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REVIEW

Moth hearing and sound communication

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Abstract Active echolocation enables bats to orient and hunt the night sky for insects. As a counter-measure against the severe predation pressure many nocturnal insects have evolved ears sensitive to ultrasonic bat calls. In moths bat-detection was the principal purpose of hearing, as evidenced by comparable hearing physiology with best sensitivity in the bat echolocation range, 20–60 kHz, across moths in spite of diverse ear morphology. Some eared moths subsequently developed sound-producing organs to warn/startle/jam attacking bats and/or to communicate intraspecifically with sound. Not only the sounds for interaction with bats, but also mating signals are within the frequency range where bats echolocate, indicating that sound communication developed after hearing by "sensory exploitation". Recent findings on moth sound communication reveal that close-range (~ a few cm) communication with low-intensity ultrasounds "whispered" by males during courtship is not uncommon, contrary to the general notion of moths predominantly being silent. Sexual sound communication in moths may apply to many eared moths, perhaps even a majority. The low intensities and high frequencies explain that this was overlooked, revealing a bias towards what humans can sense, when studying (acoustic) communication in animals.

Keywords Co-evolution · Sensory exploitation · Ultrasound · Echolocating bats · Predator-prey

Introduction

Insect hearing and sound communication is a fascinating subject, where the combination of many classical studies and recent progress using new technological and molecular methods provide an unsurpassed system for studying and understanding the evolution of acoustic communication, intraspecific as well as between predator and prey. Sound is fairly easy to quantify allowing for estimates of communication distances and thus inferences about communication partners. Also, we can simulate sounds and therefore do experiments to test the importance of specific acoustic features in the sound signals.

Moths have been particularly attractive because the predator, echolocating bats, is so well defined and the predator–prey interaction restricted to audition. These facts probably explain that the bat–moth model has found its way into many textbooks as a clear-cut example of co-evolution, leading to adjustment of sensory physiology as well as behaviors in predator and prey.

Several authors beginning with the "father of moth hearing physiology", Roeder (Roeder 1974) and later many others, in particular Fullard (Fullard 1998), have written excellent broad reviews outlining the sensory ecology of

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acoustic adaptations of many moth species from areas with different selection pressure from a varying number of sympatric bats. Our aim with this review is not to repeat what they already did, but to build upon their data and update with many new findings.

Moth hearing

Ears have evolved independently in many insect groups, presumably reflecting the fact that with an exoskeleton it is "easy" to make an ear from mechanoreceptors attaching to the surface (Fullard and Yack 1993; van Staaden and Römer 1998). In moths, tympanal hearing organs have evolved independently at least five times (Minet and Surlykke 2003; Greenfield 2014). In the superfamily Noctuoidea, the ear is placed on the metathoracic segment and has two sensory cells, A1 and A2, except in the Notodontidae, where only one A-cell is found. In Geometroidea and Pyraloidea, as well as in Drepanoidea the ears are found at the base of the abdomen and have four sensory cells, A1-A4. In those Sphingidae (Bombycoidea) species, which can hear, ears are located on the proboscis. Thus, moth ears are highly diverse in placement and morphology, but quite similar in shape of the threshold curve. Even in Hedyloidea, the nocturnal sister group to butterflies, the ears at the wing base are tuned to ultrasonic frequencies comparable to other nocturnal Lepidoptera.

The frequency range of hearing is roughly the same in all moth groups: the ears are most sensitive to ultrasonic frequencies with best frequencies ~20–60 kHz for the most sensitive A-cell, A1 (Fig. 1). In general, there is a correlation between size and best frequency, such that large moths are tuned to lower frequencies than smaller moths (Surlykke et al. 1999). In moths with two or four sensory receptors, the A2-A4 cells have higher thresholds, extending the dynamic range of the ear from the approximate 20 dB of each cell. In all moths, where threshold curves

