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REVIEW

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**‘UN CHANT D’APPEL AMOUREUX’: ACOUSTIC COMMUNICATION IN MOTHS**

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**Summary**

**Tympanal sound receptors in moths evolved in response to selective pressures provided by echolocating insectivorous bats. The presence of these ultrasound detectors also set the stage for the later evolution of ultrasonic courtship signals in the tympanate moth families. Male moths have repeatedly exploited the bat-detection mechanisms in females for the purpose of finding, identifying and obtaining mates. Ultrasonic courtship has been described in several members of the moth families Arctiidae, Noctuidae and Pyralidae, and ultrasound is predicted to play a significant role in the courtship of other tympanate moths including the Sphingidae, Lymantriidae, Notodontidae and Geometridae. Ultrasonic signals are**

**involved in species recognition, in male–male competition for mates and in female mate-choice systems.**

**Pre-existing motor systems, including those involved in bat defence, have also been exploited for the purpose of generating high-frequency courtship signals. Sound production mechanisms in moths include thoracic tymbals, tegular tymbals, alar castanets and genital stridulatory organs. Thus, in both their sensory and motor aspects, the weapons of bat/moth warfare have frequently evolved into components of courtship systems.**

Key words: ultrasound, courtship, sexual selection, bat, moth, communication.

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**Introduction**

Any insect that flies at night must deal with echolocating insectivorous bats. The most common response to this potent predation pressure has been the development of insect ears whose sensitivity extends into the ultrasonic frequencies (i.e. above 20 kHz). Insects that hear the echolocation cries of bats include members of the insect orders Dictyoptera, Orthoptera, Neuroptera, Coleoptera and Lepidoptera (Fullard and Yack, 1993; Hoy, 1989). Sound receptors appear to have evolved repeatedly and easily from vibration-sensitive proprioceptors (Fullard and Yack, 1993; Yack, 1992; Yack and Fullard, 1990; Yack and Roots, 1992) in multiple locations on the insect body. The Lepidoptera have evolved numerous sound receptor organs, including metathoracic tympani, abdominal tympani (on segments 1, 2 and 7) and acoustically sensitive appendages on the head (Scoble, 1995). All are used to detect bat echolocation cries as the first step in evading bats (Roeder, 1962, 1964, 1965, 1966a,b, 1967, 1970; Roeder and Treat, 1957, 1970; Roeder et al., 1970; Treat 1955, 1956, 1963). The frequency-sensitivity of moth ears usually nicely mirrors the power spectrum of sympatric bats, and moths either physically or temporally isolated from bats sometimes begin to lose their ultrasonic hearing (Fullard, 1987, 1988, 1994, 1998; Fullard et al., 1997; Rydel et al., 1997; Surlykke, 1986; Surlykke and Treat, 1995; Surlykke et al., 1998). The evolution of ultrasonically sensitive ears in moths also had a second

important effect. It set the stage for the repeated evolution of the intraspecific communication systems that I will describe below.

Certain moths do more than listen for and evade bats. These, most notably the Arctiidae, answer the cries of bats with ultrasonic clicks of their own (Blest, 1964; Blest et al., 1963). The clicks are produced by tiny blisters of cuticle called tymbal organs located on the metathorax (Fig. 1). The tymbals are modified metepisternites marked on their forward edge by a series of striae called microtymbals (Fenton and Roeder, 1974; Forbes and Franclemont, 1957). As the tymbal organs are flexed inwards, the microtymbals buckle sequentially from top to bottom producing a burst of microclicks referred to by Fullard and Fenton (1977) as the active modulation half-cycle. During relaxation, the microtymbals pop back out in reverse order, producing a second burst of clicks, the passive modulation half-cycle. There is a brief silent period between the flexion and relaxation called the intracycle silent interval. Modulation (mod.) cycle repetition rates ( $\text{cycles s}^{-1}$ ) are quite variable (8.5–90  $\text{cycles s}^{-1}$ ) among and within species. The two tymbals can be activated in or out of phase with each other (Fullard and Fenton, 1977; Fullard and Heller, 1990; Simmons and Conner, 1996). The clicks produced by arctiids are typically broadband with much of their energy in the ultrasonic region of the sound spectrum, features that are dictated by the

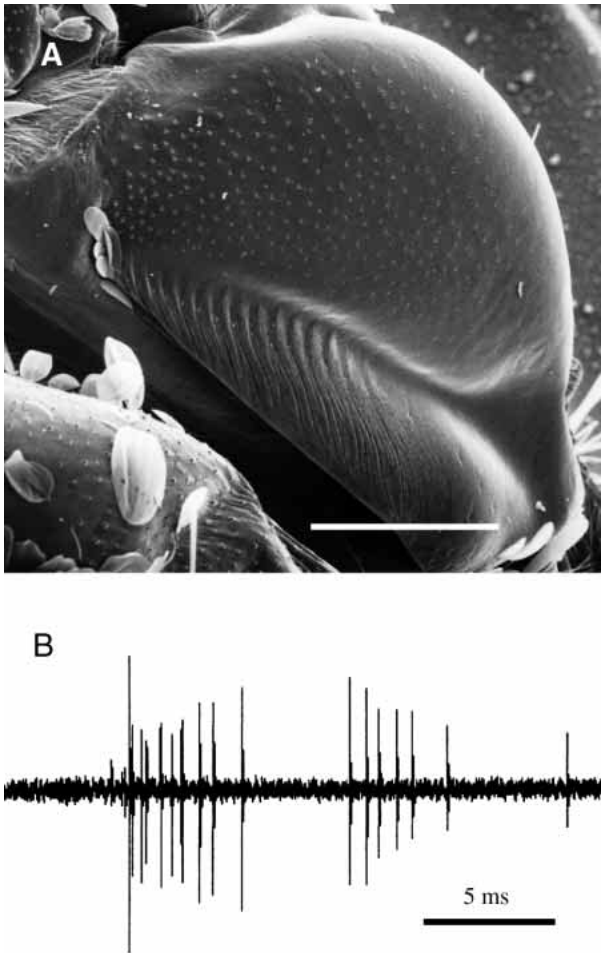


Fig. 1. Sound production in *Cycnia tenera* (Arctiidae). (A) Scanning electron micrograph of the thoracic tymbal with microtymbalar ridges (striated band) along the anterior edge. Scale bar, 0.5 mm. (B) One modulation cycle of tymbal sound. Note the initial burst of clicks produced during flexion (active modulation half-cycle), the second burst produced during relaxation (passive modulation half-cycle) and the intracycle silent interval.

mechanism of sound production and by the small dimensions of the tymbal organs (Bennet-Clark, 1998).

