# Ultrasonic hearing in moths

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**Abstract.** Many moths possess ultrasound-sensitive ears, directly resulted from bat predation. Moth ears display an abundant diversity due to their body location, accessory structures, and number of auditory sensory cells. Anatomically, the moth ears are the simplest hearing organs in insects and most are tympanal organ with a tympanum. Eared moths have an optimal frequency range between 20 kHz and 50 kHz, which coincides with the peak frequency used by most insectivorous bats. The primary function of the moth ear is to detect and avoid the hunting of bats. Eared moths show a series of defensive behaviors, when they are exposed to the cries emitted by insectivorous bats. The presence of these tympanal organs also set the stage for the later evolution of ultrasonic courtship signals in the eared moth families. Over the years, entomologists worldwide have performed large numbers of studies on hearing of moths and their interactions with bats. This paper presents an overview of moth hearing, focusing on morphology, neurophysiology, and behavioral ecology.

Résumé. L'audition ultrasonique chez les papillons nocturnes. Beaucoup de papillons de nuit ont des organes d'audition sensibles aux ultrasons, ce qui résulte d'une adaptation à la prédation par les chauve-souris. Ces organes d'audition présentent une abondante diversité en ce qui concerne leur position sur le corps, leur structure, et par le nombre de cellules sensorielles. Anatomiquement, ces organes d'audition ont une fréquence optimale de réception comprise entre 20 et 50 kHz, ce qui coincide avec le pic des fréquences utilisées par la plupart des chauves-souris insectivores. La fonction primaire de ces organes est de détecter la chasse par les chauves-souris et de permettre d'y échapper. Les espèces pourvues de ces organes présentent toute une série de comportements défensifs dès qu'elles sont exposées aux cris émis par les chauves-souris. La présence d'organes tympaniques parvient à un stade tel qu'elle permet l'évolution de signaux ultrasoniques de parade nuptiale chez plusieurs familles. Depuis longtemps, les entomologistes du monde entier ont fait de nombreuses études sur l'audition des papillons nocturnes et ses interactions avec les chauves-souris. Le présent article présente une revue de l'audition de ces lépidoptères, avec une attention particulière sur la morphologie, la neurophysiologie et l'éco-éthologie.

Keywords: Moth, ultrasound, tympanal organ, neurophysiology, behavioral ecology.

I nsects can detect a broad range of acoustic signals transmitted through air, water, or solids. In moths, hearing plays an important part in detecting and evading predators and in locating and selecting appropriate mates (Skals *et al.* 2003; Waters 2003). It is believed that moth ears evolved from internal proprioceptors (Fullard & Yack 1993), and directly resulted from bat predation (Miller & Surlykke 2001). Hearing in moths has evolved independently at least seven times (Yack 2004), and has led to an equally rich diversity of ears. These tympanal organs are found at various body locations, including the thorax (e.g. Noctuoidea), mouthparts (e.g. Sphingoidea), wings (e.g. Thyridoidea) and abdomen (e.g. Geometroidea), and have distinct designs (Yack & Fullard 1993; Surlykke *et al.* 2003; Yack 2004), but with common features, like a scolopidial sense organ. Phylogenetic comparison revealed that scolopidial sense organs are in the same place in hearing and non-hearing species, while hearing species having external structures elaborated for perception of ultrasound. Thus, the scolopidial sense organs of non-hearing species represent the evolutionary prototype to hearing species tympanal organs (Yack & Fullard 1990; Yack *et al.* 1999).

In 1877, White first suspected that moths have ears used to hear the calls of the bats (Payne et al. 1966). Studies of moth hearing have not attracted great interest among entomologists, until a report showing that moths respond to ultrasound with a number of avoidant maneuvers was published by Treat in 1955 (Waters 2003). Minet (1983) and Spangler (1988) had

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Oscillogram of the auditory (top trace) and tymbal response (bottom trace) in *Cycnia tenera*. A, A1 cell; B, B cell, (after Fullard *et al.* 2003)

reviewed the previous studies on the anatomy of moth ears, defensive behavior in response to ultrasound and ultrasonic communication. But following the development of new acoustic, biomechanical, and physiological techniques, scientists have explored the key elements involved in moth hearing and have provided new ideas for understanding the ultrasonic hearing of moths.