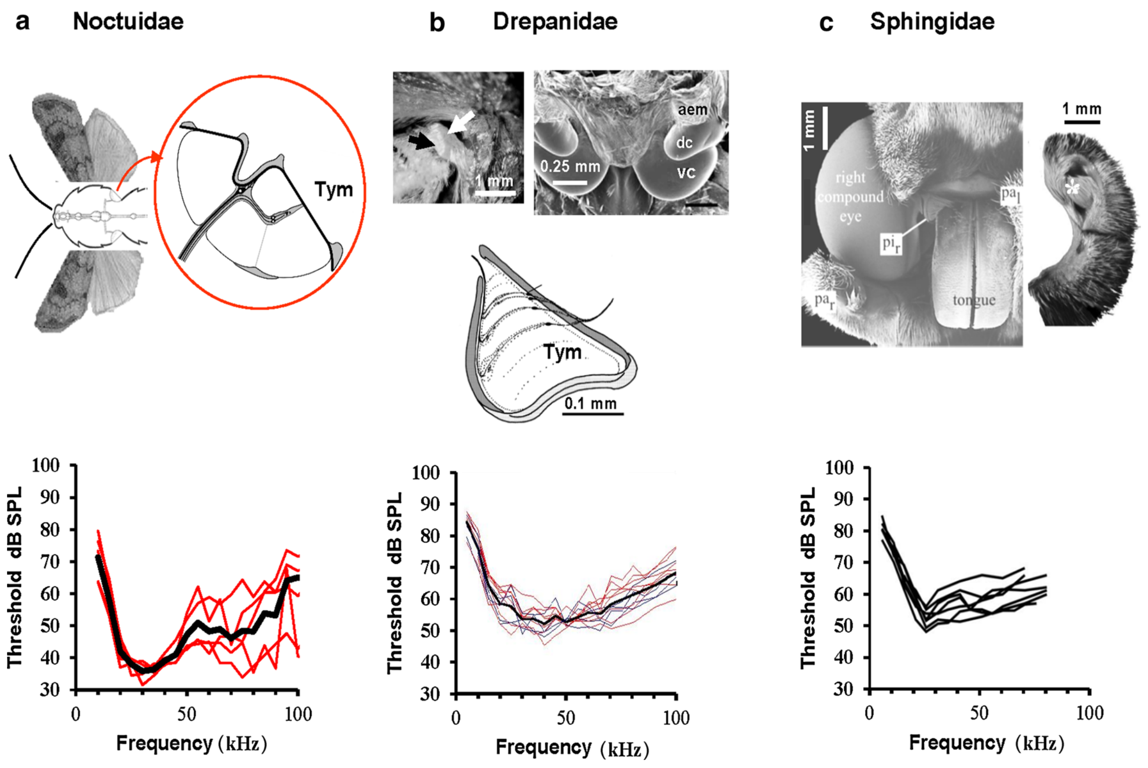

Fig. 1 Hearing in moths. Ears and hearing threshold curves for moths from three different superfamilies. **a** Noctuoidea have ears on the metathorax with two sensory cells attached directly to the tympanum (Tym). The *lower panel* shows individual and average thresholds for the most sensitive A-cell in *Axylia putris* (Noctuidae) from Denmark. **b** Drepanoidea, hook tip moths, have ears (*upper left*, *black* and *white arrows* showing location) with internal tympanal membranes as a partition wall between the dorsal (*dc*) and ventral (*vc*) air chambers. Sound presumably enters through the anterior external membrane (*aem*). Below representation of the curved tympanic membrane (*Tym*) in its frame with scolopidia 1–4 viewed from the dorsal chamber. The *lower panel* shows threshold curves for female (*red*), male (*blue*), and average (*black*) *Drepana arcuata.* (Surlykke et al. 2003). **c** Some hawkmoths, Sphingidae (Bombycoidea) have ears made of the palp and pilifer mouthparts. In upper left panel the right palp (pa_r) of the Death's head moth, *Acherontia atropos*, has been deflected to show the pilifer (pi_r). The scale-plate (*asterisk*) on the palp functions as tympanum. Threshold *curves* for *A. atropos* are shown below (adapted from Göpfert et al. 2002)

have been determined also for less sensitive sensory cells, the best frequency (frequency with the lowest threshold) is the same for all the A-cells of the ear, which means that moths are tone-deaf and cannot discriminate between different frequencies (Miller and Surlykke 2001; ter Hofstede et al. 2011, 2013). The sensitivity at the best frequency is in the range of 25–45 dB SPL. Sensitivity is also correlated to size, such that larger moths are not only tuned to lower frequencies, but also more sensitive (Surlykke et al. 1999). Moth species vary greatly in size, and larger moths should be more conspicuous to bats because they provide a larger reflective surface for echolocation calls and thus a greater target strength, which will enable echolocating bats to detect them at greater distances than small moths. The lower thresholds of larger moths compensate for their increased conspicuousness to bats by enabling them to also detect bats at greater distances, and relative detection distances are roughly constant across moth sizes: In spite of less sensitive hearing, moths can detect bats around ten times the distance where bats can detect moths, because moths are detecting the outgoing sound, while bats detect the small fraction of sound returned as an echo. Thus, moths can detect bats at ca. 20–100 m, while bats can detect moths (1–10 m) (Surlykke et al. 1999; Surlykke and Kalko 2008).

There are several facts strongly suggesting that moth ears evolved to detect echolocating bats: (1) the tuning of all moth ears to bat frequency range in spite of morphological differences (Fig. 1), (2) the positive correlation between how actively moths fly at night and their auditory sensitivity (ter Hofstede et al. 2008), (3) the absence of intraspecific acoustic communication in most moths (but see Sect. 4 below), (4) the evasive maneuvers and acoustic defenses elicited by bat sounds (Fullard 1998; Conner 2014; Greenfield 2014; see article in this volume by Pollack, G.S.), and (5) the correlation between bat predation pressure and moth hearing thresholds: Moths from Hawaii, with only one bat species, are tuned to the specific frequency of the sympatric bat (Fullard 2001). Moths that have escaped the predation by bats by being geographically isolated at remote islands without bats (Surlykke 1986; Fullard et al. 2007a) or, even more efficiently, by being temporally isolated by flying during the daytime or the winter time when no bats fly (Fullard et al. 1997; Rydell et al. 1997) show reduced hearing sensitivity. A comparison of hearing sensitivity of moths from Canada, Denmark, and the UK corroborated this pattern by showing that the British moths were more sensitive to very high frequencies than moths from the two other areas, probably reflecting the predation pressure from rhinolophid bats echolocating above 80 kHz in the UK (ter Hofstede et al. 2013).

The fact that those few moths, which use their ears for long-distance intraspecific acoustic communication, produce sounds in the bat frequency range also supports the notion that moth ears evolved originally to detect bats. If moth ears pre-existed sound production, the sensory bias (Ryan et al. 2001) forced males to produce sounds that would fall into the sensitive frequency range of the females (Nakano et al. 2013; Greenfield 2014). In the following section, we will discuss the three main scenarios for sound communication in moths: (1) interspecific acoustic interaction with bats, (2) long- and short-distance loud intraspecific sexual communication, and (3) short-distance whispering “private” intraspecific communication.

