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Sound generation in *Mantis religiosa* (Mantodea: Mantidae): stridulatory structures and acoustic signal

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Abstract

Several species of mantids perform defensive displays during close-range encounters with predators. In adult *Mantis religiosa*, this display entails both visual and acoustic components, the latter being abdomino-alary stridulation. Stridulatory modifications of the abdomen and hindwings and acoustic properties of the defensive sounds of *M. religiosa* are characterized here for the first time. Defensive sounds are generated via an abdomino-alary mechanism involving contact between teeth found on the longitudinal veins of the metathoracic wings and pegs located on the abdominal pleura. Defensive stridulation in *M. religiosa* is highly variable in both spectral and time domains. Inter-individual variability may be stochastically greater than intra-individual variability for at least one acoustic parameter (peak frequency). The loudest portion of a sound emission (syllable), or down-pulse, has an average duration of 195 ms and features an abrupt rise to maximum amplitude. Inter-syllabic intervals are irregular and rate of syllable production depends on a mantid's sex. The acoustic output of *M. religiosa* is nonresonant, broadband, and of relatively low intensity. A minor ultrasonic component may be present in the spectra of these mantids (particularly in males). The modal peak frequency range (4 kHz interval) is 8-12 kHz (mean range ~7.4-9.4 kHz). Acoustic parameters which appear to vary between the sexes and/or among females at different reproductive stages, may be related to the sexual size dimorphism of this species and morphological constraints associated with egg-bearing. The acoustic output of *M. religiosa* is considered with reference to its intended receivers and plausible mechanisms of predator deterrence.

Key words

mantid, acoustic, defense, display, stridulation, disturbance

Introduction

During a close-range encounter with a predator, the European mantid, *Mantis religiosa* L. may perform a dramatic defensive or startle display, sometimes also termed a deimatic reaction (Maldonado, 1970); this fascinating behavior has been well-documented in the literature (e.g., Dufour 1841, Goureau 1841, Wood-Mason 1879, Fabre 1897, Coupin 1899, Stäger 1928, Chopard 1938, Judd 1950, Edmunds 1972, Holroyd 1975). As a secondary defensive strategy, the display constitutes a facultative behavior, adopted only after the primary defensive strategy of a mantid (cryptic behavior) has failed (definitions of primary and secondary defense after Robinson 1969a).

The defensive display of adult *M. religiosa* is similar to that of some other mantid species and, when maximally expressed, entails the following behavioral components: 1) visual fixation on the predator, 2) opening of the mandibles, 3) elevation of the prothorax, 4) elevation, abduction, and lateral extension and/or flexion of

the prothoracic legs, 5) dorsal flexion, and often lateral extension of the abdomen, 6) elevation and partial extension of the wings, and 7) sound production. Lunging, sidling and/or striking in the direction of the perceived threat are sometimes incorporated into the defensive display.

Defensive, disturbance (Haskell 1964), or protest stridulations characterize numerous insect orders (Table 1) and are broadly similar among taxa (Masters 1980, Schmitt & Traue 1990, Montealegre-Z *et al.* 2003). In particular, most such sounds are produced by nonresonant mechanisms and consequently feature a broad band of frequencies (Haskell 1964, Masters 1980, Tschuch & Brothers 1999).

A bimodal, visual-acoustic, defensive display, such as that which occurs in *M. religiosa* is not uncommon among mantids. A summary of defensive sound generation mechanisms within the Mantodea is included in Ramsay (1990). A few mantids have evolved specialized sound-producing structures, most notably members of the Empusidae, which bear stridulatory files on the anterior edges of the tegmina (Wood-Mason 1878, Williams 1904, Willey 1918, Varley 1939, Ramsay 1990). Empusids, including *Gongylus gongyloides* Linnaeus and *Idolum diabolicum* Saussure, generate sound by rubbing their metathoracic legs against tegminal files (Williams 1904, Willey 1918, Carpenter 1921, Ramsay 1990).