Tymbal sounds are readily triggered by the echolocation cries of bats, and they are therefore thought to function primarily to deter bats (Dunning and Roeder, 1965; Fullard and Fenton, 1997). Precisely how the deterrence works is a matter of debate. Fullard and his colleagues (Fullard et al., 1979, 1994; also see Møhl and Surlykke, 1989; Tougaard et al., 1998) argued that the clicks are processed as echoes and, because of their inappropriate timing, ‘jam’ the bat’s echolocation processing system. Some have suggested that the sounds startle bats (Bates and Fenton, 1990; Edmunds, 1974), and still others suggest that tymbal sound functions as an acoustic warning of unpalatable prey (Acharya, 1995; Acharya and Fenton, 1992; Coutts et al., 1973; Dunning, 1968; Dunning and Krüger, 1995; Dunning et al., 1992; Eckrich and Boppré, 1990; Surlykke and Miller, 1985). These hypotheses need not be mutually

exclusive. Indeed, they may operate differently in different species (bats or moths) and/or may depend on the age and experience of the bat (Bates and Fenton, 1990; Dunning et al., 1992; Fullard, 1987; Fullard et al., 1994; Miller, 1991). I will argue that, regardless of their function *vis-à-vis* bats, the presence of the tymbals also increases the probability that ultrasonic communication systems have developed or will develop in the moths that possess them. The diversity of independently derived acoustic communication systems found in this group stands as evidence in support of this hypothesis.

### Arctiidae

Alexandre Laboulbène, a French entomologist, correctly predicted that arctiids use sound in courtship. In 1864, Laboulbène wrote an article about ‘l’organe musical’ of moths. Curious about an unknown sound that he heard at night, he tracked it to the arctiid *Chelonia pudica* and correctly identified the tymbal organ as the sound source in both sexes. The first definitive proof of ultrasonic communication in an arctiid came from *Cycnia tenera*, the dogbane tiger moth and the subject of much research on the defensive use of ultrasound (Dawson and Fullard, 1995; Fullard, 1977, 1979, 1982, 1992; Fullard et al., 1979). The initial steps in the courtship of *Cycnia tenera* are typically mothlike. The female releases a sex attractant just prior to dawn (Rodgers, 1991). Males detect the pheromone and fly upwind seeking the female. What makes the courtship unusual is what happens when the male reaches the female. In response to high concentrations of the female sex attractant, the male emits a burst of tymbal-generated ultrasound (50 kHz, approximately 40 mod. cycles  $s^{-1}$ ) and simultaneously everts pheromone-disseminating structures called coremata. Either the pheromone or the sound is a signal sufficient to stimulate the silent female to accept the male. When both signals are removed artificially, males have considerably more difficulty procuring a mating (Conner, 1987). Sound production by the male in the final moments before mating appears to be a common and perhaps primitive form of acoustic communication in arctiids. Mating systems with a similar acoustic component have been described for *Euchaetes egle* and *E. bolteri* (Simmons and Conner, 1996).

Slightly more complicated communication systems operate in the euchromiine genus *Empyreuma*. The results of early experiments on *Empyreuma affinis* (incorrectly referred to as *E. pugnione*) led Frank Coro and his colleagues at the University of Havana to argue that *E. affinis* was using an ultrasonic communication system. They based their arguments on a variety of neurophysiological characteristics of the ear of *Empyreuma* (Pérez et al., 1988). More importantly, they also found that the mating activity of caged *Empyreuma* diminished when the tympanic membranes of either sex were sealed with wax (Portilla et al., 1987). Wind-tunnel experiments in 1995 confirmed that *Empyreuma affinis* males find the females pheromonally and produce a burst of tymbal sound (34 kHz; 27.8–58.7 mod. cycles  $s^{-1}$ ) in the final approach to the female. The female often answers them with a sexually dimorphic

(approximately 15 mod. cycles  $s^{-1}$ ) acoustic reply (Sanderford et al., 1998). A similar mating system appears to be operating in *Empyreuma pugione* found in Puerto Rico (R. Wilson, personal communication).

The most elaborate acoustic communication system in arctiids is possessed by the polka-dot wasp moth *Syntomeida epilais*, a species that feeds on the leaves of the ornamental *Nerium oleander* in south and central Florida. The sex pheromone glands of female *Syntomeida epilais* are very small, suggesting a de-emphasis of pheromonal communication (Sanderford, 1992). Indeed, the female sex attractant is necessary only to turn on the acoustic communication system. When a male detects the sex attractant, he begins a staccato of very intense (119.4 dB peak at 2 cm re 20  $\mu$ Pa) doublet clicks (flexion followed by relaxation). The doublets are produced at a rate of 8.5 doublets  $s^{-1}$  with a peak frequency of 32 kHz. The female answers with a somewhat muted but sexually dimorphic (15.0 doublets  $s^{-1}$ ) reply. They click back and forth as the male homes in on the female, much like a male firefly homing in on the flash response of a conspecific female. Their coupling is accompanied by a nearly indecipherable crescendo of clicks (Sanderford and Conner, 1990).

In the absence of the female's acoustic reply, male *Epilais* are unable to locate the female. Sanderford showed this in an experiment in which he paired aphonic females capable of releasing pheromone with females incapable of releasing pheromone but still able to reply acoustically. The females were placed on adjacent oleander bushes. Free-flying males preferentially approached and mated with phonic females, and they approached by circling the female, not from downwind as would be expected in a pheromonally mediated orientation system (Sanderford and Conner, 1995).

The arctiines *Pyrrharctia isabella* and *Phragmatobia fuliginosa* provide an interesting twist to the story (Krasnoff and Yager, 1988). When males of either species evert their coremata (scent-disseminating structures) during courtship, the females respond with tymbal clicking. Indeed, the female's acoustic response can be used as an extremely sensitive bioassay for hydroxydanaidal, a common chemical constituent of the male's scent. Surprisingly, Krasnoff and Yager (1988) were unable to find a function for the clicking in the courtship of either species and concluded that this clicking is the vestige of a once-functional communication system (Krasnoff and Roelofs, 1991). Additional field studies of this potential communication system are needed especially to determine whether the clicks have an effect on heterospecific males that may mistakenly approach pheromone-releasing female *Pyrrharctia isabella* or *Phragmatobia fuliginosa*. If the system is truly behaviorally vestigial, perhaps one day we will find a species in these genera in which it is still operational.