Moth sound communication

Loud sound production for interspecific interaction with bats

Many species from one family, Arctiidae (subfamily Arctiinae in the family Erebidae), within the superfamily Noctuoidea, have evolved sound-producing organs, tymbals, on the metathorax. Both males and females react to bat sounds by emitting intense ultrasonic clicks, either single clicks or trains of clicks depending upon whether the tymbal is smooth or striated with microtymbals. It seems obvious that the clicks increase the survival chance of the moth, but also evaluate the distance to the approaching bat based on the repetition rate of the bat calls to elicit clicking (Fullard et al. 2007b; Ratcliffe et al. 2009). However, the exact function of clicks has been much debated. The three most likely, non-mutually exclusive, hypotheses are startle, warning, or jamming. Many arctiid moths are toxic and brightly colored so for moths with smooth tymbals producing single clicks a warning function may seem most likely (Surlykke and Miller 1985; Acharya and Fenton 1992), but startle may also play a role (Stoneman and Fenton 1988). Jamming, i.e., interrupting the bat’s own range discrimination based on echo delay (Fullard et al. 1979), would require clicks arriving at the bat’s ear within a short time window around the arrival of the echo. In a stimulating series of recent experiments this has in fact been shown to be the case for a very active clicking tiger moth producing long series of very frequent click, which interfere with echolocating bat’s precise assessment of target distance because the high click density ensures overlap with the bat’s own echoes (Corcoran et al. 2009; Corcoran and Conner 2012). For aposematic species, clicks emitted by tiger moths in the context of bat defense are intense, around 70–90 dB SPL at 10 cm (Surlykke and Miller 1985; Nakano et al. 2009a; Corcoran et al. 2010) so bats can easily hear them even at distances where they would probably not yet have detected the echo from the moth. If a flying bat has a detection threshold of 20 dB SPL, the estimated detection distance for a 80 dB moth click with most energy around 40 kHz (atmospheric attenuation 1 dB/m) would be ca. 17 m. Moth hearing thresholds are much higher than bats'. Based on a threshold of around 40 dB at 40 kHz, moths' detection distance for clicks would be 5–6 m. Very recently, Geometridae were added to the group of moths producing loud sounds for bat–moth interaction: the non-toxic orange beggar moth (*Eubaphe unicolor*) produce loud clicks by prothoracic tymbals in response to bat sounds (Corcoran and Hristov 2014).

Loud sounds for intraspecific communication

In contrast to the sound producing Arctiidae species and the geometrid beggar moth, where both species generally produce sound when hearing bat calls, only males produce sounds in the relatively rare examples of intense sound production in Noctuoidea, indicating that their sounds are for intraspecific communication. While ears in all Noctuoidea evolved once and are homologous, the wide diversity of sound-producing organs show that sound production has evolved independently several times (Conner 2014; Greenfield 2014). Noctuoidea ears are located on the metathorax, but sound-producing organs may be located in a variety of places and sound production mechanism may also vary for example males of the winter-flying species *Rileyana* (former *Thecophora*) *fovea* (Noctuidae) stridulate by scraping the modified hindleg against a bubble (fovea) on the hindwing (Surlykke and Gogala 1986). Male Nolidae of the species *Pseudoips prasinana* and *Bena bicolorana* produce high intensity clicks (100 dB SPL at 10 cm) using ventral tymbal organs located in a cleft in the second abdominal sternite. Interestingly, these two species show the same correlation between structure and function as in arctiid moths: the tymbal may be smooth as in *P. prasinana*, which produces a single click for each tymbal buckling, or with striae on the medial part, as in *B. bicolorana*, which accordingly produces many clicks per buckling (Skals and Surlykke 1999). Percussive sound production also occurs: males of diurnal Australian whistling moths, *Hecatesia* spp. (Noctuidae), strike the forewings above the back to produce sounds, which play a role in agonistic interaction with males and in female attraction (Bailey 1978). There seem to be only a few Arctiidae species, mainly from the Ctenuchinae (tribe Ctenuchini in Arctiinae), where clicks function in intraspecific communication (Sanderford et al. 1998; Conner and Corcoran 2012), although future research is likely to unravel more examples. Loud sound production has not been reported from Drepanidae, but there are several examples of loud ultrasonic sound production in Pyralidae (reviewed in Greenfield 2014).

In almost all cases studied so far, the loud sound production is done by one gender, the males. The temporal patterns and the duty cycle of the sounds differ between species, but the frequency ranges are quite comparable, 20–60 kHz, a bit higher for the smaller pyralids. The bandwidths of the communication sounds are more narrow compared to clicks produced for bat defense by arctiid moths (Fig. 2), but the

