communication signals of terrestrial predators of insect prey be recorded and played back to assess their responses.

Flying insect predators and parasitoids: Sounds made and insect responses

Many insects are attacked by flying insect predators or parasitoids (e.g., flies, wasps, and dragonflies) (Greathead 1963; Steiner 1981; Alonso-Mejia and Marquez 1994; Hedwig and Robert 2014). Aerial insect enemies produce flight sounds as they approach a prey. As noted in the previous section of this review, flying insects generate sounds with frequencies extending up to 5 kHz (e.g., Offenhauser and Khan 1949; Sotavalta 1963; Raman et al. 2007; Rashed et al. 2009; Potamitis and Rigakis 2016). These sounds overlap with the hearing sensitivity of insects that possess both near-field and far-field hearing organs (Figs. 2 and 3). There are several examples of insect prey detecting and responding to the sounds of aerial insect enemies (Table 2). Several

species of caterpillars, including those of monarch butterflies and cabbage moths, respond to simulated sounds of flying insects by flicking or dropping from a plant (e.g., Myers and Smith 1978; Tautz and Markl 1978; Taylor and Yack 2019). There is increasing awareness that near-field sound reception is widespread in insects, but in most cases, the function and mechanisms of this form of hearing have not been well documented. These near-field receptors are likely an important mechanism for risk assessment in insect prey attacked by aerial invertebrate enemies and the topic warrants further investigation.

Sounds made by nonpredators

In the first part of this review, we saw that vertebrate prey commonly attend to sounds of nonpredators, and in particular, the alarm calls of both conspecifics and heterospecifics. To the best of our knowledge, there are no examples of insect prey listening to the passive or active sounds of nonpredators. All examples of acoustically-mediated alarm signals in insects are those communicated by solid-borne vibrations (see Virant-Doberlet et al. 2019).

Conclusions

The main goal of this study was to assess how insects use their hearing to detect and avoid predators. While many insects have ears, little is known about how hearing is used to assess the risk of attack by nonbat predators. To identify the kinds of sounds that insect prey might use, we reviewed the literature on hearing-mediated predator avoidance in vertebrates. We identified a variety of sound sources that vertebrate prey use to assess risk, including incidental sound cues and communication signals generated by predators and nonpredators. We then reviewed the literature to assess whether predators of insects produce similar types of sounds, and if insects pay attention to these sounds. Some important insights emerged from our review. First, there is a lack of research on the passive sound cues generated by predators of both vertebrates and insects, and correspondingly, how prey use these sounds in risk assessment. Such sounds include those produced as byproducts of flying, splashing, or moving through vegetation. Considering that predators regularly use incidental sound cues to detect prey, it is highly probable that, on the flip side, prey use incidental sound cues to detect predators. Second, there are numerous examples of vertebrate prey eavesdropping on the calls and songs of their predators to assess predation risk, yet there are very few examples of insect prey listening for such sounds, aside from

bat echolocation calls. Likewise, there are many examples of vertebrate prey attending to alarm calls of conspecifics or heterospecifics, but there are no reported examples of insects using such sounds. Third, many eared insects are capable of detecting the sounds generated by nonbat predators. For example, diurnally active butterflies and many grasshoppers have ears that are broadly tuned to sounds <20 kHz. These insects do not produce sounds for communication and do not fly at night, yet have well developed hearing. So we propose that these insects, like nonsound producing vertebrate prey (e.g., rabbits and some lizards), use their ears primarily to detect nonbat predators. Also, while many insect ears are considered to be “dedicated” for a specific purpose, such as mate recognition or bat detection, they may also function to detect nonbat predators. Many insect ears are complex organs with multiple sensory cells and capable of discriminating temporal, frequency, and amplitude characteristics of sounds, and their capabilities for functioning in more than one context may be underestimated. We recommend that further research be conducted to test the hypothesis that insects use their ears to assess risk of attack by predators other than aerial hunting, echolocating bats. This research should include recordings of ecologically relevant sounds produced by predators, nonpredators, and parasitoids, and playback studies that assess neurophysiological and behavioral responses to these sounds. When assessing behavioral responses to sound, it is important to consider that insects may respond by not responding at all, or by becoming sensitized to other threatening stimuli, and assessments of hearing-mediated risk assessment in insects should not focus exclusively on classic escape behaviors. While this article focused on hearing-mediated risk assessment, it is important to note that prey may require input from other sensory modalities (e.g., vision and tactile) in combination with hearing to initiate a defensive response, and such multimodal stimuli should also be incorporated into future studies.

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