# SOUND PRODUCTION AND HEARING IN THE PYRALID MOTH *SYMMORACMA MINORALIS*

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## Summary

Males of the moth *Symmoracma minoralis* (Snellen) (Lepidoptera: Pyralidae, Nymphulinae) were observed producing a high-intensity calling song (95 dB SPL at a distance of 10 cm) with a complex amplitude and frequency modulation (peaks of carrier frequency at 60 and 120 kHz). This sound is produced by a hitherto unknown type of sound organ located in the last abdominal (genital) segment, which may act as a tymbal. The observed directionality of sound output is probably achieved by means of a hollow cone surrounding the sound organ. Electrophysiological recordings revealed that the tympanal organs of *S. minoralis* are most sensitive in the frequency range from 50 to at least 100 kHz, which is distinctly higher than the minimum threshold levels in most other moths yet examined. The origin of genital sound production is discussed with respect to abdominal pheromone glands and pheromone-releasing movements.

## Introduction

Ears have evolved in a large number of moth families. Apart from the palpal hearing system of the Sphingidae, moth ears are tympanal organs which are assumed to have evolved independently several times in response to bat predation (Cook and Scoble, 1992). Since the pioneering work of Roeder and Treat (1957), the hearing range and sensitivity of moths and bat–moth interactions have been studied in detail (for a review, see Surlykke, 1988), but most studies have concentrated on the ears of Noctuoidea (Noctuidae, Arctiidae and Notodontidae), which are located in the metathorax. Only a few studies (Roeder, 1974; Fenton and Fullard, 1979; Fullard *et al.* 1983) have examined the physiology of the ears of the Geometridae. Of the family Pyralidae, whose ears are situated ventrally in the first abdominal segment, only four species have been investigated physiologically. This family is, however, not only one of the largest (more than 25 000 described species; Scoble, 1992), but also one of the most ecologically diverse and economically important amongst tympanate moths. To determine hearing range and sensitivity, measurements have been performed on the European corn borer moth *Ostrinia nubilalis* (Belton, 1962; Agee, 1969), the wax moths *Galleria mellonella*

(Belton, 1962; Spangler and Takessian, 1983) and *Achroia grisella* (Spangler and Takessian, 1983) and the flour moth *Ephestia kuehniella* (Pérez and Zhantiev, 1976).

Pyralid moths, however, do not use their ears only for predator detection. Recently, intraspecific communication by ultrasound has been demonstrated or proposed in several species of this family (see Spangler, 1988, for a review). The males of some galleriine moths produce sounds by means of tegular tymbals (*Achroia grisella*, Spangler *et al.* 1984; *Galleria mellonella*, Spangler, 1985; *Corcyra cephalonica*, Spangler, 1987; *Eldana saccharina*, Bennett *et al.* 1991). In all four species, the sound intensity is rather low (below 80 dB SPL at 10 cm) and the acoustic signals probably operate only for close-range communication. In *Syntonarcha iriastis* (subfamily Odontiinae), however, the males emit a high-intensity song by means of genital stridulation (Gwynne and Edwards, 1986). In all pyralids, the carrier frequency of the song is very high, with peaks between 42 and 125 kHz.

Here we describe sound production and hearing in another species of pyralid moth, *Symmoracma minoralis*, which belongs to a third subfamily of the Pyralidae, the Nymphulinae. Sound production in this species has already been mentioned by Bailey (1991). *Symmoracma minoralis* also uses genital structures for calling, but the mechanism is quite different from that found in *Syntonarcha iriastis*. Acoustic behaviour in the field has been described by K.-G. Heller and R. Achmann (in preparation).

## Materials and methods

*Symmoracma minoralis* (wing expanse about 20 mm) belongs to the pyralid subfamily Nymphulinae. It occurs from Sri Lanka to Thailand (Bailey, 1991) and in North Australia. We studied it in Malaysia at the Ulu Gombak Field Studies Centre of the University of Malaya (3°20′N, 101°45′E) in March 1992. Neurophysiological studies were performed in Erlangen with animals collected in December 1992 in Malaysia.