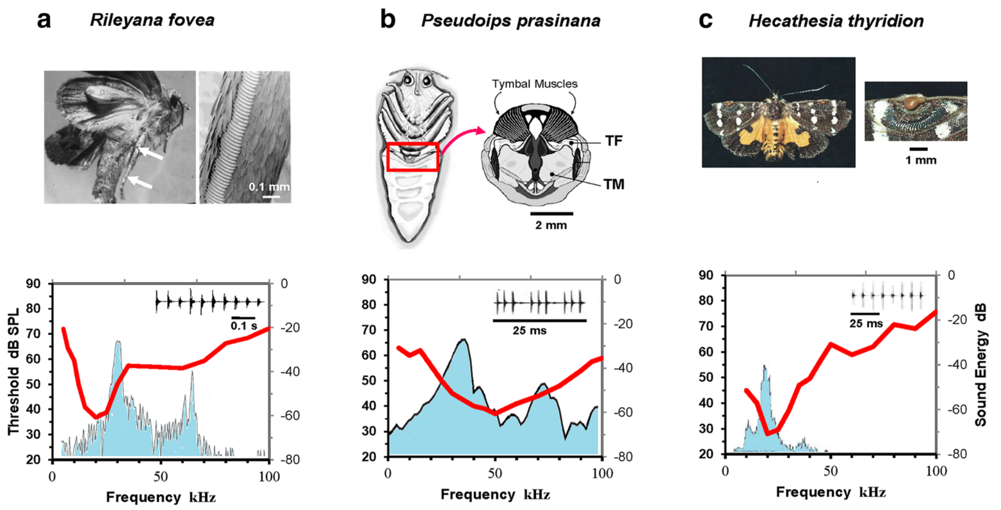

Fig. 2 Sound production in moths. Loud sound production in Noctuidae show correlation between the moths' own average hearing thresholds (*red curves*, *left y*-axis) and sound spectra (*blue areas*, *right y*-axis). **a** *Rileyana fovea* males produce pulses (*inset lower panel*) by scraping a file on the hindleg (*white arrows*, and *right*) against the "fovea" a bubble on the hindwing (Surlykke and Gogala 1986). **b** *Pseudoips fagana* (Nolidae) males produce triplets of pulses (*inset* in *lower figure*) by buckling internal tymbal organs by powerful tymbal muscles, not found in females (Skals and Surlykke 1999). **c** In flight *Hecatesia thyridion* males can produce trains of pulses by striking knobs (castanets) on the forewings together above the back. *Upper right* shows close-up of castanets and surrounding corrugated membrane. (Bailey 1978; Surlykke and Fullard 1989)

best frequency of hearing is within the frequency range, where all moths, also silent moths, are most sensitive, and thus within the frequency range of the echolocation calls emitted by insectivorous bats (Schnitzler and Kalko 2001; Schnitzler et al. 2003) supporting the hypothesis that ears evolved first for bat detection in moths, and sound communication followed later by sensory exploitation (Nakano et al. 2013). Contrary to the whispering courtship song (Sect. 3.3), the frequency of the loud calling songs is not always tuned to the best hearing frequency as shown in Fig. 2, in particular in Nolidae (2b), while the match is good in the two species *Rileyana fovea* and *Hecatesia thyridion,* which are temporally isolated from bats. Nolidae are nocturnal and active at summer suggesting that (female) hearing must not only detect males, but also all the sympatric bat species, hence requiring broad tuning. Due to more severe atmospheric attenuation of high frequencies, male calling sounds in the lower end of the female spectrum give longer communication distances than a frequency tuned to the females' best frequency. The sound pressures of these loud communication sounds are in the order of 90–100 dB SPL at 10 cm and thus comparable to sound pressures of the clicks arctiid moths emit in response to bat calls. Depending on species and emitted sound pressures (when reported) it is likely that the maximal communication distance can be estimated to approximately 10–20 m on the basis of hearing threshold, and transmission loss (40 kHz). Thus, the high intensity sounds probably play a role for sexual communication at mid-range distances, shorter than maximum communication distance with moth sex pheromones, which may be 200–500 m (Schlyter 1992), but longer distance than the close range, where the sexual mating behavior takes place.

However, some male moths generate loud ultrasonic courtship songs at close distances. The examples are from the Pyraloidea, where long-distance acoustic signaling has also been reported (Gwynne and Edwards 1986). In the bee moth, *Aphomia sociella* (Pyralidae), males attract females by sex pheromones (male odor) and subsequently produce loud courtship song (96 dB SPL at 10 cm, i.e., 1,585 times louder than the song of *Ostrinia furnacalis*, see Sect. 3.3) in close proximity to a female to stimulate her to assume a mate-acceptance position (Kindl et al. 2011). Males of *A. sociella* seem to have a mating territory and emit a rival song against intruding male(s), not unlike the system in the Australian whistling moths (Noctuidae). *Galleria mellonella,* belonging to the same subfamily as *A. sociella* also emit ultrasonic rival songs for male–male interaction. The function of the rival songs is unclear. Apparently, females cannot discriminate since they assume a mate-acceptance posture in response to the rival song as well as to true courtship songs. Male yellow peach moth *Conogethes punctiferalis* (Crambidae) also produce loud courtship songs close to a female. After approaching a female releasing sex pheromones, the male hovers around her generating a series of brief pulses and then one long loud (83 dB SPL at 10 cm) pulse (Fig. 3a) (Nakano et al. 2012a, b), causing the female to raise her wings upright and accept copulation (Fig. 3b). This specific "wing-raising" reaction is essential for copulation triggering the male's landing and attempting genital coupling. Wing-raising is evoked by any "long" ultrasonic pulse with duration of >200 ms (Nakano et al. 2014) (Fig. 3c). The series of short pulses (duration 28 ms, inter-pulse interval 26 ms) emitted before the long pulse

