Chapter 6
Acoustic Communication in the Nocturnal Lepidoptera

Michael D. Greenfield

Abstract Pair formation in moths typically involves pheromones, but some pyraloid and noctuoid species use sound in mating communication. The signals are generally ultrasound, broadcast by males, and function in courtship. Long-range advertisement songs also occur which exhibit high convergence with communication in other acoustic species such as orthopterans and anurans. Tympanal hearing with sensitivity to ultrasound in the context of bat avoidance behavior is widespread in the Lepidoptera, and phylogenetic inference indicates that such perception preceded the evolution of song. This sequence suggests that male song originated via the sensory bias mechanism, but the trajectory by which ancestral defensive behavior in females—negative responses to bat echolocation signals—may have evolved toward positive responses to male song remains unclear. Analyses of various species offer some insight to this improbable transition, and to the general process by which signals may evolve via the sensory bias mechanism.

6.1 Introduction

The acoustic world of Lepidoptera remained for humans largely unknown, and this for good reason: It takes place mostly in the middle- to high-ultrasound frequency range, well beyond our sensitivity range. Thus, the discovery and detailed study of acoustically communicating moths came about only with the use of electronic instruments sensitive to these sound frequencies. Such equipment was invented following the 1930s, and instruments that could be readily applied in the field were only available since the 1980s. But the application of such equipment

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for studying acoustic animal species has accelerated in recent years, and we now know that certain moth species in several families use ultrasound for communication in much of the same way as Orthoptera and Cicadidae, as well as other acoustic species such as anurans, use audible sound. Scientists have known for a longer period that hearing, and specifically sensitivity to ultrasound, occurs in several major families of moths, that such perception is involved in the detection and evasion of predatory bats, and that some moth species also produce their own ultrasound emissions in the context of interacting with bats (see Chap. 5 by Conner). But if we define communication as an exchange of information between members of the same species, or at least as an event where both signaler and receiver benefit from the exchange (Hauser 1996; Greenfield 2002), then acoustic communication in moths is a rare behavior that has come to light only recently.

6.2 Lepidopteran Acoustics: Perception and Sound Production

Hearing, with specific sensitivity in the ultrasound frequency range, is very widespread in three major superfamilies of the Lepidoptera: Pyraloidea, Geometroidea, and Noctuoidea (Scoble 1992; see Minet 1983, 1985 for the Pyraloidea); these groups include over 90,000 species, comprising 55 % of lepidopteran species. The vast majority of pyraloid, geometroid, and noctuoid species hear, and those that do not may represent secondary loss of acoustic perception and tympanal organs. Ultrasound hearing is also found in the Drepanoidea, Thyridoidea, and Hedyloidea as well as in some Tineoidea, and Bombycoidea. In addition some butterflies (Papilionoidea) have tympanal hearing organs sensitive to sound in the audible frequency range. Considering both phylogeny and the homology of hearing organs it appears that hearing evolved independently 5–10 times in the Lepidoptera (Scoble 1992; Hoy and Robert 1996; Yack and Fullard 2000). The several groups have tympanal organs located in different body segments, including the abdomen (Pyraloidea, Geometroidea, Tineoidea, Drepanoidea), thorax (Noctuoidea), wing bases (Thyridoidea, Hedyloidea, Papilionoidea), and even the proboscis (Bombycoidea). A reanalysis of relationships among the lepidopteran superfamilies based on an extensive molecular dataset provides an improved phylogeny (Mutanen et al. 2010), and it may resolve previous uncertainty over clades and thereby allow a more definitive assessment of the evolution of hearing in the order.

Phylogeny combined with historical biogeography and the evidence from fossil Lepidoptera indicate that the evolutionary origins of lepidopteran hearing, with the possible exception of that in the Tineoidea (Davis 1998), occurred not earlier than 60 mya (Yack and Fullard 2000). This date suggests strongly that lepidopteran hearing originated in response to predatory bats hunting aerial insects via echolocation. The predation pressure from bats may have been critical in maintaining hearing in the Lepidoptera, as hearing and tympanal organs are reduced or even lost in pyraloid, geometroid, and noctuoid species inhabiting regions free of insectivorous bats (Fullard 1994). Similarly, species that have escaped bat predation temporally by activity during times of the day or year when bats are not active also show hearing loss (Fullard et al. 1997; Surlykke et al. 1998). It has been suggested that the Papilionoidea (butterflies), which generally do not hear, at least not ultrasound, have escaped bat predation by evolving from an ancestral state of nocturnal behavior to their present daytime activity (Yack and Fullard 2000). Some anatomical features of butterflies can be interpreted as vestiges of ancestral hearing organs, and interestingly their sister group, the Hedyloidea, are nocturnal and do hear ultrasound. The anatomical and neural apparatus necessary for hearing may come with a cost, and when hearing is no longer needed the investment devoted to these features is reduced (cf. Yager 1999).