Song recordings were made by means of a 6.35 mm microphone (Brüel & Kjaer 4135), measuring amplifier (B & K 2231) and a high-pass filter (1.3 kHz) on a modified videorecorder (frequency response of the system $\pm 3$ dB up to 130 kHz). The same microphone and amplifier were used for intensity measurements (dB SPL; re 0.02 mPa). The recordings were re-recorded on a Racal store 4DS tape recorder operating at $152.4 \, \mathrm{cm \, s^{-1}}$ for analysis. Time patterns were analyzed using a liquid-jet oscillograph (Siemens Oszillomink L) and a computer (program Turbolab 4.0, Fa. Stemmer). Frequency analysis was performed on a Mosip computer (program Spektro 6.0, Fa. Medav). To register the temporal pattern of the song, the output of a bat-detector tuned to 60 kHz was recorded with a Sony WM-D3 cassette tape recorder.

The sound organs were examined under a dissecting microscope. Hearing thresholds were determined by neurophysiological experiments. The moths were briefly anaesthesized with $CO_2$. The wings and legs were removed. The head and notum were attached to a free-standing holder with a wax–resin mixture (dorsal side down). Thus, the abdomen with the tympanal organ was exposed, and its position was similar to that of a male in the singing position. The pterothoracic ganglion complex was exposed by removing the first and second pairs of coxae. This preparation is quick and easy, and the

acoustic properties of the tympanic organ should not have been impaired very much. In order to avoid desiccation, the thorax was filled with Ringer solution (Pearson and Robertson, 1981).

The experiments were performed in an anechoic Faraday cage at room temperature (21–22 °C). The stimuli were delivered *via* a condensor speaker (Müller BBN) located 11 cm from the preparation. The amplitude of the sine-wave stimuli (Burchardt Akustischer Stimulator II) was modulated by a computer (AIM 65, Rockwell) and sound intensity was adjusted with a 6.35 mm microphone (Brüel & Kjaer 4135) located on site. The stimulus duration was 96 ms (5 ms rise and fall times).

To measure acoustic sensitivity, the activity of auditory neurones within the pterothoracic ganglion was registered. The best signal-to-noise ratio was obtained when the polyethylene suction electrode touched the ventrocaudal surface of the ganglion. Therefore, the monitored reaction to the acoustic stimulation cannot be specifically assigned to the receptor cells, but may result from the activity of thoracic interneurones as well. The electrode signal was amplified and monitored on an oscilloscope. Thresholds were determined acoustically *via* headphones.

## Results

### *Analysis of the song*

The song is produced by the male moth, usually sitting on the edge of the underside of a leaf with his ventral side directed upwards (Fig. 1). The animals call throughout the night with very short pauses between bursts of calling activity. The song will be referred to as the 'calling song' (see K.-G. Heller and R. Achmann, in preparation).

### *Intensity and directionality*

The intensity of the song, measured ventrally at a distance of 10 cm vertical to the body axis, was 95.5±1.0 dB SPL (mean ± S.D.; $N$=21; peak measurement).

To estimate the directionality of sound output, we measured intensity in the horizontal and vertical planes around the animal in 45 ° divisions. The caudal position was taken as a reference point for the calculation of a mean curve. As can be seen in Fig. 2, the sound intensity is about 6 dB higher in the direction of the opening of the sound organ, which points ventro-caudally, than in the opposite direction.

### *Amplitude pattern of the calling song*

The calling song consists of a continuous sequence of chirps (Fig. 3) produced at a rate of 3.4 Hz ($N$=32). The duration of a chirp period ranged from 260 to 370 ms in various animals (mean ± S.D. 298±21 ms; $N$=32; all recordings were made between 20:00 and 22:00 h at a temperature of 22–25 °C). Variation in the data from single animals was much smaller, with a standard deviation not exceeding 8 ms. Each chirp is composed of about 30 syllables, arranged in a syllable group, with amplitude increasing from a very faint start to an intense end, and one isolated syllable of lower intensity, following 23±2 ms ($N$=8) after the end of the syllable group (Fig. 3). When an animal stopped singing, sound production ended with the isolated syllable. The duration of a syllable period (measured