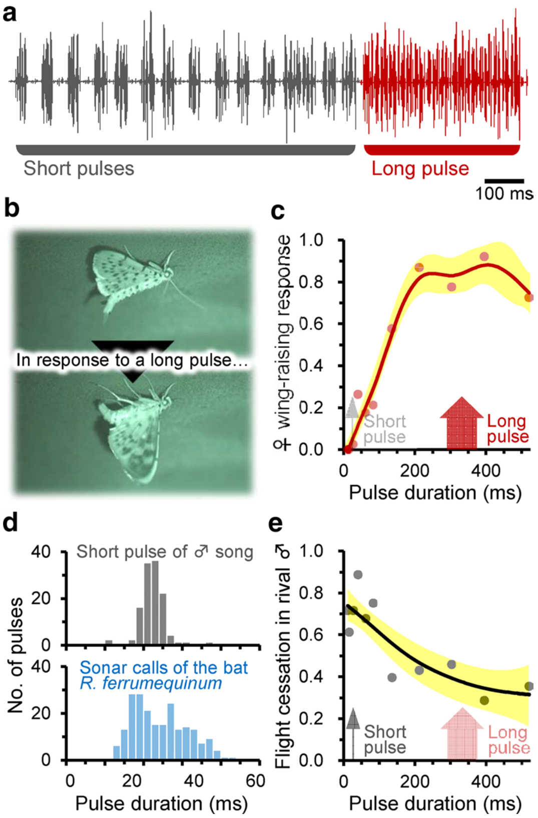

Fig. 3 Communication with loud sounds. Acoustic communication with loud courtship song in a crambid moth *Conogethes punctiferalis*. **a** Oscillogram of male courtship song composed of short pulses in the early phase (*black*) and a long pulse in the late phase (*red*). **b** Females raise their wings in a mate-acceptance posture in response to a long (>200 ms) ultrasonic pulse. **c** The proportion of virgin receptive females raising their wings increases with duration of male courtship pulse. The response curve (*solid line*) is estimated from averages of binary data (*circles*) with 95 % confidence intervals (CI) indicated by the *yellow band*. The width of *two arrows* on the *x*-axis denotes the 95 % CI of the mean durations of short pulses (*gray*; 26.8–28.8 ms) and long pulse (*red*; 297.0–380.9 ms), respectively. **d** *Histograms* of pulse duration of short pulses emitted by males of *C. punctiferalis* (*top*, *black*) and that of approach-phase echolocation calls in the greater horseshoe bats *Rhinolophus ferrumequinum* (*bottom*, *blue*). **e** Flight suppression effect of male courtship pulses on males flying toward a female. *Symbols* are same as **c** (adapted from Nakano et al. 2012a, b, 2014)

do not seem to directly affect female's mate-acceptance. However, the temporal pattern is comparable to approach calls of horseshoe bats *Rhinolophus* spp. a moth-foraging-bat species, which elicits flight cessation in moths. Thus, a possible function of the short pulses may be to suppress the flight of rival males (Fig. 3d, e), indicating a dual function of male courtship songs in *C. punctiferalis* to fend off rivals with the short pulses and make the female accept mating with the long pulse. The evidence from both *A. sociella* and *C. punctiferalis* suggest that the high sound pressure of the male courtship song might have developed for communication with rival males whereas for communicating with the females the loudness is mainly a "byproduct" of using the same sound-producing mechanism for rival songs and courtship songs. However, recently new data have revealed very quiet acoustic communication in a number of moth species. We will focus on this "private whispering" in the remaining part of the review.

Quiet sound communication in *Ostrinia* moths

Males of the Asian corn borer *Ostrinia furnacalis* (Crambidae) produce ultrasonic courtship songs of extremely low intensity (46 dB SPL at 1 cm = 26 dB at 10 cm, 48 kHz) in close proximity (≈1 cm) to a receptive female (Fig. 4) (Nakano et al. 2006, 2008). The females' threshold (38 dB SPL) at their best frequency (46 kHz) allows females to detect the male song only when a male is singing within 3 cm of the female (Fig. 4b) (Nakano et al. 2008). Males produce these sounds by stridulation; they rub specialized scales on their wings against scales on the thorax (Fig. 4a) (Nakano et al. 2008). Simple sound-producing scales on the body may have evolved more easily than other more elaborate cuticular sound-producing apparatuses, requiring major modifications of the integument. The male songs suppress the escape behavior of the stationary female releasing sex pheromones, thereby increasing the male's success in copulation, i.e., genital coupling with the motionless female (Nakano et al. 2008).

Quiet sound production has also been discovered in two other *Ostrinia* species, *O. nubilalis* and *O. scapulalis*. The sound levels are quite similar (23–26 dB SPL at 10 cm). Also hearing thresholds are comparable (38–44 dB SPL at the best frequency), indicating that sound communication functions only at very close range in all three species (Fig. 4c). However, the spectral features and the temporal patterns differ reflecting the phylogenetic relationships of *Ostrinia* moths (Fig. 4c). The songs of male *O. nubilalis* and *O. scapulalis* consist of pairs of pulses, whereas *O. furnacalis* males emit pulse-group songs (Fig. 4c) (Takanashi et al. 2010) with a higher frequency (peak frequency, 48 kHz; bandwidth 3 dB below the peak, 38–60 kHz) than in *O. nubilalis* (39 kHz; 31–45 kHz) and *O. scapulalis* (38 kHz; 29–45 kHz) (Fig. 4) (Nakano et al. 2008; Takanashi et al. 2010).