This paper reviews studies on moth hearing, especially focusing on the morphology, neurophysiology and behavioral ecology of moth ears. Furthermore, some problems involved in the understanding of moth hearing are highlighted.

### Auditory system

Anatomically, moth ears are among the simplest of all insect hearing organs. They have only 1–4 auditory A cells and a non-auditory B cell, depending on the species. Typical extracellular neurophysiological recording made from the noctuid tympanum is shown in fig. 1, illustrating how the noctuid A1 cells respond to an ultrasonic stimulus, and also showing the firing of the B cell. For example, the ears of notodontids have a single A cell, noctuids have two A cells, and geometrids, pyralids and drepanids have four A cells (Surlykke 1984; Surlykke & Filskov 1997; Fullard *et al.* 1998; Roeder 1998). Most moth ears are tympanal organs, which are usually defined by the presence of a tympanal membrane. There are three sub-structures to



Figure 2

Horizontal section through the right ear of a noctuid. Modified from Treat & Roeder (1959).

characterize the tympanal ears, which are the tympanal membrane, a large tracheal sac that opens to the outside, and chordotonal organs associated with the tympanal membrane (Fig. 2) (Hoy & Robert 1996; Yack 2004). Tympanal hearing has been well documented in ten superfamilies of Lepidoptera (Yack & Fullard 1993; Surlykke *et al.* 2003; Yack 2004) (Fig. 3).

The ear of noctuid is a typical tympanal ear (Fig. 2) and has been studied in great detail (Roeder 1998; Blackburn 2007). Noctuid ears are positioned on the lateroposterior edge of the metathoracic segment, and comprise a tympanum and associated structures (Eaton 1987). The tympanum is normally covered by a thin layer of fine scales and lies in a shallow cavity that in most cases has a movable covering or "hood". It is an approximately 0.5–2 mm diameter circular and 0.5–1 µm thick membrane depending on the moth size (Yager 1999). A countertympanic membrane behind the air sac faces the countertympanic cavity, opening to the outside. The auditory sensory cells (A1 and

A2 cells) bear a fine distal process ending in a minute refractile structure that extends toward the tympanum. The B cell attaches to a short projection, the Bügel, which extends into the body from the medial rim. Centrally, all cells project via the tympanal nerve to the pterothoracic ganglion (Boyan *et al.* 1990; Roeder 1998).

Notodontid moths possess paired ears similar to the noctuid family, but with a single sensory cell (Fullard *et al.* 1998). The B cell lies on the wall of the tympanic cavity, as notodontid moths do not have the Bügel structure. In addition, the notodontid ear has no abdominal hood covering the tympanic cavity and no nodular sclerite, making the conjunctiva continuous with the tympanum (Fig. 4) (Surlykke 1984).

Surlykke and her colleagues (2003) find the ears of drepanid moths have an internal tympanum in which auditory cells are embedded. This is structurally different from other moth ears. The drepanid ears are located at the first abdominal segment, near the base of



#### Figure 3

Diagrammatic view of a "generalized" moth, which shows the locations on the body where tympanal hearing organs have been descrided in various species of moths. Modified from Fullard (1998).

the sternum. The tympanum is a smooth, transparent membrane, formed by two layers of tracheal epithelial tissue that stretch across an opening between two cuticular oval chambers. The tympanal nerve arises from the anterior branch of the first abdominal ganglion, and enters the tympanic cavity medially, terminating in four sensory cells. Each sensory cell belongs to a scolopidial unit (Fig. 5). The scolopidia are "sandwiched" between two layers of tympanum (Yack 2004). Two larger scolopidia span the midregion of the tympanum, while the two smaller ones occur at the median end of the sclerotized tympanal frame (Surlykke *et al.* 2003).

The ears of geometrids are also on the pleural-ventral surface of the first abdominal segment (Surlykke & Filskov 1997). In geometrid moths, the two ears are served by a common tracheal air sac. A sclerotized bridge (the ansa), which is unique to Geometridae, extends across the tympanum. The dendrites of four sensory cells attach to the tympanum and fold back on themselves.