After working for several years on acoustic communication in arctiids, I was delighted to discover a doctoral dissertation by Karel Cerný (1990) of Innsbruck University on ultrasonic communication in the genus *Setina* (*Endrosa*). This study added examples of ultrasonic communication within the little-studied arctiid subfamily Lithosiinae. Following up on

observations made by Peter (1912), Cerný found a diurnal communication system similar to the communication systems of *Syntomeida* and *Empyreuma*. Males are initially attracted by the sex pheromone of the female as in *Empyreuma*. At a distance of 3.5 m, males begin to click and females to answer acoustically but distinctively, as in *Syntomeida*.

Although the sounds of arctiids have considerable fine structure (e.g. intrapulse intervals within the modulation half-cycles and the intracycle silent intervals), most are too rapid to be encoded by the firing rates of insect auditory neurons. In spite of the fact that the vibrational time constant of the tympanum of the noctuid *Argrotis segetum* has been shown to be sufficient to resolve sound pulses separated by 150  $\mu$ s or more (Schiolten et al., 1981), the neural response apparently cannot keep pace. In a recent study, Sanderford et al. (1998) showed that the only temporal characteristic of the sounds of *Empyreuma affinis* and *Syntomeida epilais* that is faithfully encoded is the modulation cycle rate, the grossest temporal characteristic of the call. However, the fine structure of the calls may still have a function in intraspecific communication because it lends a finite duration to each click cycle that is greater than would be produced by a tymbal without stria. The increased duration may be necessary to reach the duration threshold of some sensory receptors. The fine structure of tymbal sound may, of course, also play a role in the interaction between moths and bats (Fullard et al., 1994).

When one maps the examples of acoustic communication on a phylogeny of the arctiids recently developed by Jacobson and Weller (1999), a pattern becomes obvious (Table 1; Fig. 2; Weller et al., 1999). Acoustic communication has developed repeatedly within the family: once in the genus *Setina*, a member of the basal Lithosiinae; at least once in the Arctiini in the genera *Phragmatobia* and *Pyrrharctia*; at least once in the Callimorphini within *Cygnia* and *Euchaetes*; and at least once within the Euchromiini in *Empyreuma* and *Syntomeida*. The different details of the ways in which ultrasound is used

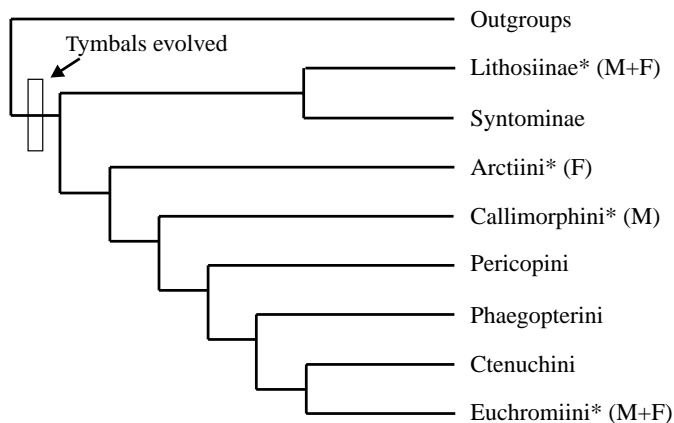


Fig. 2. Phylogeny of the Arctiidae simplified from Weller et al. (1999). An asterisk indicates that some, but not all, representatives of a group use ultrasound during courtship. F, female; M, male.

Table 1. Taxonomic distribution of acoustic communication in moths

Family	Subfamily	Species	Sex	Structure	Frequency (kHz)	References	
Arctiidae	Lithosiinae	<i>Setina aurita</i>	M,F	Thoracic tymbal	32–42 M 35–40 F	Cerný (1990)	
		<i>S. alpestris</i>	M,F	Thoracic tymbal	35–53 M 45–65 F	Cerný (1990)	
		<i>S. irrorella</i>	M,F	Thoracic tymbal	50–60 M –	Cerný (1990)	
		<i>S. roscida</i>	M,F	Thoracic tymbal	60–80 M 75–90 F	Cerný (1990)	
	Arctiinae Arctiini	<i>Phragmatobia fuliginosa</i>	F	Thoracic tymbal	20–80	Krasnoff (1987)	
		<i>Pyrrharctia isabella</i>	F	Thoracic tymbal	20–80	Krasnoff and Yager (1988)	
	Callimorphini	<i>Cyenia tenera</i>	M	Thoracic tymbal	50(p)	Conner (1987)	
		<i>Euchaetes egle</i>	M	Thoracic tymbal	40–64	Simmons and Conner (1996)	
		<i>Euchaetes bolteri</i>	M	Thoracic tymbal	30–60	Simmons and Conner (1996)	
	Euchromiini	<i>Empyreuma affinis</i>	M,F	Thoracic tymbal	34(p)	Sanderford et al. (1998)	
		<i>Syntomeida epilais</i>	M,F	Thoracic tymbal	32.4(p) M 31.9(p) F	Sanderford and Conner (1990) Sanderford and Conner (1995)	
	Noctuidae	Agaristinae	<i>Hecatesia thyridion</i>	M	Alar castanets	18(p)	Bailey (1978); Alcock et al. (1989)
			<i>Hecatesia exultans</i>	M	Alar castanets	30(p)	Alcock and Bailey (1995)
		Acontiinae	<i>Amyna natalis</i>	M	Alar tymbal	60–80	Heller and Achmann (1993)
<i>Rileyana fovea</i> <sup>1</sup>			M	Wing-scaper Leg-file	32.2(p)	Surlykke and Gogala (1986)	
Pyralidae		Gallerinae	<i>Achroia grisella</i>	M	Tegular tymbal	70–130	Dahm et al. (1971); Greenfield and Colfelt (1983); Spangler (1984a,b); Spangler et al. (1984); Snedden et al. (1994); Jang and Greenfield (1996); Jang et al. (1997)
			<i>Galleria mellonella</i>	M F	Tegular tymbal Wings	72(p) 0.0386 Hz	Spangler (1987b) Bennet (1989)
	<i>Corcyra cephalonica</i>		M	Tegular tymbal	125(p)	Spangler (1987a)	
	<i>Eldana saccharina</i>		M	Tegular tymbal	–	Zagatti (1981)	
	Nymphalinae	<i>Symmoracma minoralis</i>	M	Abdominal tymbal	42–118	Heller and Krahe (1994); Heller and Achmann (1993)	
	Odontiinae	<i>Syntonarcha iriastis</i>	M	Genital stridulation	37.5–97	Gwynne and Edwards (1986)	
	Sphingidae		<i>Psilogramma</i> sp.	M	Genital stridulation	–	Mell (1922)

(p), peak sound intensity; <sup>1</sup>formerly *Thecophora fovea*.

in courtship argue that ultrasonic communication is not a plesiomorphic character, but rather that it has evolved repeatedly in insects preadapted by the existence of ears and sound-producing structures present for defensive purposes.