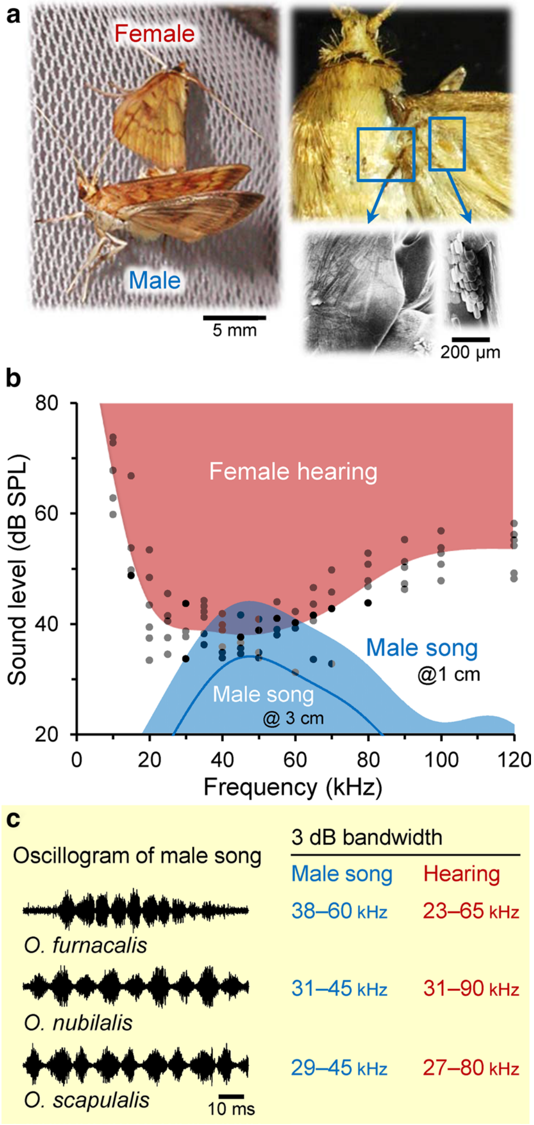

Fig. 4 Quiet sound communication. Ultrasound communication in a crambid moth *Ostrinia furnacalis*. **a** Courting males rub specific scales on the base of forewings against scales on mesothorax to emit ultrasonic songs. **b** Spectrum of the male ultrasound at a distance of 1 cm (at the female's ear; *blue area*) has main energy around 48 kHz, which corresponds to the most sensitive frequency range of female hearing (*red area*). At a distance of 3 cm the male ultrasound (*blue line*) is below the hearing threshold of the female, so she cannot hear him >3 cm away. The *gray circles* show individual hearing threshold values with overlapping data points indicated by a *deeper color*. **c** Oscillograms of male songs with pulse structures, bandwidths of the songs and hearing thresholds for three *Ostrinia* species. Adapted from Nakano et al. (2009a) and Takanashi et al. (2010)

Although sounds are used for sexual communication in *Ostrinia* moths, the physiological threshold and hearing range have been conserved as a result of predatory pressures imposed by insectivorous bats (Takanashi et al.

2010). Thus, also for those “soft spoken” Crambidae, the most likely evolutionary scenario is that evolution of ultrasonic hearing for bat detection came first and later ancestral males of *Ostrinia* species acquired the ability to produce courtship songs that can be heard only by females in close proximity. For the functions of the male courtship songs, we highlight them in Sect. 5.

Is intraspecific moth sound communication really so uncommon?

Ultrasonic sexual communication was first reported in the wax moths *Achroia grisella* and *Galleria mellonella* (Pyralidae) in the late twentieth century (Spangler et al. 1984; Spangler 1985), whereas production of ultrasonic clicks in both sexes of arctiid moths in defense against bats was described already in 1963 (Blest et al. 1963). Technological advances since then have made it a lot easier to record and analyze high frequency sounds. Nonetheless there are still only few known examples of ultrasonic intraspecific communication (see Sect. 3.2). Thus, sexual sound communication has been regarded as rare in moths. However, this impression may possibly be wrong, based on a failure to notice (male) courtship songs in many species using low intensities and high frequencies.

Loud acoustic signals in particular at lower frequencies are favorable for sexual communication over long distances. However, such signals lend themselves to eavesdropping by unintended receivers such as predators, parasitoids, and conspecific rivals (satellite males) (Zuk and Kolluru 1998; Gerhardt and Huber 2002; Hedwig and Robert 2014). In singing insects, loud sound signals are matters of life and death: predatory gleaning bats and auditory parasitoid flies locate sound-producing insects using passive hearing in nature (Belwood and Morris 1987; Zuk et al. 2006; Alem et al. 2011; Siemers et al. 2012). In contrast, the quiet male courtship songs in the corn borer moths *Ostrinia* spp. (Crambidae) (Sect. 3.3) suggested that whispering “soft” ultrasonic courtship songs might be widespread among moths, partly because the drawback of loud sounds does not apply to quiet sounds, which would be less susceptible to eavesdropping by predators and rivals (Nakano et al. 2008). In