Although hearing is widespread in moths, sound production in the context of mating communication occurs only in isolated genera and species scattered among various clades within the Pyraloidea and Noctuoidea (Conner 1999). Some of these acoustically communicating species also broadcast sounds in the context of interacting with bats (cf. Dunning and Roeder 1965), and in several cases the same sounds serve both as mating signals and during interactions with predators (Conner and Corcoran 2012). However, in most acoustically communicating moths the sounds produced serve only in mating. That is, these moths may typically hear and respond evasively to the echolocation signals of bats, but echolocation signals do not elicit any sounds from the moths that might serve in jamming, warning, or startling bat predators. Whereas tympanal hearing organs within the Pyraloidea and Noctuoidea appear to be homologous within each superfamily, sound producing structures are situated on many different locations (Greenfield 2002; Nakano et al. 2009b). These points have major implications for the evolution of acoustic communication in the Lepidoptera and in general.

6.3 Acoustic Communication in the Lepidoptera: History of a Discovery

The death's head hawkmoth (*Acherontia atropos*; Sphingidae: Sphinginae), in which the adults enter colonies of bees to imbibe honey, was perhaps the first acoustic lepidopteran whose sounds drew human attention (Kitching 2003). Adult *A. atropos* emit sounds by expelling air through the mouthparts when disturbed, and it had been proposed that these emissions mimic the 'piping' sounds of the queen and thus inhibit worker honeybees from attacking the moths while they are feeding (Kettlewell 1978), a suggestion however questioned by Moritz et al. (1991). During the nineteenth century several reports described sounds emitted by various species of moths and butterflies, and the presence of 'tympaniform' organs, assumed to be involved in hearing, was noted as well (Laboulbène 1864; review in McLachlan 1877). Some of the sounds reported occur during interactions with bats, and they are audible because of their broadband nature. It was even suggested that lepidopteran acoustic signaling may be ‘more general than commonly believed’ (McLachlan 1877).

The first definitive report of sound used in mating communication in the Lepidoptera was made in the Lesser waxmoth (*Achroia grisella*; Pyralidae: Galleriinae), a species with distinctive pair formation wherein males attract females up to 1 m distant with a high-frequency song (Spangler et al. 1984). In most species of moths females emit an advertisement pheromone that attracts males over relatively long distances (Greenfield 1981). Males may also emit a close-range courtship pheromone that influences female acceptance, but the basic scheme of signaling females and searching males is the rule in moths. *A. grisella* is an exception to this rule, as males attract females with what appeared to be some type of mechanical stimulation (Dahm et al. 1971). Males generate this stimulation by continuously fanning their wings while remaining stationary on the substrate (Kunikë 1930; Greenfield and Coffelt 1983). Neighboring males may occasionally run toward and butt a wing-fanning individual, which results in a brief scuffle, repositioning, and resumption of wing-fanning by one or both of the males. A female will move among the males and eventually run toward a given individual, her trajectory becoming rather direct once she begins the final approach. Although females too may fan their wings while approaching, males do not move or even turn toward the approaching female until she makes physical contact, at which time a brief courtship and mating ensue. These observations, combined with knowledge that the moths can hear very high-frequency ultrasound (Spangler and Takessian 1983), suggested that *A. grisella* was an acoustic species and that the male wing-fanning was generating an acoustic mating signal. Sound recordings then showed that while females are mute, male wing-fanning caused a pair of tymbal organs situated on the tegulae, small sclerites at the bases of the forewings, to resonate and to produce rhythmic trains of 100 kHz pulses. Female muteness reflects their lack of tymbals. Behavioral tests demonstrated that wing-fanning males whose tegulae were ablated did not attract females, but broadcasts of synthetic male song from a loudspeaker were as attractive to females as wing-fanning males (Spangler et al. 1984). The findings on *A. grisella* demonstrated that moths do use sound for purposes other than sending signals to predators or hosts, and that when they do communicate acoustically the broadcasts are likely to be in the ultrasound frequency range. Similar findings were later made in other moth species, revealing male songs involved in long-range advertisement as well as close-range courtship.

6.4 Acoustic Communication in the Lepidoptera: Phylogenetic Survey

To date, acoustic communication has been reported in the Pyraloidea (Pyralidae, Crambidae), Noctuoidea (Noctuidae, Arctiidae), and Papilionoidea (Nymphalidae). This section provides an overview of which groups and species broadcast mating songs and the manner in which these songs are produced and function. Systematic treatment follows the phylogeny of the Lepidoptera presented in the Tree of Life Web Project 2010 (www.tolweb.org; Fig. 6.1).

6.4.1 *Pyraloidea*

Several species of galleriine pyralid moths produce male courtship songs that influence female response, including *Aphomia sociella* (Figs. 6.2a and 6.3a; Kindl et al. 2011) and *Eldana saccharina* (Bennett et al. 1991), and possibly *Galleria mellonella* (Spangler 1985, 1986). Only *Achroia grisella* is known to produce a long-range male advertisement song (Spangler et al. 1984). Songs that give the appearance of functioning in courtship but which have not been tested experimentally are observed in *Corcyra cephalonica* (Spangler 1987) and *Achroia innotata* (personal observations), a congener of *A. grisella*. In all of the above species males sing while stationary and fanning their wings, which causes tymbals on the tegulae to resonate. *Achroia*, *Aphomia*, and *Galleria* are symbionts of social bees, in whose colonies the moth larvae develop. However, no observations indicate that male song in these galleriine species has any influence on bee behavior. In both *A. sociella* and *G. mellonella* males attract females with long-range sex pheromones, and the male song probably acts only in close-range courtship. *A. grisella* males also emit an odor that originates from glands on the forewings, but the role of