Fig. 1. A sound-producing male *Symmoracma minoralis*. Note the white hollow cone around the sound organ on the ventral side of the body, projected upwards because the animal is positioned on the underside of a leaf. Scale bar, 5 mm.
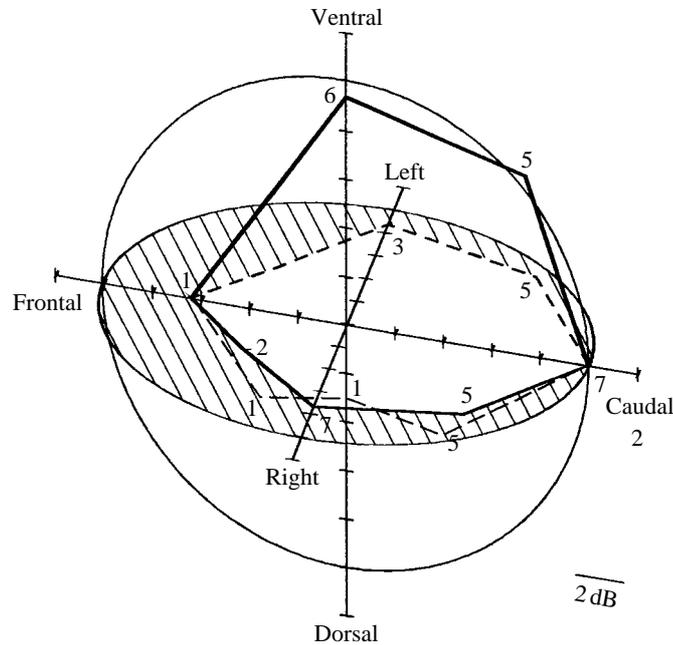
Fig. 2. Directionality of sound output. Owing to the male's position on the underside of a leaf, its ventral body side is directed upwards (see Fig. 1). Numbers indicate the number of measurements in the respective position (*N*=7 different animals).

for the last 10 most intense syllables of the syllable group) ranged from 6.0 to 7.5 ms (mean ± S.D. 6.9±0.3 ms; *N*=30) and was not correlated with the duration of the chirp period ($r^2$=0.01). Each syllable consisted of two parts, a short and a long hemisyllable, each containing about the same number of sound impulses (Fig. 3). During the long hemisyllable, the 12–15 impulses were produced at a rate of 3301±180 Hz (mean ± S.D.; *N*=10 animals, mean of 10 syllables at the end of the syllable group). During the short hemisyllable, the impulse rate was much higher – approximately 15 kHz – and the impulses often could not be separated.

*Frequency pattern of the calling song*

The frequency pattern within each chirp of the calling song changed in a very regular sequence in all the animals analyzed (Fig. 4). During the first faint syllables of the syllable group, and in the isolated syllable, only high-frequency components of about 118±2 kHz were observed (*N*=10 animals, power spectra of complete syllable, middle of range 6 dB below peak). In the central part of the chirp, a lower-frequency component appeared (42±3 kHz), increasing in frequency to become the dominant 60±2 kHz component at the end of the syllable group (with an upper harmonic of 115±2 kHz). The spectra of short and long hemisyllables were similar.