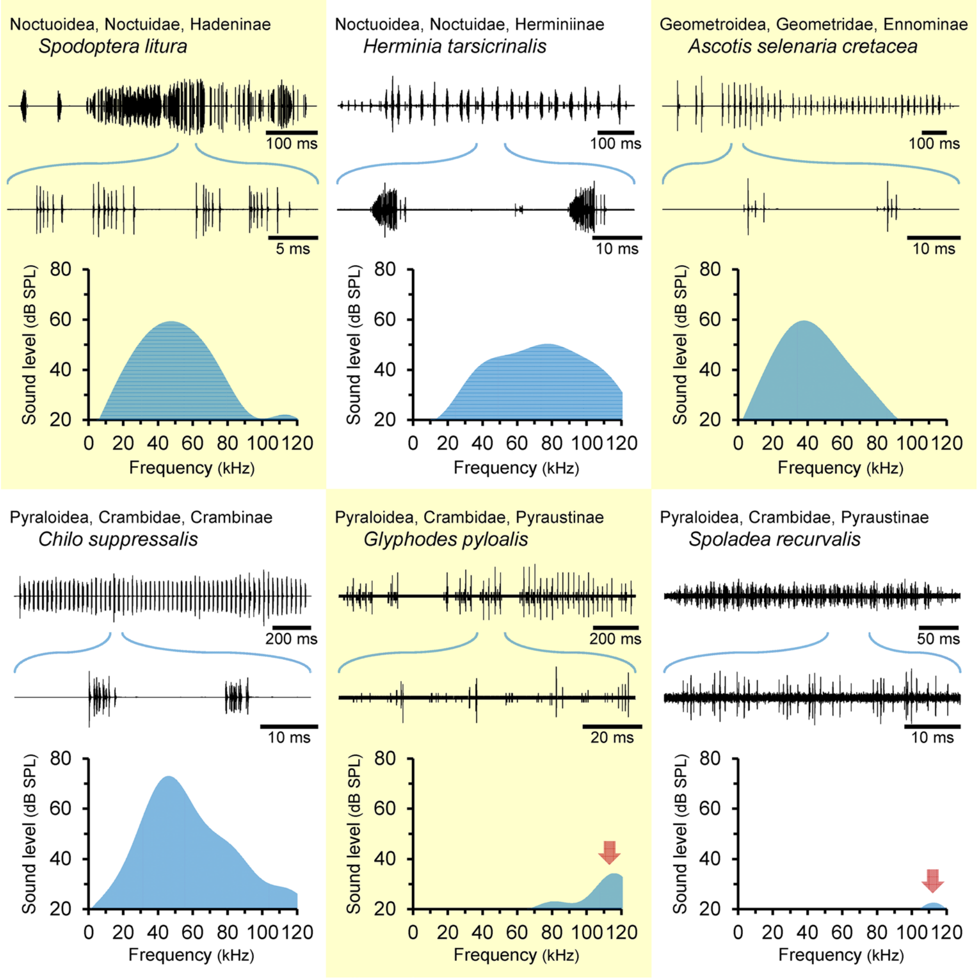

Fig. 5 Male courtship songs in seven tympanate moths. *Upper traces* (oscillograms) show time structure. *Lower figures* show power spectrum (*blue area*) of male songs recorded at a distance of 1 cm (=distance to the female’s ear) from singing males (re. 20 µPa). *Red arrows* denote underestimated sound levels because most song energy was above the appropriate recording range of the microphone (≤100 kHz). Adapted from Nakano et al. (2009b)

fact, a survey of 13 species of moths (Noctuidae, Arctiidae, Geometridae, and Crambidae) revealed that males of nine species (69 %) produced low intensity (23–56 dB SPL at 10 cm) ultrasound close to females with peak frequencies of 38 to >100 kHz (Nakano et al. 2009b). Thus, whispering courship songs were not found in all species, but were rather common. As shown in Fig. 5, temporal and spectral features of the male sounds are quite diverse, probably reflecting the different body parts involved in the two main types of sound production, click by tymbal buckling or stridulation by file-and-scraper. The fact that metathoracic tymbals are found in male *Spodoptera litura* (Noctuidae) (Nakano et al. 2010), but not in the four other noctuids we investigated, supports independent evolution of the sound-producing organs and sound communications (Nakano et al. 2009b). Hence, it corroborates the evolutionary scenario for development of loud sexual communication sounds in moths: relatively recently after speciation of ancestral species which had already developed functional hearing organs some moths have evolved sound communication with male courtship song both with low and high sound levels. The recent data suggest that whispering courtship song may be quite common in moths, because eavesdropping does not work against it as for loud conspicuous sounds.

Sensory exploitation: an evolutionary scenario of moth sound communication

As outlined above, moth sound communication has probably evolved through the exploitation of mating partners' preadaptive sensory bias toward predator cues, i.e., ultrasonic echolocation calls of attacking bats ("sensory exploitation" or "receiver bias", Endler and Basolo 1998; Ryan 1998; Greenfield 2014). Thus, distinct sound production for mating is limited to hearing moth species. However, to exploit a sensory bias to use sound signals for mating involves more than just detecting the sounds. A reversal of behavioral reaction from negative escape behaviors against foraging bat calls to positive phonotaxis and/or mate-acceptance to mating signals is also necessary (for example in the lesser wax moth, Rodríguez and Greenfield 2004; Greenfield and Weber 2000; Greenfield and Hohendorf 2009 or in the lichen moth, Nakano et al. 2013). The requirement of behavior reversal may not be as critical for very low intensity courtship songs, since they function at very close range making the positive phonotaxis superfluous, which may have been an additional factor (on top of the danger of eavesdropping) making quiet courtship songs more common than loud calling songs in moths. The sensory exploitation in moth sound communication force