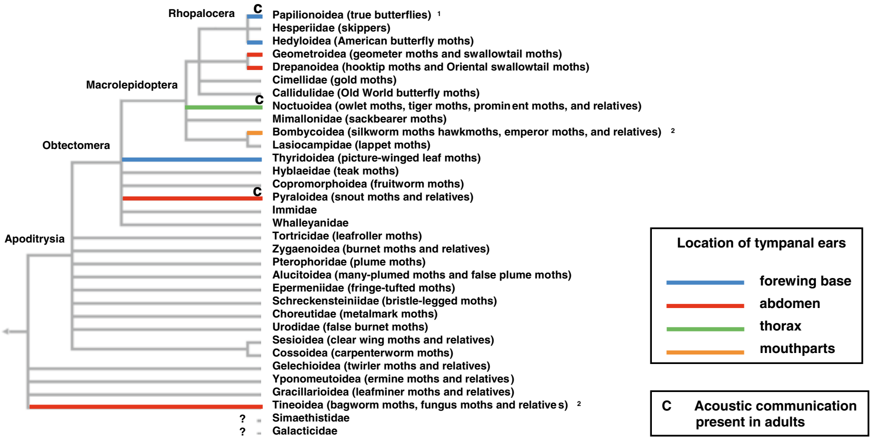

Fig. 6.1 Phylogeny of the ditrysian Lepidoptera showing distribution of tympanal ears, classified by anatomical location, and acoustic mating communication, denoted by ‘C’. Unless indicated by a superscript, tympanal ears are found in the majority of species in the clades represented by colored branches. 1 Tympanal ears in some groups of Papilionoidea are sensitive to audible sound, 2 Tympanal ears in some groups of Bombycoidea, and Tineoidea are ultrasound sensitive

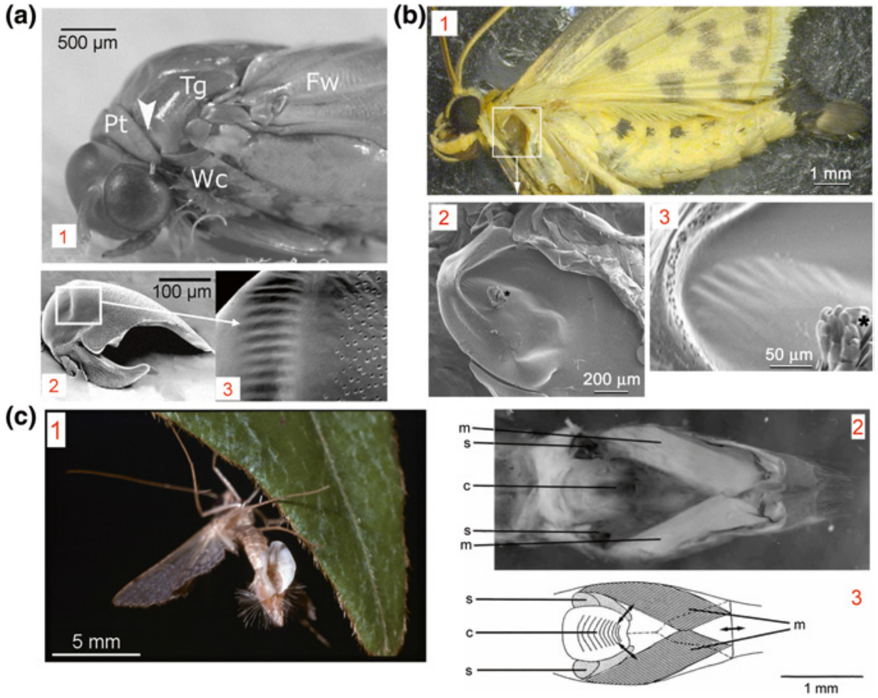

Fig. 6.2 Sound-producing structures in male pyraloid moths. **a** *Aphomia sociella*: 1. general situation of the tymbal (*arrow*) on the tegula (*Tg*), to the left of the forewing base (*Fw*) and to the right of the patagium (*Pt*), tegular wing coupler (*Wc*); 2. tymbal located on the male tegula; 3. detail of striations on the male tymbal (adapted from Kindl et al. 2011), **b** *Conogethes punctiferalis*: 1. male tymbal situated laterally on the mesothorax, indicated by box (adapted from Nakano et al. 2012b); 2 and 3. scanning electron micrographs showing detail of membrane on male tymbal; black asterisk, indicating a group of scales that had fallen on the membrane, serves to relate the higher magnification Figs. 6.2–6.3 (photos courtesy of Ryo Nakano), **c** *Symmoracma minoralis*: 1. singing male (photo courtesy of Klaus-Gerhard Heller); 2. anterior of last abdominal segment of male, dorsal view; 3. schematic representation of photograph shown in part 2, indicating cavity (*c*) with ribbed bottom serving as sound chamber, sclerotized wall (*s*) of cavity, muscles (*m*), and proposed sound-producing movement (*arrows*) (adapted from Heller and Krahe 1994)

this scent in pair formation is not clear. By itself, the odor does not influence female behavior, although it may enhance female response to male song (Greenfield and Coffelt 1983; Spangler et al. 1984).