In two distantly related subtribes of Sphingidae, the Choerocampina and the Acherontiina, the labral pilifers and the labial palps form hearing organs (Göpfert & Wasserthal 1999a b; Göpfert *et al.* 2002). In both subtribes, the labial palp serves as an accessory auditory structure that increases the acoustic sensitivity and a single auditory sensory cell is located in the labral pilifer. Choerocampine ears use a thin area of cuticle backed by a large air sac that serves as a tympanum. However, overlapping scales functionally replace the tympanum in hearing Acherontiina.

# Neurophysiological properties

# **Frequency tuning**

Frequency content is one parameter of sound carrying special information for insects. To enable frequency discrimination, individual receptors differ in their relative sensitivities to sounds of different frequencies (Mason & Faure 2004). However, the ears of most noctuid moths have only two auditory cells, with identical tuning curves (Waters 1996). It has been suggested that noctuid moths have no capacity for frequency analysis (Wyttenbach & Farris 2004).

It has been shown that the frequency-sensitivity range of moth ears nicely reflects the frequency range of the echolocation calls of sympatric bats (Rydell et al. 1997; Jones & Waters 2000; Pavey & Burwell 2005; Barber & Conner 2006). Electrophysiologyical data suggest that noctuid moths are able to hear ultrasound in the range from 10 to 100 kHz with an optimal frequency range between 20 and 50 kHz. For example, a noctuid moth audiogram is shown in Fig. 6. The echolocation calls of many bat species, calls used to hunt prey, are generally within this frequency range (Norman & Jones 2000). The optimal frequencies of moth ears differ between taxa. The ears of Sphingidae are syntonic with optimal frequencies between 20 and 25 kHz (Göpfert & Wasserthal 1999b). The threshold curves of geometrid moths auditory sensory cells show optimal frequencies around 20-30 kHz (Surlykke & Filskov 1997). Moreover, the ears of hooktip moths have a peak of sensitivity in the interval 30-60 kHz (Surlykke et al. 2003).



#### Figure 4

Drawings of the right ear of a notodontid *Phalera bucephala* (A) and a noctuid Barathra brassicae (B). C, conjunctiva; TM, tympanum; NS, nodular sclerite. Modified from Surlykke (1984). The mechanical properties of noctuid moth ears have been described for the species *Prodenia eridania* (Cramer) (Lepidoptera, Noctuidae) (Adams 1972). It was found that a low-threshold frequency region of the hearing of this species exist, covering the frequency range between 20 and 100 kHz, with maximum sensitivity at 60 or 70 kHz. It has been hypothesized that the frequency of the tympanic membrane mechanical resonance is not constant in flying moths. Vorotsov and Lapshin (2002) have demonstrated that noctuids have the capacity for tuning the mechanical resonance frequency of the tympanic membrane within the range



#### Figure 5

Tympanal scolopidia of a male *Drepana arcuata*. AC, attachment cell; E, enveloping cell; F, system of longitudinally oriented fibrils; P, perineurium cell; Sc, 'scolopale' region, with scolopale rods, cap and dendritic cilium; SC, sensory cell; SU, scolopidial unit; TN, tympanal nerve. Modified from Surlykke *et al.* (2003).

of several dozens of kilohertz.

Surlykke *et al.* (1999) first reported that the body size of eared moths could affect auditory receptor sensitivity. The ears of large moths are more sensitive than those of small species. The relationship between body size and the frequency that optimally stimulate bat echolocation calls have been investigated in a range of noctuid moths (Norman & Jones 2000). The data indicate that larger moths have lower thresholds at their optimal frequency than smaller moths. There is a linear relationship between the moth wing-length and the wavelength of sound at the optimal frequency. Norman and Jones (2000) suggest that moth size may partly constrain the optimal frequency.

A sex-based auditory dimorphism in Lymantriidae was first reported in 1988 (Cardone & Fullard 1988). The ears of male gypsy moths are tuned to the echolocation range of 30–50 kHz, however females of the species are tuned to peak frequencies of 10–20 kHz. Cardone and Fullard (1988) suggest that a possible explanation for the auditory sexual dimorphism of *Lymantria dispar* (Lepidoptera, Lymantriidae) is that only the males of the species are exposed to the predation pressures of insectivorous bats but that the female species are not exposed to those pressures and possess ears that are degenerated.