### Noctuidae

Many noctuid moths have been shown to produce ultrasound when touched or stimulated by bat cries, or even during unmolested free flight (Agee, 1971; Zhantiyev et al., 1993). Only a few species have proved to use sound during courtship. Among these are males of the Australian whistling moths *Hecatesia exultans*, *H. fenestrata* and *H. thyridion* (Agaristinae, Noctuidae), which possess castanet-like structures on the leading edge of the forewing. Each consists of a cuticular knob surrounded by a pleated band of pliant cuticle (Fig. 3). During sound production, the wings are repeatedly clapped together above the thorax and cupped, forming a resonant chamber that increases the efficiency of sound production (Bailey, 1978). *H. exultans* produces an amazingly pure ultrasonic tone centered on 30 kHz, whereas *H. fenestrata* and *H. thyridion* produce broad-band clicks that have significant energy in both the ultrasonic and the audible ranges (Alcock and Bailey, 1995; Bailey, 1978).

In Western Australia, males of *H. exultans* perch on low vegetation and call nearly continuously at midday. The call is composed of chirps produced at a rate of  $5\text{ s}^{-1}$ . The chirps are composed of a train of doublet and triplet sound pulses (Fig. 3). Each doublet and triplet is thought to be the result of a single wing clap. Calling males move frequently from perch to perch and, through their movements, define a territory 10–20 m in diameter. Calling males modify their calls in response to heterospecifics, dead conspecifics of either sex and paper models of conspecifics. In each case, they increase the duration of each chirp, sometimes to the point of calling continuously (Alcock and Bailey, 1995).

The signals function primarily in a mate-attraction mode. Females approach calling males and solicit copulations. The mating system of *Hecatesia* appears to be an example of lek polygyny. Males defend territories that lack resources or oviposition sites. Females visit such sites solely to acquire sperm. By doing so, they may acquire mates that have proved their quality through their interactions with other males (Alcock and Bailey, 1995). Male–male agonistic interactions are also mediated by acoustic signals. Males frequently approach males calling nearby, and territorial ‘buzz-bumping’ matches result in which vigorous calls are interspersed with attempts to butt the intruder.

*H. thyridion* and *H. fenestrata* have similar acoustically mediated mating systems. Males in these species call during special upwind zigzagging display flights over their territories. Males also appear to scent-mark within their territories. Scent-marking males drag their bodies while walking up plant stems and large leaves, all the while whirring their wings. Instead of ‘buzz-bumping,’ territorial males participate in buzzing aerial ‘dogfights’ with intruding males. Playback experiments using

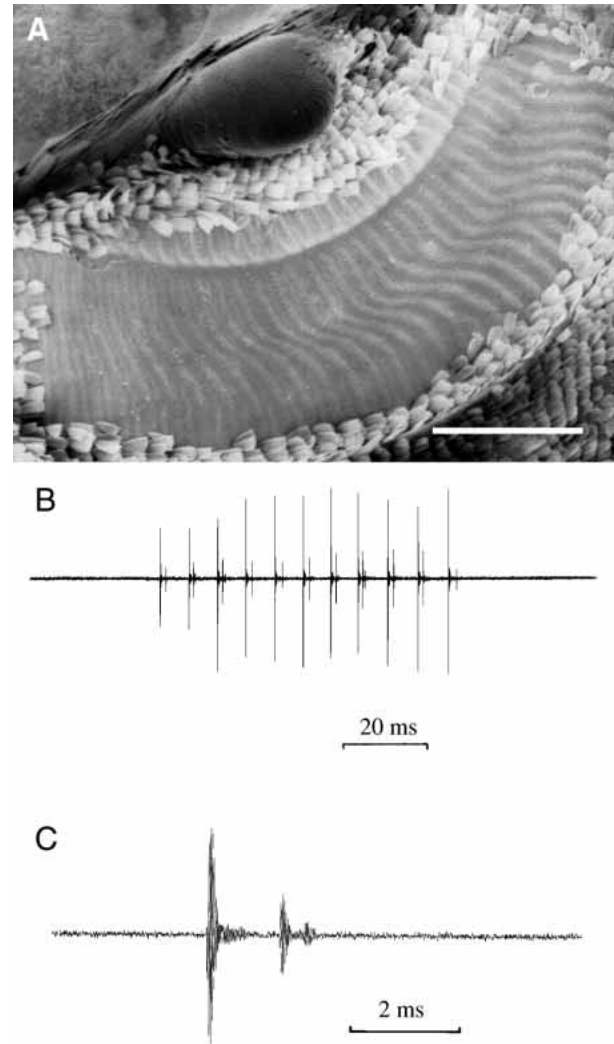
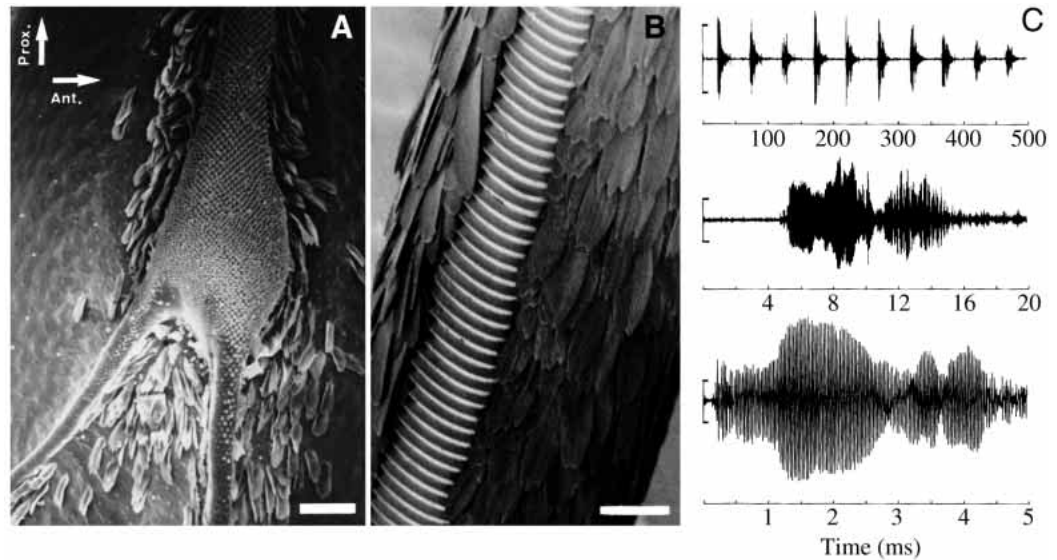