*Sound production*

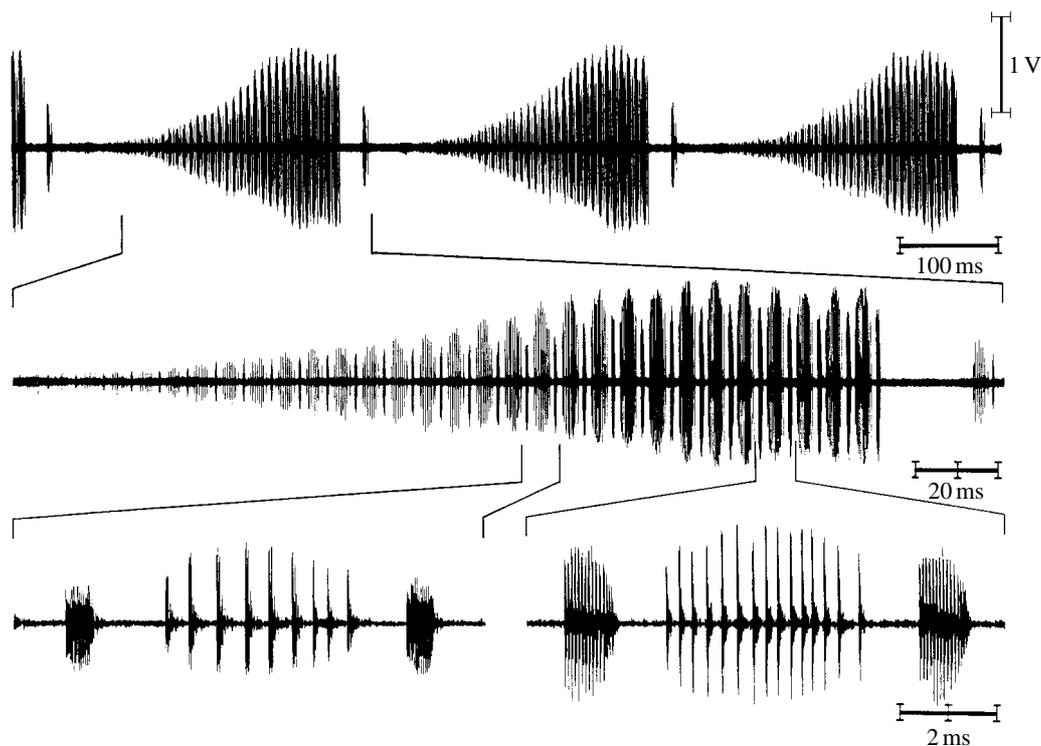The sound organ is a very complex structure and does not contain a file-scraper system.

Fig. 3. Time pattern of the male calling song. (A) A sequence of three chirps. (B) A syllable group and an isolated syllable. (C) Several syllables (each example includes two short and one long hemisyllable).

It is located in the last abdominal segment. If the animal is not prepared to sing, this segment is almost completely retracted into the anterior segments. It is extruded immediately before the animal starts to call (Fig. 1). A white membranous hollow cone opens on its ventral side as a result of this movement. Because the male is positioned on the underside of a leaf, this structure is normally directed upwards. The walls of the cone are pushed open and stabilized by three sclerotized elements directed anteriorly. In the centre of the hollow cone is situated a deep concavity, or 'sound chamber', which almost reaches the dorsal body wall. A series of parallel ribs (Fig. 5) can be seen at the bottom of this hole, and parallel folds can be found in both side walls.

At the upper edge of both lateral sides of the cavity, heavily sclerotized elements are integrated into the wall. Posterio-laterally to the cavity two large muscles are to be found, one on each side (Fig. 5). We propose that the segment is shortened and deformed by the contraction of these muscles (against the elastic body wall). As a result of this action, the sclerotized elements are moved (Fig. 5), deforming the bottom and walls of the sound chamber, which thus acts as a tymbal. During calling, slight movements of the cuticle in this region could be observed in time with the chirp rhythm. Since the animals, however, did not sing in captivity, full details of sound production have yet to be clarified.
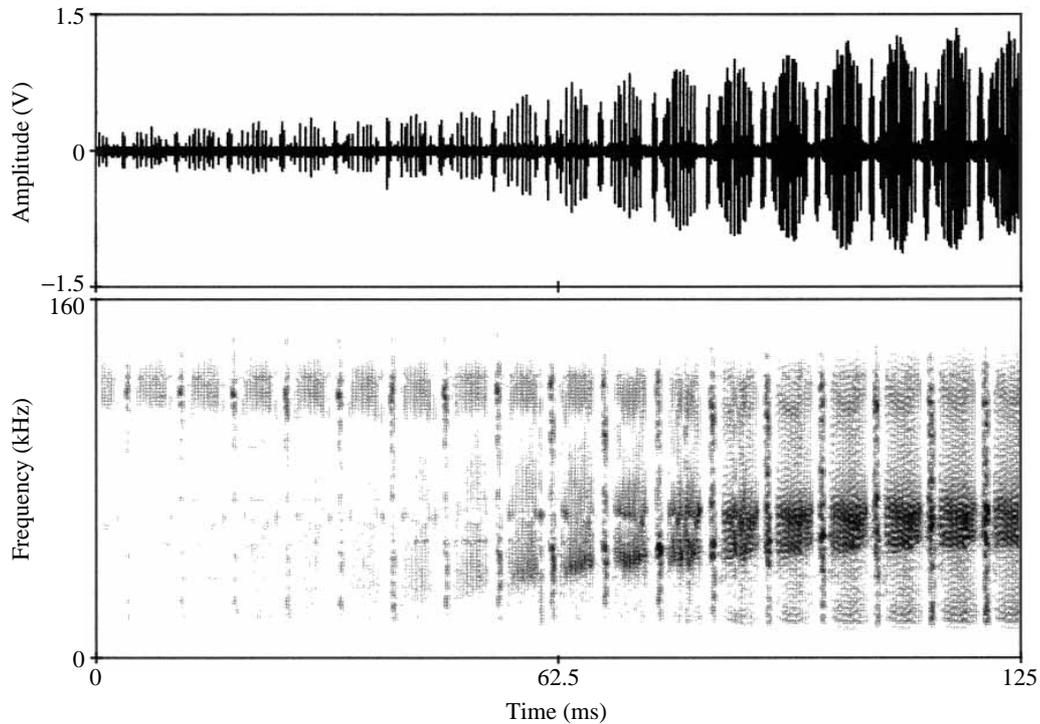
Fig. 4. Time (oscillogram; above) and frequency pattern (sonogram; below) of the calling song.