Among phycitine pyralid moths, male songs have been recorded in several species (*Ephestia cautella*, *E. kuehniella*, *Plodia interpunctella*). These moths exhibit typical pair formation, long-range female pheromones, and short-range male courtship pheromones, and it is suggested that the songs act in concert with the latter (Trematerra and Pavan 1995). The sound-producing structures in phycitine moths have not been described.

Loud male advertisement songs have been recorded in several species of crambid moths (Figs. 6.2b, c and 6.3b, c). In *Syntonarcha iriastis* (Crambidae:

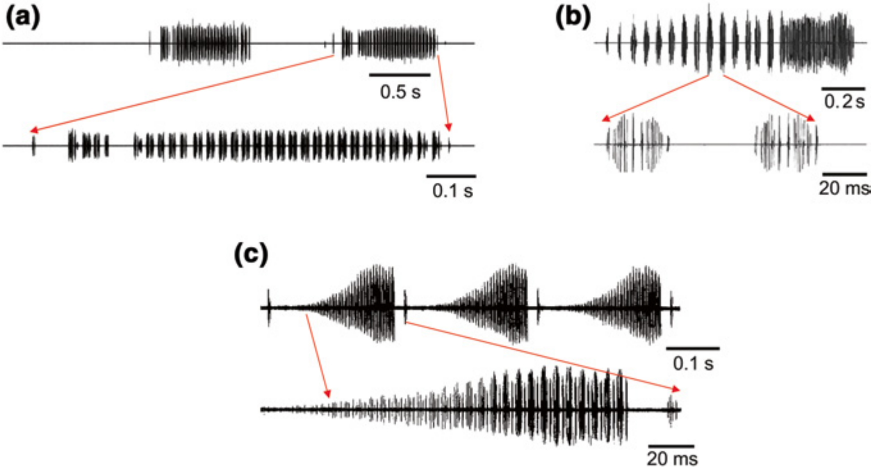

Fig. 6.3 Male songs in pyraloid moths. Oscillograms show representative segments of ultrasound song in: **a** *Aphomia sociella* (adapted from Kindl et al. 2011), **b** *Conogethes punctiferalis* (adapted from Nakano et al. 2012a), **c** *Symmoracma minoralis* (adapted from Heller and Krahe 1994), **a** and **b** are courtship songs, **c** may be an advertisement song, but its function is not yet confirmed

Odontiinae) and *Symmoracma minoralis* (Crambidae: Spilomelinae) songs are produced by structures on the genitalia; in the former the structure is stridulatory (Gwynne and Edwards 1986) whereas in the latter it is a tymbal organ (Heller and Krahe 1994). In *Conogethes punctiferalis* (Crambidae: Spilomelinae), sound is produced by a tymbal organ situated on the mesothorax, and the role of male song in courtship has been confirmed (Nakano et al. 2012a, b).

Songs in the above species of Galleriinae and Crambidae are all broadcast at amplitudes ≥80 dB SPL at 1 cm from the singing male (Nakano et al. 2009b). In other species of Crambidae, as well as Noctuidae and Arctiidae, males have been found to whisper ‘soft songs’ at much lower amplitudes, <60 dB SPL at 1 cm (Nakano et al. 2009a). These songs may be produced by stridulation with specialized scales on the wings and thorax (Nakano et al. 2008). The extremely low amplitude, nonetheless detectable by the female, may prevent eavesdropping predators or rival males from localizing a courting pair. In *Ostrinia* spp. (Crambidae), the role of quiet songs in courtship has been confirmed by testing males whose specialized scales were ablated (Takanashi et al. 2010).

6.4.2 Noctuoidea

Acoustic communication has been reported in four noctuoid families, Nolidae, Lymantriidae, Arctiidae, and Noctuidae. Mating songs are best known in the Arctiidae, where they are reported in the Arctiinae, the Lithosiinae, and the

Syntominae and appear to have evolved independently (Simmons and Conner 1996; Weller et al. 1999; DaCosta et al. 2006).

Loud male songs that probably function in advertisement are found in the Nolidae and the Noctuidae. In the Nolidae (*Pseudoips prasinana*; *Bena bicolorana*), tymbals located ventrally on the abdomen serve as the sound producing organs (Skals and Surlykke 1999), whereas in the Noctuidae sound is produced by forewing tymbals (*Amyna natalis*) (Heller and Achmann 1995), stridulation between the metathoracic leg and the hindwing (*Rileyana* (formerly *Thecophora) fovea*) (Surlykke and Gogala 1986), and the percussion of castanet structures on the forewings (*Hecatesia exultans*, *Hecatesia thyridon*) (Bailey 1978). Males sing while at rest except in *H. thyridion*, where song in the audible frequency range is produced while flying low over the vegetation during the day (Alcock et al. 1989). In both *Hecatesia* species, males exhibit agonistic interactions and defend small territories at which females arrive (Alcock et al. 1989; Alcock and Bailey 1995). The attraction of local males to loudspeakers broadcasting male song indicates that sound plays an important role in these interactions and territorial defense.