#### Figure 6

Audiogram of the A1 and A2 cells of the noctuid moth Agrotis segetum (N = 10 individuals) (after Waters 2003).

### Intensity coding

Intensity coding enables the moth ear to detect relevant ultrasonic signals in complex surroundings. The intensity of an ultrasound signal is coded in the A cell discharge of the noctuid as: the numbers of A spikes per second, the activity in one or in both A cells, the duration of the after-discharge and the response time (Roeder 1998).

The auditory sensory cells differ by 20-30 dB in noctuid moths, and A1cells are more sensitive than A2 cells. It has been suggested that the intensity range fractionation provided by the A1 and A2 cells underlies a switch in the type of escaping behavior as the distance between bat and moth decreases (Yager 1999). The form of the intensity characteristic strongly depends on the stimulus duration (Adams 1971). The response is approximately an impulse response with a short-duration stimulus as opposed to a nonmonotonic response, with a very long stimulus. The stimulus level required to produce regular A1 cell spike trains is greater with short-duration stimuli than with stimuli of long-duration (Fig. 7) (Waters 1996). It was subsequently suggested that the non-monotonic characteristics are attributed to intensity-related changes in response adaptation (Adams 1971).

The A1 cell shows a non-monotonic intensity response function with stimulus durations of 45 ms to 1 s, while the A2 cell displays a monotonic increase in spike rate with intensity. The relationship between the increase of A2-cell response and the decrease of A1-cell response is linear and significant (Fig. 8) (Coro & Pérez 1984). A possible explanation is that an inhibitory interaction exists between the two cells and is a mechanism for the decline in A1 cell responses at high intensities. Fullard *et al.* (1998) has tested this hypothesis using notodonid moths, with singlecelled ears. In their experiments, the A1 cells of the moths showed non-monotonic response curves at high stimulus intensities and no relationship with the B cell. They conclude that the non-monotonic firing response of the A1 cell is caused by tympanal motion non-linearity and cellular adaptation in both singleand multi-celled moth ears.

# Time

The ability of moth ears to hear bat echolocation calls is not only affected by the frequency parameters of the calls but also by the time parameters of the calls (Jones & Waters 2000). For example, the echolocation pulse period is used by Cycnia tenera (Hübner) (Lepidoptera, Arctiidae) to discriminate an attacking bat (Fullard et al. 2007). A female Achroia grisella (Fabricius) (Lepidoptera, Pyralidae) only uses pulse rate to discriminate male calls that attract receptive females within a radius of several meters from bat echolocations (Greig & Greenfield 2004). Many tests of temporal sensitivity have measured either integration (the summation of information over time) or resolution (the detection of rapid changes) (Wyttenbach & Farris 2004). The Integration time is often used to express temporal integration, and has been measured several times in noctuid moths (Surlykke et al. 1988; Waters & Jones 1996; Tougaard 1996 1998).

It is believed that the integration time of the moth ear that behaves as an energy detector is 25 ms (Surlykke *et al.* 1988). In the amplitude modulation experiments, the degree of the auditory response synchronization depends on the temporal cues but not on the type of carrier. It has been confirmed that the temporal cues are foundations for amplitude



#### Figure 7

The number of stimulus-locked A1 action potentials for three stimulus durations with increasing stimulus intensity (N = 3 individuals, N = 5 stimulus presentations per individual) (after Waters 1996).

modulated detection. The thresholds of two species of noctuid moths for single clicks and pairs of clicks with a separation of 1-20 ms were measured. With a 1ms separation, the thresholds for single clicks were higher than the thresholds for double clicks. A comparison between these results and previously published results with pure tone intensity/duration trading indicates that a common underlying mechanism exists based on the passive electric properties of the receptor cell membrane (Tougaard 1996). In addition, different time constants can characterize the temporal integration in the noctuid ear. The information for temporal integration and receptor cell resolution can be provided by the intrinsic time constant that is measured in doubleclick experiments (Tougaard 1998). Though a lot of information about temporal integration in the moth ear is known, further studies are needed to establish its overall importance.