Fig. 3. Sound production in *Hecatesia thyridion* (Noctuidae). (A) Scanning electron micrograph of the alar castanet of a male *H. thyridion*. Scale bar, 0.5 mm. (B) Sound chirp produced during calling behavior of male *H. exultans*. Each doublet of sound pulses is thought to be the result of a single wing clap. (C) A closer examination shows that some sound doublets are actually triplets (taken from Alcock and Bailey, 1995, with permission).

simulated clicks elicited approaches by territorial males, but it is not yet clear whether the females respond to the acoustic signals of the males (Alcock et al., 1989; Surlykke and Fullard, 1989).

The noctuid *Rileyana (Thecophora) fovea* has a different mechanism of sound production. The male produces stridulatory sounds by rubbing a transversely ridged tarsal segment of the hindleg (the ‘*Schrilleiste*’ or stridulator) across a peg-covered swelling of the hindwing (the ‘*Schallblase*’) (Hanneman, 1956). The *Schallblase*, or sound-producing bubble, is a transparent swelling formed through the expansion of the radial vein on the underside of the hindwing (Fig. 4). The bubble acts as a mechanical resonator excited by the first tarsal segment of the hindleg. The metatarsus has approximately 100 transverse ridges that are raked across the

Fig. 4. Sound production in *Rileyana* (*Thecophora*) *fovea* (Noctuidae). (A) Scanning electron micrograph of a peg-covered swelling of the radial vein on the underside of the hindwing called the *Schalblasse*. Scale bar, 0.2 mm. (B) Scanning electron micrograph of a tarsal segment of the hindleg showing the *Schrilleiste* or file. Scale bar, 0.1 mm. The *Schrilleiste* is rubbed across the *Schalblasse* to produce the sounds shown in C (taken from Surlykke and Gogala, 1986, with permission).



bubble, producing a train of sound pulses at a rate of 20 pulses  $s^{-1}$ . Surlykke and Gogala (1986) showed that the main acoustic energy is at 32.2 kHz, with a secondary peak between 60 and 70 kHz. Audiograms show that the hearing of *Rileyana fovea* is reasonably well matched to this sound output. In northern Yugoslavia, pairs have been noted 'dancing' in flight at dusk in the vicinity of prominent oak trees, suggesting male–male agonistic behavior similar to that of *Hecatesia thyridion* (Surlykke and Gogala, 1986). Similar sound-producing structures have also been described for male *Pemphigostola synemonistis* and *Musrugina laeta* from Madagascar and for *Aegocera mahdi* (Noctuidae: Agaristinae) (for details, see Hannemann, 1956). Few behavioral observations have been made of these species.

*Amyna natalis* is a small (16–22 mm) acontiine noctuid widespread from tropical Asia into northern Australia. Singing males perch on well-exposed vegetation and call by holding their wings vertically above the body while twisting them at high frequency. The twisting motion activates a thinly scaled forewing 'tymbal'. The call of *Amyna natalis* is described as a continuous buzzing. The sound consists of a train of sound pulse quadruplets produced at a rate of 170 quadruplets  $s^{-1}$ . Each quadruplet is composed of two resonant pulses at approximately 60 kHz followed by two broadband pulses centered on 75–80 kHz. The structure of the quadruplets suggests that the wings may be twisted out of phase with each other. Sound production in this species may be associated with the release of a pheromone from putative scent-disseminating structures on the underside of the forewing tymbal (Heller and Achmann, 1993).

### Pyralidae

Hayward Spangler was the first to document ultrasonic communication in moths in 1984 with his seminal observations of the courtship of the greater (*Galleria mellonella*) and lesser (*Achroia grisella*) wax moths (Spangler, 1984a–c, 1985,

1986a, 1988a; Spangler et al., 1984). Both species have tegular tymbals that cover the forewing insertions. In *Achroia*, stroboscopic observations showed that a tegular wing coupler driven by wing motion twists the base of the tymbal. This twisting action causes the tymbal to buckle inwards, producing a short, highly damped ultrasonic click in the middle of the downstroke. The upstroke is accompanied by a recovery click. If the two wings are slightly out of phase, a doublet of sound pulses is produced on both the downstroke and the upstroke (Fig. 5). The tegulae are elevated during sound production by a small resonant air pouch underlying them (Spangler and Takessian, 1986). The tegulae of *Achroia grisella* and *Galleria mellonella* are finely corrugated. In other species, such as *Corcyra cephalonica*, *Aphomia sociella* and *Eldana sacharina*, the tegulae are more deeply striated, reminiscent of the thoracic tymbals of arctiids. Depending on the species and the degree of striation, the tymbal may produce a single click on the upstroke and a single click on the downstroke or up to 18 clicks on both the upstroke and the downstroke (Spangler, 1988a).

*Achroia grisella* males take up positions on or near the wax combs of honeybee colonies (a food resource) and call continuously (50 doublets  $s^{-1}$  at 70–130 kHz) (Greenfield and Coffelt, 1983; Snedden et al., 1994). Males simultaneously wing-fan and release a two-component sex pheromone composed of *n*-undecanal and *n*-11-*cis*-octadecenal (Dahm et al., 1971), but the directed movements of the female to the male are clearly mediated by the acoustic signal alone (Spangler, 1984b; Spangler et al., 1984). The female uses binaural cues to approach to a distance of 1 or 2 cm, and the male then begins circling until contact is made (Spangler, 1988b; Spangler and Hippenmeyer, 1988). Jang and Greenfield (1996) have shown that females given a choice between calls prefer to approach synthetic calls with greater pulse amplitude, pulse duration, pulse repetition rate and degree of pulse asynchrony (which is a function of the asynchrony of the wing movements that produce sound).