In the Arctiidae acoustic communication is often related to sounds produced in the context of interacting with bats. Male *Euchaetes egle* and *Euchaetes bolteri* produce species-specific songs with thoracic tymbal organs when courting females. These songs are acoustically identical to the sounds that both sexes emit for warning or jamming bats, and there is no sexual dimorphism in tymbal structure (Simmons and Conner 1996). In other species (e.g. *Phoenicoprocta capistrata*) the tymbal structure and the sounds differ between the sexes (Rodriguez-Loeches et al. 2009). In *Empyreuma affinis* and *Syntomeida epilais* both sexes sing in a duetting fashion (Sanderford and Conner 1995, 1998), while in *Pyrrharctia isabella* it is only the female who sings, which she does in response to the male courtship pheromone (Krasnoff and Yager 1988). The female acoustic reply in *P. isabella* is identical to the sound she emits when disturbed. Male songs are necessary for courtship success in some species, but in others (e.g. *Cycnia tenera*) they may be critical only in the absence of male courtship pheromone (Conner 1987). Sanderford (2009) presents a more comprehensive survey of acoustic communication in the Arctiidae.

In the Lymantriidae soft songs are reported in several species and may be similar to those described in the previous section except that they are produced by the female, not the male, during courtship (Rowland et al. 2011). The mechanism of sound production is unknown.

6.4.3 Papilionoidea

Several species of *Hamadryas* butterflies (Nymphalidae) produce audible clicks by percussion of veins in the forewings. These sounds are generally emitted by both sexes in a defensive context. Males also click during agonistic interactions with neighbors, and in at least one species the sounds represent a courtship song (Monge-Najera et al. 1998).

6.5 Physiology and Behavior of a Model Acoustic Species, *Achroia grisella*

6.5.1 Mating Communication

The galleriine pyralid moth *Achroia grisella* (Fig. 6.4a) has served as a model species in the study of sexual selection over the past 20 years. I present this example to illustrate how sound can function in mating communication in the Lepidoptera, and also to infer the evolution of acoustic communication in the order.

A. grisella adults normally remain in the immediate vicinity of honeybee (*Apis mellifera*) colonies, and signaling and mating behavior take place there (Greenfield and Coffelt 1983). Males begin singing at dusk and continue more or less uninterruptedly for 6–10 h. This activity starts on the evening following adult eclosion and is repeated each night over 7–10 d until senescence and death. The male song is a series of brief ultrasound pulses (~100 μs, 70–130 kHz) delivered at a regular rhythm ranging from 80–100 pulses·s^{-1} among individuals within a population (Jang and Greenfield 1996; Jang et al. 1997; Fig. 6.4d). The pulse rhythm increases linearly with temperature (Greenfield and Medlock 2007) and reflects the rate of wing beating, which generates two pulses during each complete cycle of wing movement. A given pulse represents the strongly damped resonance of the tymbals on the tegulae (Fig. 6.4b, c), which are knocked by the wing bases during the upstroke and again during the downstroke. Closer analysis reveals that most

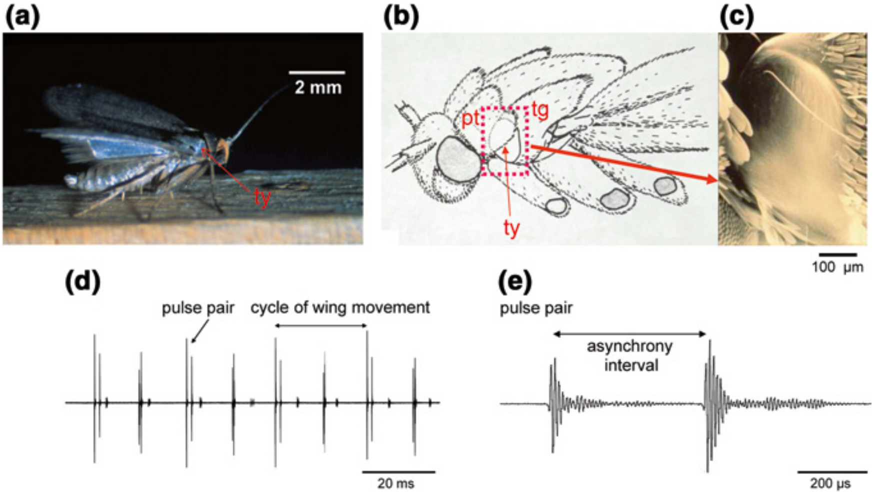

Fig. 6.4 Sound production and ultrasound advertisement song in male *Achroia grisella*. **a** singing male with sound producing tymbal (*ty*) shown, **b** schematic representation of tymbal (*ty*) situated on the tegula (*tg*), posterior and ventral to the patagium (*pt*), **c** scanning electron micrograph showing tymbal, the scale-less frontal area of the tegula (adapted from Spangler et al. 1984)

resonances are actually ‘double pulses’ (Fig. 6.4e) in which a brief (~100–500 μs) delay, termed the ‘asynchrony interval’, separates two individual pulses. The delay arises because movement of the left and right wings is not perfectly synchronous, and the two sides generate two non-overlapping pulses.