## *Hearing*

The structure of the ear of *S. minoralis* is typical for a member of the pyralid subfamily Nymphulinae; the tympanal membrane is divided in two parts with a decided angle between them (crambiform arrangement; Scoble, 1992; Minet, 1985). Ventrally, both ears are separated by a large praecinctorium, a median expansion of the intersegmental thoraco-abdominal membrane (Scoble, 1992), closing the gap between the base of the abdomen and the coxae of the hindlegs.

The neurophysiologically determined hearing threshold was similar in all four animals studied (Fig. 6). The animals were most sensitive between 60 and 90 kHz (lowest threshold 43 dB). Sensitivity decreased sharply towards lower frequencies, but only slightly towards high frequencies and the animals may well be able to hear sounds above 100 kHz.

Fig. 5. (A) Ventral view of the last abdominal segment of a male prepared to sing (anterior to the left, posterior to the right). (B) Lateral view of the last abdominal segment. The lateral body wall, including a large portion of the muscles and of the hollow cone, has been removed. (C) Frontal section of the last abdominal segment, dorsal part. (D) Schematic presentation of the proposed sound-producing movement (see text); *c*, cavity (sound chamber) with ribbed bottom; *g*, genitalia; *h*, hollow cone with three stabilizing elements; *m*, muscles; *s*, sclerotized structures within the cavity wall.
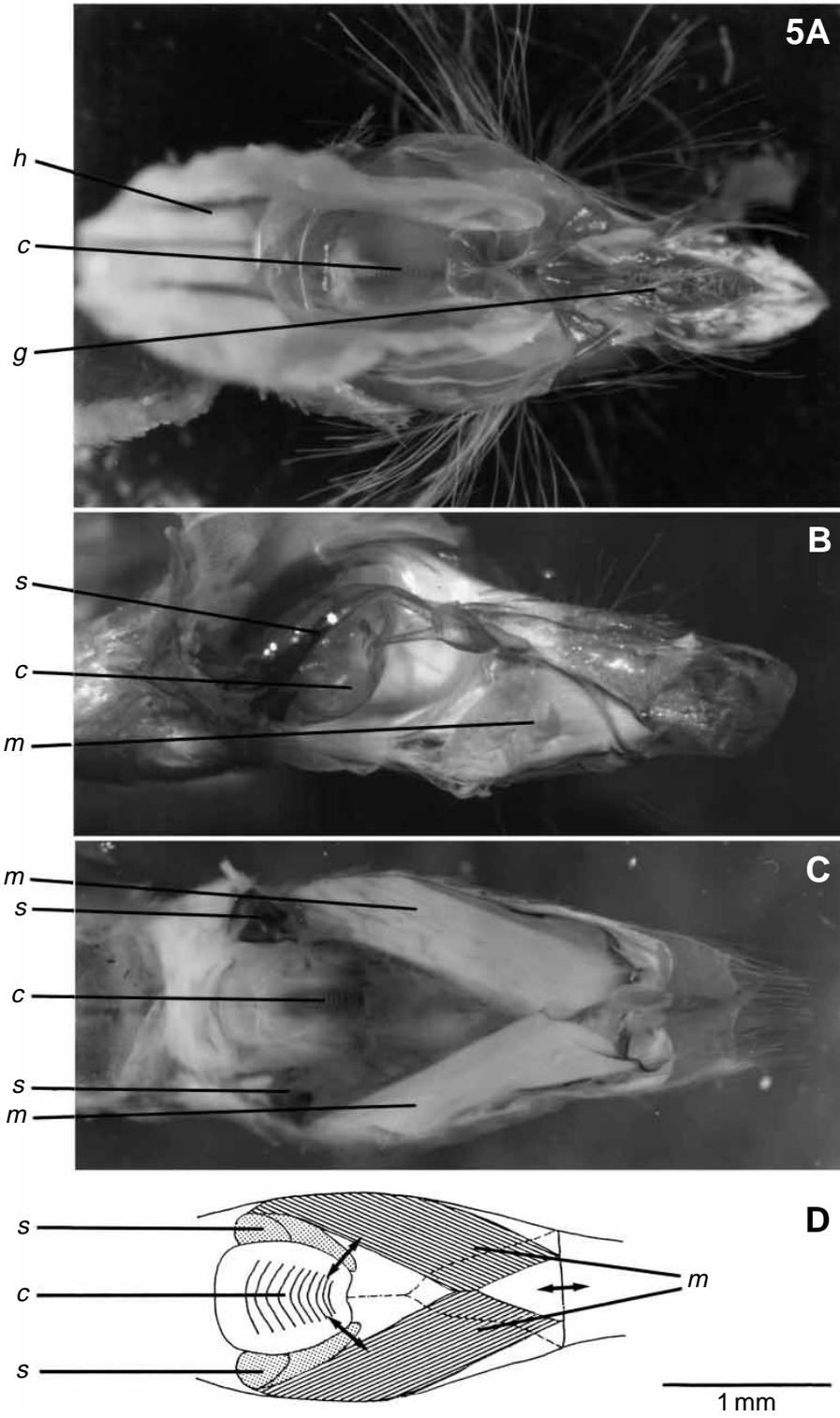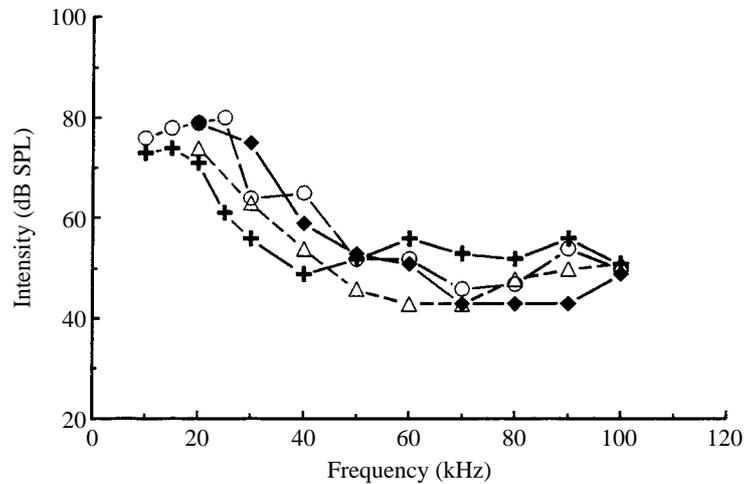