### B cell

In previous studies, there have been different views about the role of the B cell in the interpretation of ultrasonic signals. Some studies indicate that the B cell is inhibited by pulsed ultrasonic stimuli. Lechtenberg (1971) monitored spike activity of the B cell during both stationary flight and acoustic stimulation. During stationary flight, acoustic stimuli could affect the B cell spike repetition rate that was unaffected by the wing movements. This suggests that a significant function of the B cell is not proprioception of flight activity. The inhibition of the B cell varies with pulsed, relatively intense bursts of ultrasound. Lechtenberg (1971) speculated that a possible function of the B cell was in relation to avoidance behavior of flying moths. Lapshin and Fyodorova (2000) found that mechanical pushing of the thorax caused either an increase in the average spiking frequency of the B cell or a phasic response timed changes of stimulus in conditions of acute experiments. The morphological characteristics of the cells B and A1 indicate that the B cell is a receptor of the self-generated clicks of nocturnal acoustical moths (Lapshin & Fyodorova 2000).

However, there has been indirect evidence that the B cell can be driven at various discharge frequencies by the thoracic deformations associated with wing-beats (Payne *et al.* 1966). These discount the role of the B cell as an auditory receptor. A series of subsequent studies supported the conclusion that the B cell is not an auditory receptor (Surlykke 1984; Yack & Fullard 1990; Fullard *et al.* 2003). Recordings from *Pheosia tremula* Clerck (Noctuoidea, Notodontidae) have shown that the spikes from B cells are not affected by sound stimuli. Extracellular recordings of the tympana nerve in *Actias* 

*luna* (Linnaeus) (Bombycoidea, Saturniidae) revealed that the B cell spontaneously fires in a regular pattern. A recent study by Fullard and his colleagues (2003) showed that the B cell plays no auditory role during an attack of natural durations, repetition rates and intensities. They concluded that the B cell responded to the ultrasounds used in Lechtenberg's experiments (1971) because the ultrasounds were powerful enough to artifactually elicit the proprioceptive responses of the B cell. However, it is far from clear what role the B cell really plays in moth hearing.

#### **Behavior responses**

### **Predator detection**

The primary function of the moth ear is to detect and avoid the hunting of bats (Conner 1999). It is well known that most moths use their ears solely to detect the echolocation calls of bats and activate evasive behaviors. When eared moths are either spatially or temporally separated from bats, they will lose their ears completely or retain fully functional ears for non bat-detecting purposes (e.g., conspecific calls) (Fullard 1994; Fullard *et al.* 1997; Fullard *et al.* 2004; Muma & Fullard 2004; Fullard *et al.* 2007). The absence of bats in the islands of Tahiti and Moorea has caused



#### Figure 8

Relation between stimulus intensity and tympanic organ responses to acoustic pulses (34 kHz and 45 ms) (after Coro & Pérez 1984).

the neural circuitry that normally controls the acoustic startle response behavior in bat-exposed moths to become decoupled from the functionally vestigial ears of endemic Tahitian moths (Fullard *et al.* 2004). *Archiearis parthenias* (L.) (Geometridae, Archiearinae), which is a dayflying moth, is practically deaf at bat-relevant frequencies (above 25 kHz) (Surlykke & Skals 1998). A reasonable hypothesis is that the moth ear derives from the predation pressure exerted by bats. A number of studies on the interaction between bats and moths have been performed in the field and laboratory (Miller & Surlykke 2001; Hristov & Conner 2005; Fullard *et al.* 2007).

The avoidance behaviors of moths are usually similar among species and depend greatly on the location of the echolocating bat. Noctuid moths have a stereotyped two-phased behavior in response to the calls of an approaching bat. Moths will make negative phonotactic maneuvers when bats are distant and more erratic nondirectional responses when bats are close. In the woodland, flying geometrid moths respond to sound bursts imitating the echolocation calls of aerial-hawking bats. They may quickly dive or circle towards the ground or rapidly shift their flight course one or more times (Svensson & Rydell 1998). In the laboratory, moths respond to bat-like sound, with turns, loops, dives, and a number of other maneuvers (Dawson et al. 2004; Svensson et al. 2004). A series of research investigations in the field have confirmed that these escape maneuvers are efficient (Acharya & Fenton 1999). Moths that hear the calls of a bat and show escape behaviors have a considerable survival advantage (Fullard 1991; Rydell & Lancaster 2000).