Female response to and preference for males is strongly influenced by the acoustic characters of the male song. Females move toward songs that are delivered at a faster pulse-pair rate, that include longer pulses and pulses with a higher peak amplitude, and whose pulse pairs encompass a longer asynchrony interval (Jang and Greenfield 1996; Limousin and Greenfield 2009; Alem and Greenfield 2010). Most of these preferences represent choice for higher acoustic energy or power and may be based on greater afferent activity. There is no evidence that females evaluate the carrier frequency of male song, which is not surprising given that the *A. grisella* ear has only 4 afferent neurons, each attached to the tympanum at the same central location. The tympanum is broadly tuned between 40 kHz and at least 100 kHz, and its peak sensitivity, between 90 and 100 kHz, matches the dominant frequencies of male song (Rodriguez et al. 2005). Females also exhibit a threshold response to the pulse-pair rate of male song (Brandt et al. 2005) and will not move toward a single song stimulus if it is delivered below a minimum rate ranging from 20–80 pulse pairs$\cdot$s^{-1}. Behavioral tests with live males demonstrated that females evaluate the overall attractiveness of song based on a multivariate function of the several signal characters (Jang and Greenfield 1998), which may vary among individuals (Jang and Greenfield 2000) and between populations (Zhou et al. 2008).

Male song also evokes several male responses in *A. grisella*: Neighboring singers stimulate a male to initiate song at the beginning of the night, and a particularly close neighbor can elicit a 4–10 % increase in pulse-pair rate for 15–20 min during a singing bout (Jia et al. 2001). These responses may be forms of signal competition in which a male can match or exceed the quality of a neighbor’s signaling and thereby attract local females. Singing males often gather in small clusters, which can be interpreted as lekking aggregations, and agonistic interactions commonly occur between neighbors (Cremer and Greenfield 1998). Males who sing in these aggregations enjoy a higher per capita attractiveness to females than males singing alone (Alem et al. 2011).

6.5.2 Sexual Selection

Male *A. grisella* who broadcast attractive songs expend more energy than males who broadcast songs of inferior attractiveness (Reinhold et al. 1998). Song attractiveness, as determined by the signal characters influencing female preference, is phenotypically and genetically correlated with a male’s body mass at adult eclosion, the duration of his nightly singing period, and his adult longevity (Brandt and Greenfield 2004). That is, song attractiveness is ‘condition’ dependent, and in the laboratory there is no evidence of a trade-off between sexual attractiveness and survival.

Quantitative genetic analyses showed that the various male signal characters are heritable traits (Collins et al. 1999; Brandt and Greenfield 2004; Zhou et al. 2011). Similar findings, albeit based on fewer data, were obtained for the female preference function (Jang and Greenfield 2000) and response threshold (Rodriguez and Greenfield 2003). But contrary to some expectations from sexual selection theory, no genetic covariance has been found between the male signal and female preference and response traits in *A. grisella* (Zhou et al. 2011; Limousin 2011; Limousin et al. 2012). Both male signaling and female preference are influenced by several quantitative trait loci (QTL) that are distributed among the 29 chromosomes. One QTL that is specifically associated with the pulse-pair rate of male song exerts a very major influence on this song character, but none of the song QTL are located on the same chromosomes as the preference QTL. The findings on the number and strength of QTL influencing song are similar to those in Hawaiian cricket species (Shaw et al. 2007).

6.5.3 *On the Bat-Moth Interaction*

In *A. grisella* behavioral responses to predatory bats and their echolocation signals occur in flight and also on the substrate, where males exhibit very different behavior from females (see Chap. 5 by Conner). Flying *A. grisella* cease beating their wings and drop toward the ground upon hearing echolocation signals (Rodriguez and Greenfield 2004). This response can be elicited by a single pulse of ultrasound (40–100 kHz) that exceeds a minimum duration of 1 ms and amplitude of 70 dB. Response latencies decrease as the pulse lengthens, the amplitude increases, or the pulses are delivered more rapidly and may be as short as 50 ms.

Because a considerable proportion of *A. grisella* activity takes place on the substrate, we asked whether the moths also respond to echolocation signals in this situation. Whereas foraging bats are not likely to enter wooden honeybee hives and prey on the moths, it is critical to recognize that these enclosed hive boxes have only been employed in apiculture since the middle of the nineteenth century. Moreover, much signaling and mating behavior in *A. grisella* takes place in the vicinity of the honeybee colony rather than within it. Thus, *A. grisella* would have been exposed to bat predation, particularly from bat species that glean their insect prey from the substrate, for most of their evolutionary history, and they remain exposed today. We found two basic responses of *A. grisella* to echolocation signals while on the ground: Singing males become temporarily silent (referred to as a ‘silence response’), and females who are running, as during their approach to a singing male, cease movement (referred to as a ‘stationary response’; Greenfield and Weber 2000; Greenfield and Baker 2003). Male and female responses are elicited by ultrasound pulses that exceed a minimum of 75 dB SPL and a duration of 1 ms but are delivered at a relatively slow rate, <30 pulses·s^{-1}. This last criterion reflects the slow pulse rate of bat echolocation signals broadcast during the ‘search phase’ of predation. It is inferred that *A. grisella* discriminate singing male conspecifics from searching bats on the basis of pulse rate rather than pulse length (Greenfield and Weber 2000). Whereas bat echolocation signals are normally much longer than the pulses in *A. grisella* male song, female *A. grisella* will respond positively to artificially lengthened pulses as if they are super-normal stimuli (Fig. 6.5).