Fig. 6. Hearing thresholds in four males of *Symmoracma minoralis*.

Taking into account a sensitivity of the pyralid ear of 45 dB SPL at 60 kHz and an atmospheric attenuation of 2.5 dB m$^{-1}$ (Lawrence and Simmons, 1982), the range of the moth's song for intraspecific communication can be estimated to be not more than 6 m.

## Discussion

The most striking differences between *Symmoracma minoralis* and the other known acoustically active moths concern the location and structure of the sound-producing organs. Genital sound production is only known in two families of Lepidoptera. In Sphingidae, the relatively faint stridulatory sound is assumed to have both a defensive function and to be part of courtship behaviour. It is produced through contact between the eighth abdominal segment and the valvae (for references, see Nässig and Lüttgen, 1988). The only other species in which genital sound production has been reported belongs, like *Symmoracma minoralis*, to the family Pyralidae (*Syntonarcha iriastis*; Gwynne and Edwards, 1986) but to another subfamily. In this species, an asymmetrically constructed file scraper system was observed (Gwynne and Edwards, 1986). In *Symmoracma minoralis*, however, the structures responsible for sound production are symmetrical and, considering the ribbed structure of the bottom and walls of the sound chamber, which resembles the microtymbals of Arctiidae (Blest *et al.* 1963), a tymbal mechanism of sound production seems most probable.