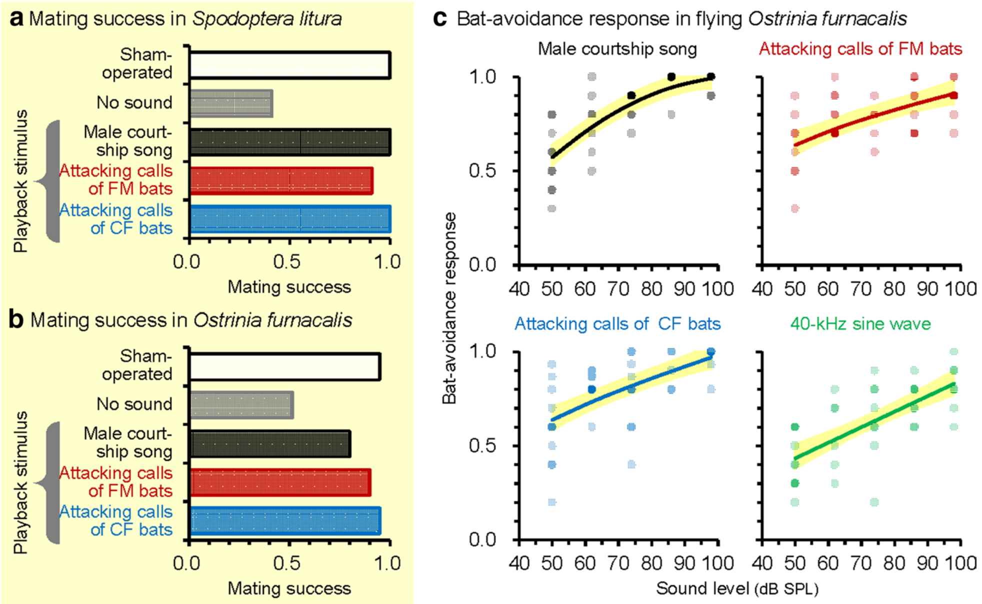

Fig. 6 Sound communication by sensory exploitation. Behavioral evidence of sensory exploitation in moth sound communication. Females' mate acceptance of muted males (ablated sound-producing organs) in a noctuid moth *Spodoptera litura* (**a**) and a crambid moth *Ostrinia furnacalis* (**b**) increased with simultaneous playback of male courtship song as well as playback of simulated bat calls [frequency-modulated (FM) pulses from big brown bat or constant-frequency (CF) pulses from greater horseshoe bat]. **c** The frequency of bat-avoidance behaviors (freeze response or evasive flight) to playback of male courtship song and simulations of bat calls in flying tethered *O. furnacalis*. The lower right panel shows the effect of playback of a 40 kHz pure tone sine wave without pulse structure. Each *circle* represents individual data point. *Yellow bands* around *solid lines* (estimated averaged response curve) show 95 % confidence intervals. Adapted from Nakano et al. (2010, 2013)

signal features to fall within the receiver's detection range, i.e., high frequencies of bat calls. Subsequently both signal and the receiver's response have coevolved through sexual selection (Greenfield 2014). Thus, a prerequisite for establishing sensory exploitation in moth sound communication is to ascertain that preference to mate's signal evolved after development of evasive reaction to bat ultrasounds. We review examples indicating such a sequence of events in the next section.

Male *Spodoptera litura* and *Ostrinia furnacalis* emit courtship songs with low sound levels (Sect. 3.3), and females do not distinguish male songs from bat calls, but copulate with muted males not only with concurrent playback of male sounds (70 and 46 dB SPL at the female's ear (≈1 cm from the speaker), respectively) but also of simulated bat calls (100 and 74 dB SPL, respectively) (Fig. 6a, b) (Nakano et al. 2010, 2013). Females' response to bat calls and conspecific male songs are similar: they "freeze", which is an anti-bat reaction helping stationary moths avoid being targeted by bats. By exploiting females' freeze response to ultrasounds males can increase copulation success because the female is motionless. When flying, both sexes of *O. furnacalis* also freeze (drop to the ground) or take evasive maneuvers to simulations of both bat calls (big brown bat *Eptesicus fuscus* and greater horseshoe bat *Rhinolophus ferrumequinum*) and playbacks of male courtship song, if these ultrasounds are presented at >70 dB SPL at the female's ear (Fig. 6c). Because male *S. litura* and *O. furnacalis* songs are not loud, moths in flight do not react with drastic evasive maneuvers to their courtship songs; however, it is inferred that females mistake males' "soft" song for bat echolocation calls emitted from afar and remain motionless to avoid being detected by the bat. Thus, the identical reaction of females to bat call and to male song supports the sensory exploitation hypothesis in the evolution of moth sound communication. After developing ultrasound detection ability as a countermeasure to ultrasonic echolocation calls of predatory bats, some moth species incidentally emitted faint ultrasounds, probably as a by-product of mating displays such as wing-fanning for diffusing the male pheromone to the female or detecting the female pheromone (Obara 1979; Spangler 1988; Kindl et al. 2011). The implication is that some females could detect the incidental ultrasounds and reacted with a freeze response, which caused mating success to increase. Hence, this promoted the evolution of males' deceptive courtship songs due to the absence of females' mate-preference/-recognition based on the male song traits (pulse pattern etc.). By contrast, if males' primordial mating ultrasounds were sufficiently different from bat calls, they would not elicit anti-bat reactions in females, because eared moths are not supposed to react by evasive responses to all the detectable sounds. Species capable of distinguishing between male ultrasounds and bat echolocation calls could develop "true" mating songs with female mate-preference/-recognition via co-evolutionary sexual selections (Endler and Basolo 1998; Ryan 1998; Greenfield 2014).

Perspectives on moth sound communication

There is an increasing number of reports of moths in which males produce ultrasounds for courtship (Conner 1999; Nakano et al. 2009b; Greenfield 2014), but in most cases the functions of these courtship sounds are not confirmed by behavioral experiments with muted males and deafened females and/or with playbacks of courtship sounds. Thus, it is uncertain whether males' ultrasounds are mating signals or not. Depending on the receiver's reaction, moth courtship songs are divided into two functions: "deceptive" function found in e.g., the noctuid *Spodoptera litura* and the crambid *Ostrinia furnacalis* (Sect. 5) (Nakano et al. 2010, 2013) or "true" mating signal in the pyralid *Galleria mellonella* and the arctiid *Eilema japonica* (Spangler 1985; Nakano et al. 2013). Only in case of "true" mating signals can females distinguish between bats and mates only showing positive response in form of mate-acceptance to true courtship songs, but not to bat echolocation calls.

It is not easy to observe courtship behaviors of animals with unknown mating timing, in particular nocturnal moths, which often use sounds that we cannot hear directly, because they are soft, ultrasonic, and brief. The bias toward low frequency, high intensity sounds surely has contributed to a failure in revealing the actual number of moths communicating acoustically with courtship songs. Hence, we predict that future research will uncover more and more moths, and in fact more and more other animals too, using quiet sound for private communications. We further predict that many of these sounds will subsequently be confirmed to function as mating songs. Such less biased results will be important for understanding the evolutionary process of moth sound communication, and how auditory recognition based on the neural processing evolved in general in animals.

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