A similar mating sequence appears to operate in the rice

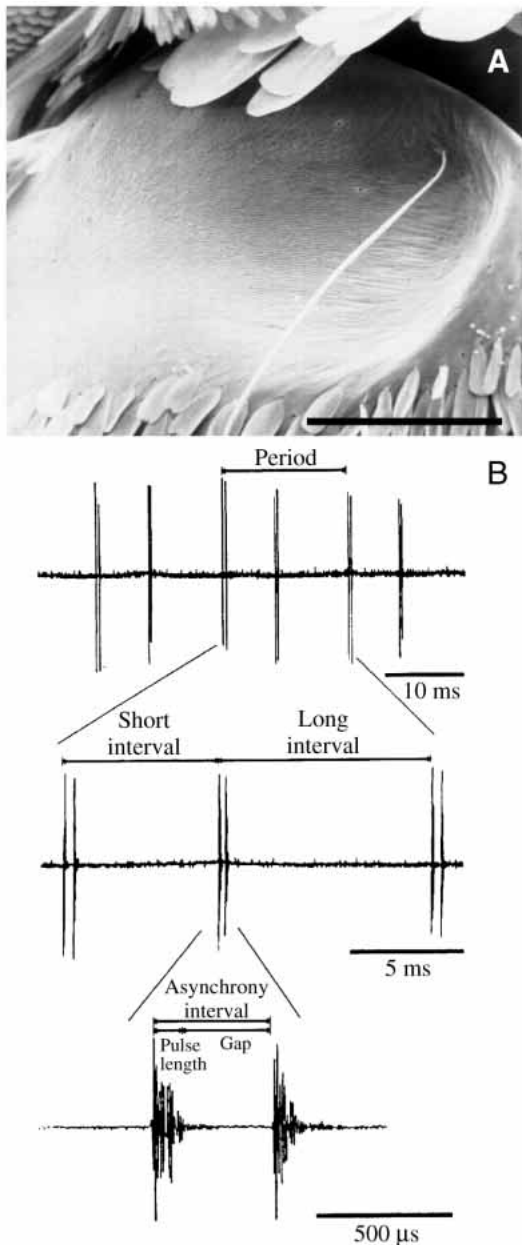


Fig. 5. Sound production in *Achroia grisella* (Pyrilidae). (A) Scanning electron micrograph of the tegular tymbal in a male. Scale bar, 0.15 mm. (B) Clicks produced during calling (taken from Jang and Greenfield, 1996, with permission).

moth *Corcyra cephalonica*. In this case, each flexion and relaxation of the tegular tymbals of the male results in a burst of up to nine sound pulses corresponding to the nine striations on each tymbal. The upstroke and downstroke simultaneously activate the two tymbals and result in a burst of up to 36 pulses of ultrasound centered on 125 kHz. Burst trains are irregular, ranging in rate from 5 bursts  $s^{-1}$  during regular calling to 60–70 bursts  $s^{-1}$  during a special buzz phase (Spangler, 1987a). As in *Achroia grisella*, the sounds attract virgin females. These pyralid mating systems all appear to be classic short-range, female mate-choice systems. Jang et al. (1997) showed that

male *Achroia grisella* have sufficient repeatable variation in their acoustic signals to fuel sexual selection and that females prefer males whose signals have the highest level of acoustic energy and/or asynchrony.

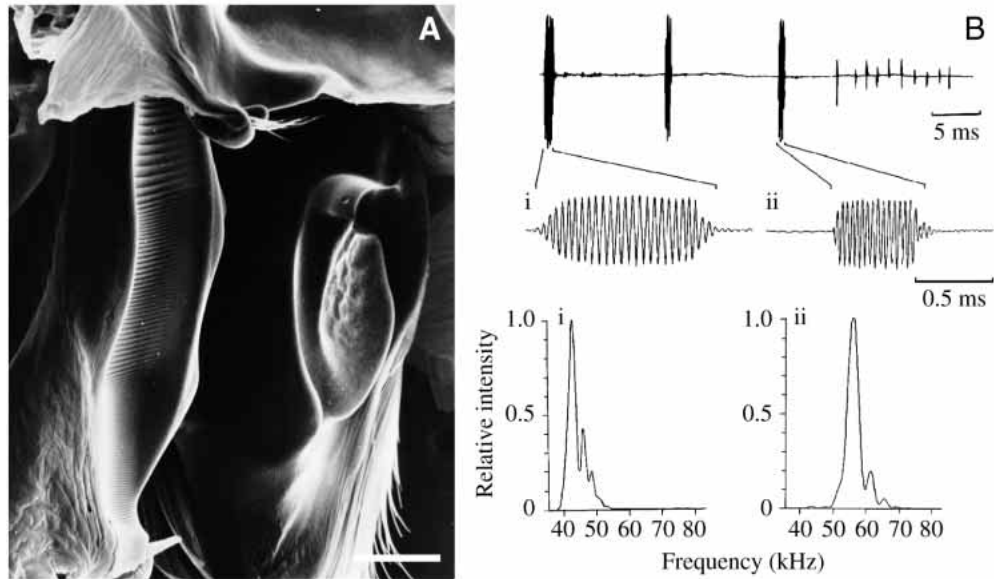
*Galleria mellonella* exhibits a different mating system in which male-produced ultrasound initiates courtship and a pheromone takes over to attract the female (Spangler, 1985). Male *Galleria mellonella* call intermittently by producing short bursts of 1–4 ultrasonic pulses (72 kHz) at a burst repetition rate of 41.1 bursts  $s^{-1}$ . The bursts are clustered in phrases composed of 1–18 bursts with a mean of four bursts. Females respond by fanning their wings, producing a 38.6 Hz wingbeat sound. The male responds to this low frequency by wing-fanning and elevating the rate of release of his sex pheromone, an odorous mixture of *n*-nonanal and *n*-undecanal (Spangler, 1985, 1987b). It is the elevated pheromone output that stimulates the final approach of the female to the male. This three-phase courtship begins shortly after sunset, and acoustic activity decreases steadily throughout the night (Spangler, 1986b).