Tests in a flight room in which *A. grisella* were exposed to live bats—*Rhinolophus ferromequinum* (greater horseshoe bat), a species that both forages aerially and gleans prey from the substrate and has no aversion to eating *A. grisella* in captivity—revealed both male silence and female stationary responses to bat echolocation signals (Alem et al. 2011). More importantly, the bats were attracted toward singing male *A. grisella*. Thus, the silence response in males is probably an adaptation that reduces the risk of exposure to bat predation. Because moths moving on substrates generate inadvertent sounds that may be perceived by gleaning bats, the stationary response in females is probably a defensive adaptation as well. Life history and the 'acoustic scene' influence the balance between sexual advertisement and defensive behavior in *A. grisella*: Males and females are less likely to exhibit silence and stationary responses as they age and the probability of future mating opportunities declines (Lafaille et al. 2010). The silence response is also reduced when males join lekking aggregations because neighbors' songs mask predator signals. Moreover, the pressure of signal competition in a lek may 'motivate' males to ignore predation risks (Brunel-Pons et al. 2011).

The dual function of hearing in *A. grisella*, and in moths in general, invites questions on the genetics of sexual and defensive behavior. Do sexual and

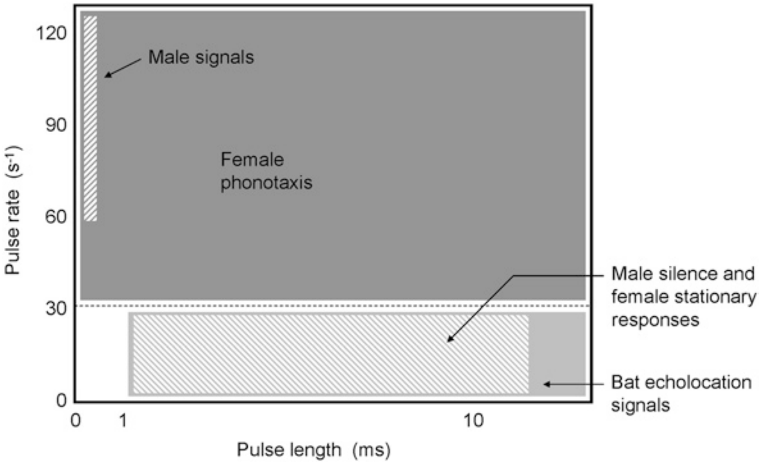

Fig. 6.5 Diagram of pulse pair and pulse rate combinations showing the range of *Achroia grisella* male song and echolocation signals of gleaning bats during their searching phase. Female responses to male song and defensive responses of male and female *A. grisella* to bat echolocation signals while on the substrate are indicated (adapted from Greenfield and Hohendorf 2009). Defensive responses while in flight are given to pulse lengths >1 ms regardless of pulse rate

defensive responses to pulsed ultrasound represent independent traits or different expressions of the same behavioral trait evoked under distinct circumstances? Similarly, do the male silence and female stationary response represent independent or linked traits? Quantitative analysis of inbred lines indicated no evidence of genetic covariance between sexual and defensive behavior (Greenfield and Hohendorf 2009), and in females the QTL that influence these two behaviors are not found on the same chromosomes (Alem 2012). On the other hand, the male silence and the female stationary responses do appear to covary (Greenfield and Hohendorf 2009). That is, they may be sex-specific expressions of the same trait, an inhibition of motor activity in response to stimuli that are normally associated with potential predators.

6.6 Evolution of Acoustic Communication: On the Role of the Sensory Bias Mechanism

The acoustic Lepidoptera offer us a valuable opportunity to probe the evolution of signals in animal communication. Because acoustic signaling used in mating communication in Lepidoptera is so rare while hearing is widespread, the evolution of perception prior to communicative signaling is inferred: One can readily conceive of the occurrence of perception in the absence of communication, and the occurrence of non-communicative acoustic signals in the absence of hearing is equally possible, as in the case of startle or aposematic signals intended for predators. However, communication requires the occurrence of both perception and signaling, with the specific stipulation that these two functions be mutually beneficial to both parties, sender and receiver. Where one function, i.e., hearing, is common while the other, i.e., acoustic signaling, is rare, it is more parsimonious to assume that the rare one evolved later in several clades as opposed to the alternative where the rare one was secondarily lost in the majority of clades.

The above evolutionary sequence implies that acoustic communication in Lepidoptera originated via the ‘sensory bias’ mechanism (sensu Ryan et al. 1990; Endler and Basolo 1998). That is, male acoustic signals originated inadvertently at some point after hearing evolved. These novel signals would have had a responsive audience—females equipped with tympanal organs and exhibiting certain behavioral reactions to pulsed ultrasound—and thus communication would have appeared without any parallel evolution on the receiver side. It is this absence of receiver evolution that distinguishes the sensory bias mechanism from the various ‘co-evolutionary mechanisms’, e.g., Fisherian, good genes, chase-away, proposed for signal evolution. The sensory bias mechanism is further supported by the homology of ears within the main acoustic clades, Pyraloidea and Noctuoidea, combined with the multiple, non-homologous structures used for sound production within these clades. This distribution of morphologies is consistent with the proposition that sound production originated on multiple, independent occasions, occurring after hearing had evolved.