Eared moths have many more subtle behavior strategies. For example, the ultrasonic calls produced by male greater wax moths, *Galleria mellonella* (Linnaeus) (Lepidoptera, Pyralidae) can elicit female's wingbeats. If females hear the calls of an echolocating bat, they will not display wing fanning. The presence of male moth calls and bat calls synchronously, will reduce the displaying rate of females (Jones *et al.* 2001). Female lesser waxmoths *A. grisella* are attracted by the ultrasonic signals of males, and then run toward signaling males. But females will cease orientation and freeze movement if simultaneously present with the hunting bat calls (Greenfield & Baker 2003).

In addition to negative defensive strategies, active defensive behaviors are present in eared moths. The high-frequency clicks emitted by certain tiger moths could cause an attacking bat to break off it pursuit (Fullard *et al.* 1994). These sounds have a broad frequency spectrum though they are rather variable, even from the same individual. Three possible defense

mechanisms have been hypothesized: the startle, aposematism and jamming mechanisms.

The startle hypothesis supposes that the clicks trigger the bat startle reflex that may allow the moth to escape. It is reported that bats would be startled by the clicks presented for the first time (Miller 1991). A second possibility is that the sounds indicate to the bat that the moth is unpalatable (Ratcliffe & Fullard 2005). In order to find out what the clicks mean, Hristov and Conner (2005) chose four species of arctiid moths, with differences in distastefulness levels and sound production. In their experiments, the bats quickly learned to avoid clicking moths only if the clicks were associated with noxious taste. Barber and Conner (2007) found that some tiger moths mimic the sounds of the noxious tiger moths to avoid being eaten by the bats. The results supported that the sounds are, in essence, a warning to the bats that the moth is distasteful. Finally the jamming hypothesis assumes that the clicks disrupt the neural mechanism for encoding the time of arrival of the echo. It was demonstrated that the clicks of dogbane tiger moth C. tenera are emitted in the terminal phase of the bat echolocation (Fullard 1994; Barber & Conner 2006). Tougaard et al. (1998) used combinations of a broadband click and a test signal to stimulate the bats. They recorded responses of single units in the nuclei of the lateral lemniscuses of bats to the stimuli. It was showed that clicks could interfere with most unit neural responses. These hypotheses are not mutually exclusive. Depending on the species (bats and moths) and the experience of the bats, clicks may work differently (Conner 1999).

# Communication

The ears of certain moths are not only used to detect bats but also to select mates (Jang & Greenfield 1996 2000; Collins et al. 1999; Skals et al. 2003; Brandt & Greenfield 2004; Nakano et al. 2006). Ultrasonic communication systems have evolved in Arctiidae, Pyralidae, Noctuidae, Sphingidae, Nymphalidae, and Crambidae (Table 1). Ultrasound plays an important role in these moths' courtship behaviors. For example, Conner (1987) reported that the production of ultrasound is sufficient to ensure copulation for C. tenera. He compared the mating capabilities of six groups of males C. tenera: normal males, males without their courtship pheromone, aphonic males, males without pheromone and sound, and control males. The mating success rate of the males without sound was 90%, and the rate of the males without both pheromone and sound was only 57%, while all the rates of the other groups were 100%. It was also reported that male-produced ultrasound serves as a courtship song in the Asian corn borer moth, Ostrinia furnacalis (Guenée) (Lepidoptera, Crambidae) (Nakano et al. 2006). A significant difference in the incidence of three behavioral responses to courting males, i.e., immediate acceptance, acceptance after walking, and rejection, was showed between deaf and hearing females in the flight tunnel experiments. Hearing females showed less 'rejection' and more 'acceptance after walking' than deaf females (Nakano et al. 2006). According to the description by Conner (1999), ultrasonic signals are involved in species recognition, in male-male competition for mates, and in female mate-choice systems.

The sounds emitted by the male greater wax moths, *G. mellonela*, have the temporal and spectral characteristics that are similar to the calls of frequencymodulated bats. Therefore, it is surmised that female moths are able to distinguish between the attractive signals of male conspecifics and similar sounds made by predatory bats. This view has been confirmed by some experiments (Jones *et al.* 2001). It has been suggested that the distinction between bats and conspecifics must be based on temporal cues (Skal & Sulykke 2000).