Several pyralids that infest stored products: *Ephestia cautella* (Walk.), *Ephestia kuehniella* (Hb.) and *Plodia interpunctella* (Hb.) have been shown to produce sounds that may prove to have signal value in courtship (Trematerra and Pavan, 1995). In these three species, wing-fanning males simultaneously emit pheromonal and acoustic signals. Females approach ‘displaying’ males and initiate copulation. The sounds appear to be produced by a tegular mechanism and range in frequency from the audible up to 80 kHz, and 14–24 ms pulses are produced at rates of 41–72 pulses  $s^{-1}$ . Matings involving males deprived of tegulae or females rendered deaf by destroying their tympani produced fewer viable eggs (Trematerra et al., 1994). Since most insect wing movements produce some low-intensity broadband sound, more research is necessary to ascertain whether these sounds are used in communication.

Some pyralids have acoustic signals that operate over distances of 10–20 m. *Syntonarcha iriastis*, an odontiine pyralid found in Western Australia, is thought to attract females over considerable distances using a combination of ultrasound and pheromones (Gwynne and Edwards, 1986). Males perch on the tips of branches of bushes and trees and call continuously from just after sunset well into the night. Signaling males separate their wings, curl their abdomen upwards and expose their genitalia. Sclerites at the base of the genitalia are highly modified to form a file with three distinct sound-producing zones demarcated by different spacing between the ridges of the file. The genitalia are asymmetrical, with the file arranged longitudinally along the left venter (Fig. 6). The signal consists of a continuous series of 24 ms phrases, each composed of three intense sound pulses followed by a buzz of 10 less-intense pulses (Fig. 6B). The peak frequencies of the pulses generally increase from 42.5 kHz (first pulse), through 54.4 kHz (second and third pulses) to 58–97 kHz (remaining pulses).

One of the most interesting sound-producing pyralids is *Symmoracma minoralis*, a nymphulinae pyralid found from

Fig. 6. Sound production in *Syntonarcha iriatus* (Pyrallidae). (A) Scanning electron micrograph of the genital file showing three zones of ridges each with distinct spacing. Scale bar, 0.2 mm. (B) Acoustic phrases produced as a scaper (not shown) is moved across the file (taken from Gwynne and Edwards, 1986, with permission).



Sri Lanka to Thailand (Bailey, 1991) and in northern Australia. The small males of this species have a median 'tymbal' on the ventral side of the terminal abdominal segment. The tymbal is found at the base of a megaphone-like structure that results in the production of a highly directional sound cone. The calling male hangs from a leaf, and the sound is projected upwards. The calling song consists of a continuous series of chirps at a rate of  $3.4 \text{ chirps s}^{-1}$ . Each chirp lasts approximately 300 ms and consists of a series of sound-pulse doublets whose structure suggests that they are produced by a slow flexion of the tymbal followed by a rapid relaxation. Each chirp starts out at low intensity and gradually increases to a sound pressure level of 95 dB at 10 cm (Fig. 7). Each chirp is followed by a small doublet of sound pulses that appears to result from the single flexion and relaxation of the tymbal. The frequency spectrum of each chirp shows a broadband structure with a high-frequency band (118 kHz) that is prominent throughout the chirp and a stronger low-frequency band that starts at 42 kHz roughly halfway through the chirp and gradually increased in frequency to 60 kHz. The acoustic display of male *Symmoracma minoralis* is accompanied by the splaying of long scent scales from the genitalia (Heller and Achmann, 1995; Heller and Krahe, 1994).

Hannemann (1956) described yet another method of sound production in male South American Chrysauginae (Pyrallidae), in which the frenulum of the hindwing scrapes along a series of ridges on the inside of the ring-shaped retinaculum (clasp) of the forewing. Vibrations may be amplified by a resonating chamber formed by a fold of the leading edge of the forewing.

Since a very low percentage of moths have been examined for the existence of ultrasonic communication, additional examples of acoustic communication will undoubtedly to be found in the Arctiidae, Noctuidae and Pyralidae. Several major moth families will almost certainly prove to use ultrasound during courtship. These include the remaining noctuid

families (the Lymantriidae and the Notodontidae), the Geometridae and the Sphingidae.

Although no definitive studies have been carried out using sphingids, a few observations strongly suggest that this group does use ultrasound during courtship. The males of some Sphingini and Smerinthini (Sphingidae) stridulate using

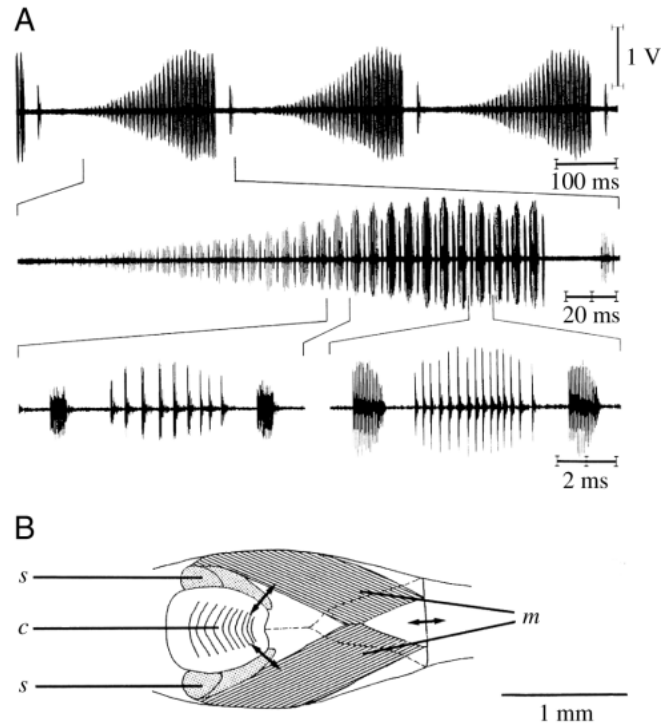


Fig. 7. Sound production in *Symmoracma minoralis* (Pyrallidae). (A) Sounds produced by a calling male. (B) Schematic diagram showing the median tymbal on the ventral side of the terminal abdominal segment with the muscles (*m*) that drive sound production. Scale bar, 1 mm. Taken from Heller and Krahe, 1994, with permission.

modified genital valves. The mechanism appears to be of the file-and-scraper type (van Doesburg, 1966). Modified scales on the genital valves act as plectra and are scraped across two files on the eighth abdominal sternum. The files are also composed of modified scales or spines. Although the sounds are clearly audible as a continuous stridulation, spectrograms suggest significant energy in ultrasonic frequencies (Lloyd, 1974). Male *Psilogramma* with splayed abdominal scent scales have been observed to stridulate while flying in the vicinity of females (Mell, 1922). Genital stridulation has also been noted in the smerinthine *Protambulyx strigilis* and in *Meganoton analis sumatranus* (Nässig and Lüttgen, 1988).