Whereas the general notion that hearing preceded sound production in the Lepidoptera may be relatively solid, the details of how acoustic communication evolved remain problematic. Those initial, inadvertent sounds produced by males would have had a female audience, but we can infer that the behavioral responses of these females were negative in terms of movement and orientation: Erratic or evasive flight and dropping to the ground if in the air, and becoming stationary if on the substrate, the basic responses to bat echolocation signals. Thus, we are faced with the challenge of deciphering the evolutionary trajectory from defensive to sexual responses in females. Otherwise stated, how could the males producing these initial, inadvertent sounds have benefited from defensive responses evoked in females such that male sound production was selectively favored? And once favored, how did these inadvertent sounds evolve toward in specialized forms of mating communication?

Various cases reviewed here, particularly those involving moth-bat interactions, provide some insight to the question of how acoustic communication may have emerged from its presumed beginnings. In some arctiid moths, the same structures and sounds are used in defensive and sexual contexts. These male courtship sounds are not identical to bat echolocation signals, but they are of similar high frequency and delivered in short pulses. This overlap suggests that the response evoked in females by the male sounds could resemble that evoked by the bat signals. Unfortunately we have relatively little information on how moths resting on the substrate, which is where courtship in arctiid moths takes place, respond to bat echolocation signals. Whereas the male sounds are known to be necessary for successful courtship in some arctiid species, the specific behavioral responses that females make to these sounds have generally not been directly studied via playback of synthetic signals, which would allow one to disentangle the effects of sound from other male signals. Consequently, we can only suggest that at some point in evolution certain males began to broadcast their defensive sounds when engaged in courtship.

Noctuid and crambid moths are not reported to broadcast sounds intended for bats, but recent findings on several species wherein males produce very low amplitude courtship songs allow comparisons of sexual and defensive responses. In *Spodoptera litura* playback of synthetic male signals to females evoked a stationary response, the freezing of all movement, similar to that observed in response to synthetic bat echolocation signals (Nakano et al. 2010a). Similar behavior also occurred in *Ostrinia furnacalis* (Nakano et al. 2010b). The implication is that females do respond to the male signals as if they were made by predatory bats, and males may benefit from this evoked defensive response because a female who remains motionless may be more easily courted.

The case of *A. grisella* (Pyralidae) is more challenging but must ultimately be analyzed to understand the evolution of acoustic communication. Female *A. grisella* do not simply freeze in response to male song, as they do when exposed to bat echolocation signals, but rather run toward the singing male. Assuming that the sensory bias mechanism accounts for the origin of acoustic communication in moths, we are faced with an inevitable modification of this evolutionary mechanism in which some change occurred in the female subsequent to male signaling. This change would have been essential for *A. grisella* females in their discrimination of male and bat signals. *A. grisella* females distinguish male song from bat echolocation signals primarily on the basis of the slow pulse rate (10–25 pulses·s^{-1}) of echolocation signals of gleaning bats. Were male signals delivered at a high pulse rate at the origin of signaling or did male pulse rate gradually evolve toward faster values alongside a female preference for faster and faster song? Was the hypothetical acceleration of pulse rate in the moth song driven by the need to be distinguished from bat echolocation signals, by sexual selection, or both? And, was the initial male song a crude imitation of bat signaling that elicited a freezing response in females by virtue of its slow pulse rate? Finally, did male pheromones allow females to discriminate males from bats when song originated? Although we cannot answer these questions definitively, it is rather certain that some modification in the female response had occurred: Female *A. grisella* exhibit an abrupt, categorical shift from a defensive to a sexual response as the rate of synthetic ultrasound pulses exceeds 30–40 pulses·s^{-1} (Greig and Greenfield 2004), a feature that would not have been expected in the ancestral state where only defensive behavior occurred.

Is this scenario presented for *A. grisella* song the exception or the rule for the evolution of signaling via sensory bias? It is tempting to propose the latter, as the need to discriminate the signaler from environmental cues will always be present (Greenfield 2002). One approach that could help to resolve questions on signal evolution via the sensory bias mechanism is analysis of genetic architecture, both quantitative and molecular. Genetic architecture has seldom been considered in this context, but information on the genes that influence female responses to male signals and environmental cues could indicate whether these two perceptual traits are controlled pleiotropically by the same locus (loci) (cf. Fuller 2009). Such control is a critical issue, as a ‘genetic imprint’ in the form of pleiotropy is predicted should the sensory bias mechanism occur in its simplest form: A male signal arises that elicits a female response to environmental cues, and this response remains fixed. However, if some change has occurred in the female response after the origin of the male signal, the genetic loci controlling the two perceptual traits may not be fully identical. Our findings on the genetics of female defensive and sexual responses in *A. grisella* are consistent with the latter situation, male acoustic signals that originated via the sensory bias mechanism and subsequent evolution of the female auditory response to those signals. Here, the genetic analysis supports the general expectation that the female sexual response will not remain unchanged over evolutionary time.

6.7 Conclusion

This chapter has presented the Lepidoptera as an eminently appropriate group in which to probe evolution of acoustic communication, and the sensory bias mechanism in particular. Acoustically communicating Lepidoptera reveal the phylogenetic imprint of the sensory bias mechanism in the evolution of male song, but they also present the dilemma of an improbable transition in the female response. Some resolution of this problem appears possible via further comparative and genetic analyses. It is hoped that evolutionary biologists will avail themselves of the unique opportunities afforded by acoustic Lepidoptera and that further inquiry of signal evolution is undertaken among these very special acoustic species.

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