The white hollow cone, which envelops the sound cavity, probably increases the directionality of sound output. The intensity of the sound was highest in the direction of the opening of the funnel. Similar differences of about 6 dB between the directions of the highest and the lowest intensities were also detected in the lesser wax moth, which uses tegular tymbals for sound production (Spangler *et al.* 1984). In this species, the sound shadow produced by the wings may be responsible for the differences in intensity.

The evolution of genital sound production is probably related to the presence of pheromone glands in the distal abdominal segments. In *Symmoracma*, their presence is

indicated by the large hair-pencils, which may be seen in Fig. 1. In other species, these glands are often exposed and moved during courtship and brought near to the female's head (for a review, see Birch *et al.* 1990). The pheromone blend from these glands is normally effective for a short distance only and is assumed to signal species identity and/or to influence intraspecific female choice (Phelan and Baker, 1987). Any sound production associated with the movements necessary for pheromone release could easily be incorporated into the courtship behaviour, since increasing female sensory stimulation seems to be common in the evolution of courtship signals (Ryan and Keddy-Hector, 1992).

A similar relationship between sound organs and pheromone glands is found in acoustically active moth species which produce sound during wing-fanning by means of tegular tymbals (Spangler *et al.* 1984) or wing tymbals (Heller and Achmann, 1993). Male wing-fanning has been observed in many non-acoustic species and improves the pheromone release from the forewing glands. Sound produced during these movements was probably integrated into mating behaviour on several independent occasions in moths.

Compared with those of other moth species, the song of *Symmoracma minoralis* exhibits by far the most complex amplitude pattern. Its spectral composition is also more complex than that of other moths. Frequency changes have been observed only in the song of *Syntonarcha iriastis* (Gwynne and Edwards, 1986), but they were less pronounced than those in *Symmoracma*.

It is likely that part of the song complexity cannot be used directly for communication; the impulse intervals within the syllables are so short that they are probably only resolved by the tympanic membrane (see Schiolten *et al.* 1981) and not by the receptor cells. Transmission of these short intervals within the nervous system through the synchronized activity of several cells, as proposed in grasshoppers (Ronacher and Römer, 1985), seems unlikely, since each pyralid ear has only four receptor cells (Eggers, 1928). The moths would hear the hemisyllables of the song as continuous sound.

The observed hearing threshold in *Symmoracma* lies between those found in other pyralid species (Spangler and Takessian, 1983; Pérez and Zhantiev, 1976). All four species previously examined seem to be relatively sensitive to frequencies above 60 kHz and up to at least 100 kHz. Other insects, whose ears are also assumed to have evolved for bat-avoidance, are far less sensitive in this frequency range (Yager and Hoy, 1989). Thus, pyralid moths may be more successful than noctuid moths in avoiding attacks by specialized moth-feeding bats, which are assumed to have evolved extraordinarily high-frequency echolocation calls outside the hearing range of moths (Fullard, 1990).

The threshold minimum of about 60 kHz in *Symmoracma* coincides quite well with the peak frequency of the song. However, even the first harmonic of the song at 120 kHz should be easily perceptible by the animals. The changes in intensity and spectral composition of the song due to atmospheric attenuation (7 dB m$^{-1}$ at 120 kHz; Lawrence and Simmons, 1982) may permit an approaching moth to use chirp duration to estimate the distance to the singing male. The high frequencies are probably also very useful for sound localization by these small animals, which have their ears situated very close together.

When comparing the song of *Symmoracma* with the simple songs of other species, factors that might be responsible for song complexity other than those improving locatability should also be considered. A species-recognition function seems improbable, since no related singing species are known at the moment. Female choice for special song parameters (e.g. Stumpner and von Helversen, 1992) in the context of sexual selection, however, could be important.

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