In the lesser wax moth *A. grisella*, male moths emit ultrasonic signals to attract receptive females within 1-2 m. When 20 cm apart, individual males significantly increase their signal rates. At separation distances of 40 cm or more, signal modification does not occur (Jia *et al.* 2001). The phenomenon is considered a form of signal competition.

It is well known that females choose males on a relative basis and evaluate primarily three signal features: signal rate, loudness, and the asynchrony interval (Jia *et al.* 2001). *A. grisella* females preferentially oriented towards the calls of males that were louder, delivered sounds with higher rates and more evenly spaced pairs of pulses, and included longer pulse lengths and longer

silent intervals within pairs of pulses. A male may have more attractiveness to females, if it sings with higher peak amplitudes and longer asynchrony intervals and for longer nightly periods (Brandt & Greenfield 2004; Brandt *et al.* 2005). Signal preference was based on acoustic energy and the power of the male signals (Jang & Greenfield 1996). In *O. furnacalis*, the ultrasound signals produced by males appears to function only near the end of the courtship. Therefore Nakano *et al.* (2006) believed that the sound appears to be important in the context of intraspecific mate choice, rather than for interspecific reasons (i.e., species recognition).

# Conclusion

During the past 50 years, researchers have gathered plentiful information on moth hearing, but there are still many fundamental questions unanswered and some areas unexplored. What mechanisms allow the two ears of geometrid moths to be served by a common tracheal air sac? What role does the ultrastructure of the tympanum play in moth hearing? Does an ultrasonic masker present in the moth hearing?

In addition, no relative report on the molecular mechanisms underlying moth hearing have been published to date, although munch molecular research is being conducted on the ears of *Drosophila* (Kim *et al.* 2003; Lu 2004; Göpfert *et al.* 2006). As a new genetic model system, the *Drosophila* auditory system is used to investigate the molecular mechanisms of insect and vertebrate hearing (Caldwell & Eberl 2002). However, the ears of moths are greatly different from those of *Drosophila* anatomically. Further study is needed on the molecular mechanisms of moth ears to understand the differences in the hearing of moth ears to those of *Drosophila*.

Family	Species	Structure	References
Arctiidae	Cycnia tenera, C. oregonensis, Euchaetes egle, Halysidota tessellaris	The modified thoracic episterna	Fullard 1992
Pyralidae	Symmoracma minoralis	The very complex structure located in the last abdominal segment	Heller & Krahe 1994
Noctuidae	Thecophora fovea	The 1. tarsal segment of the metathoracic leg and a modified part of the hindwing	Surlykke & Gogala 1986
	Pseudoips prasinana, Bena bicolorana	The ventral tymbal organ located in a cleft in the second abdominal sternite	Skals & Surlykke 1999
Sphingidae	<i>Psiligramma</i> sp.	The genital stidulation	Conner 1999
Nymphalidae	Hamadryas feronia	The wing	Yack <i>et al.</i> 2000
	Heliconius cydno alithea	The wing	Hay-Roe & Mankin 2004
Crambidae	Ostrinia furnacalis	The wing	Nakano <i>et al.</i> 2006

Table 1. The occurrence of structures of sound production in Lepidoptera.

It is well known that the larvae of a great number of moths are important agricultural pests, and existing control methods typically have negative impacts on the environment. Since eared moths respond to ultrasounds that are emitted by the bats or by intraspecific males/ females, certain frequency ultrasounds may be used to control these species. It has been demonstrated that the ultrasound frequency coinciding with the calls of local foraging bats can make the moths display a series of evasive behaviors. The echolocation calls of sympatric aerial-hawking bats also reduce the average flight time of moths (Fullard et al. 2003). In addition, ultrasound can affect spermatophore transfer, larval numbers, and larval weight of moths (Huang et al. 2003). Acoustic methods could provide effective behavioral management strategies. In contrast to driving out moths, ultrasound could also be used to trap certain moths that use ultrasonic communication systems. We can utilize male moth calls, natural or artificial, to attract female species, similar to the use of sex pheromones. Of course, the long-term safety of acoustic methods needs to be estimated.

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