Male of lymantriids belonging to 70 genera possess abdominal 'tymbals' (Zerny and Beier, 1936; Dall'Asta, 1988) on the venter of abdominal segment 3. Since abdominal flexion is an important component of copulatory attempts, such copulatory movements probably preadapted lymantriids for the development of the abdominal tymbals that may prove to be utilized during courtship. Unfortunately, no behavioral studies have focused on acoustic communication in tymballed lymantriid species.

No sound-producing structures have yet been described for the Geometridae or the Notodontidae. However, geometrids have tympani at the base of the abdomen (Kennel and Eggers, 1933), and notodontids have thoracic tympanic membranes (Richards, 1933). Additional families that possess tympanal receptors include the Tineidae, Drudgeonidae, Thyrididae, Uraniidae, Drepaniidae and Doidae (Scoble, 1992).

### Evolution of ultrasonic communication systems in moths

When discussing the evolution of behavior, it is important to distinguish between the origin of the behavior and its current adaptive value. I have divided the following discussion into two parts in order to make this distinction.

#### Origins

It is clear that acoustic communication has evolved in moths on numerous occasions and that the sound frequencies involved are most often ultrasonic (Table 1). Both the ears and the sound-producing mechanisms are clearly not homologous across species. Moths have operated essentially as opportunists, exploiting existing sensory systems (Ryan, 1997; Alcock, 1998). The presence of bat-detection systems appears to have been the most significant evolutionary factor in preadapting moths for the detection of intraspecific acoustic signals.

Several of the moths utilizing ultrasonic communication systems are diurnal. It is possible that the release from bat predation has freed the use of the tympanic membranes for other purposes (Surlykke and Gogala, 1986). Others are patently distasteful (the arctiids), a characteristic that may in essence have freed them from bat predation as well. A signaling *Syntomeida epilais*, for example, may be able to click back and forth to its mate with impunity because its cardenolide content renders it unpalatable and its acoustic signature can be recognized by echolocating bats.

It will be interesting to determine how moths have altered their sensory systems so that they function well in this new sexual context. One might expect the tuning of the ears to shift gradually from best frequencies matching bat cries to best frequencies matching better the communicative signals of their species. This should be most obvious in species that have escaped bat predation by flying during the day. This appears to have happened in *Rileyana (Thecophora) fovea*, whose ears are tuned to lower frequencies than those produced by most bats yet match the low-frequency calls of conspecifics (Surlykke and Gogala, 1986). For moths that still fly at night and are exposed to bat predation, one might expect mechanisms that will allow the moths to distinguish between bats and conspecifics. Given the small number of sensory neurons involved, it seems unlikely that frequency discrimination is an option (but see Spangler, 1984c). Either pulse repetition rate or context (e.g. the presence of a female sex attractant) may prove important. In other cases, distinguishing friend from foe may not even be necessary. By using pulse repetition rates similar to those of bats, males may utilize the identical neural pathways to 'freeze' females' (Werner, 1981) during copulatory attempts.

Sound-production mechanisms have also evolved from existing motor systems. The tymbal organs of arctiids are clear examples. Although originally developed in the context of bat defence, their function has been exploited in the context of courtship. Because acoustic responses by the moth were already acoustically triggered by bat echolocation cries, the system was primed for the development of two-way acoustic communication systems such as those found in *Empyreuma* and *Syntomeida*. High-velocity wing movements are often associated with evasive maneuvers, male-male interactions and mate-finding. It is, again, a simple evolutionary step to harness these movements for sound production, as in the noctuid *Hecatesia* and in many pyralid species. Perhaps this is the origin of tymbal sounds in arctiids as well, if the muscles used for the control of evasive maneuvers have been co-opted for sound production. Existing reproductive structures and their movements have also been exploited. This is most obvious in the use of exposed genital structures for sound production, as in *Symmoracama*. Many male moths expose their genitalia prior to mating. Genital movements are necessary for mating, and it is a simple evolutionary step to harness these movements for sound production, especially for species in which the sound receptors already exist.

#### Current adaptive value

Ultrasonic cues are probably involved in all aspects of moth reproductive behavior, including species recognition, male-male competition and mate-choice. Sound pulse repetition rate (modulation cycle rate), pulse duration, sound intensity and degree of asynchrony are the mostly likely substrates to mediate these systems, as Jang and Greenfield (1996) have shown. The sex attractant systems of moths are not always as species-specific as one might think. M. V. Sanderford (personal communication) reports that female

*Empyreuma affinis* attract males of at least two additional arctiid species. Close-range tymbal sound may prove useful in sorting out such courtship mistakes. Sexual selection in the form of male–male competition seems clear in *Hecatesia*, and female mate-choice may also be mediated by the ultrasonic emissions of moths.

In the context of sexual selection, acoustic emissions may be indicators of a direct benefit for females such as access to a defended territory for oviposition or a nutritious spermatophore. Alternatively, male emissions may provide clues to the genetic benefits with which they can provide their mates. These potential benefits include the attractiveness genes of the Fisherian model of sexual selection (Kirkpatrick, 1982; Lande, 1981) or ‘good genes’ that enhance survival and growth (Pomiankowski, 1988; Jia and Greenfield, 1997). One intriguing ‘good genes’ possibility is that the ultrasonic clicks may in some cases provide evidence of the defensive prowess of the males – perhaps their ability to evade bats in flight or their ability to respond to them acoustically. For example, the degree of tymbal asynchrony, a character proved to be chosen by male *Achroia grisella* (Jang et al., 1997), could easily be correlated with the ability to turn quickly and to carry out the maneuvers necessary to evade bats.

Many significant questions remain. These include proximate questions about how moths communicate – how they produce sounds, how they receive sounds, how they process sounds and how sounds result in motor output. They also include the ultimate questions on why communication evolved. Do sounds aid in species recognition or are they involved primarily in sexually selected intraspecific interactions? If they are involved in sexual selection, do they usually mediate male–male interactions or provide a substrate for female mate-choice? If they are involved in female mate-choice, how does the female benefit? We have much to do to build upon Laboulbène’s (1864) original functional analysis of acoustic signals of moths as ‘un chant d’apell amoureux et probablement aussi un cri plaintif’.

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