Within the Mantidae, *Choeradodis rhombicollis* Latreille and *Hierodula s.l.* Burmeister boast unusual stridulatory mechanisms. In the former species, sounds are emitted when the sides of the pronotum contact spines borne on the prothoracic legs (Robinson 1969b). In *Hierodula*, sound generation is apparently effected by rubbing of the abdomen against a tegminal file (similar to that characteristic of the Empusidae) (Wood-Mason 1878, Varley 1939, Ramsay 1990).

Ramsay (1990) asserts that adult mantids of all alate species possess some potential to generate sounds when the wings are fanned during a display and that this stridulation would occur either through abdomino-alary contact, or by moving the forewings and hindwings against each other. Stridulation in mantids has also been reported in *Hestiasula sarawaka* (Shelford 1903), *Angela guianensis* Rehn (Robinson 1969b), *Stagmatoptera biocellata* (Maldonado 1970), *Tenodera aridifolia sinensis* Saussure (Liske 1999), *Tenodera superstitiosa* Fabricius, *Stenovates strachani* Kirby, *Pseudocreobotra ocellata* Beauvois (Edmunds 1972), and of course, *M. religiosa* (e.g., Dufour 1841, Wood-Mason 1879, Simonot-Revol 1891, Fabre 1897, Stäger 1928, Judd 1950, Edmunds 1972, Holroyd 1975). In *M. religiosa*, stridulation is a conspicuous and consistent component of the full adult deimatic reaction (pers. obs.), touted by Edmunds (1972) as

Table 1. Representative insect taxa known to produce disturbance sounds.

Lepidoptera	Haskell 1961, Fullard <i>et al.</i> 1994, Simmons & Connor 1996
Coleoptera	
Carabidae	Masters 1979, 1980
Cerambycidae	Masters 1980
Chrysomelidae	Schmitt & Traue 1990
Geotrupidae	Carisio <i>et al.</i> 2004
Hydrophilidae	Masters 1979, 1980
Scarabaeidae	Dumortier 1963, Masters 1980
Hymenoptera	
Sphecidae	Coelho 1998
Apidae	Sen Sarma <i>et al.</i> 2002
Mutillidae	Masters 1979, 1980
Hemiptera	
Reduviidae	Masters 1980, Schmidt 1994, Schilman <i>et al.</i> 2001
Cicadidae	Alexander 1960, Riede & Kroker 1995
Orthoptera	
Gryllacrididae	Field & Bailey 1997
Gryllidae	Desutter-Grandcolas 1998b
Tettigoniidae	Belwood 1990, Heller 1996, Naskrecki 2000
Isoptera	Connétable <i>et al.</i> 1999
Blattodea	Dumortier 1965, Guthrie 1966, Nelson 1979, Nelson & Fraser 1980, Schal <i>et al.</i> 1982
Phasmatodea	Carlberg 1989
Mantodea	Wood-Mason 1878, 1879; Shelford 1903; Williams 1904; Willey 1918; Carpenter 1921; Stäger 1928; Chopard 1938; Varley 1939; Maldonado 1970; Edmunds 1972, 1976; Holroyd 1975

“probably the most important part of the display” in this species (p.25).

Although the acoustic component of the display in *M. religiosa* has been well-noted, an acoustic characterization of the defensive sounds and a description of the microscopic structures responsible for their production have never been published. In fact, no one has quantitatively documented the defensive sounds of *any* mantid.

In general, mantid stridulation is often qualitatively likened to a “hiss” (Maldonado 1970, Preston-Mafham 1990, Edmunds & Brunner 1999). Simonot-Revol (1891) commented that the sounds generated by *M. religiosa* were softer than those of many other orthopterans.

Published accounts of the motor movements and morphological structures associated with sound generation in *M. religiosa* have often been confused (see Wood-Mason 1879, Atwood in Slingerland 1900, Vickery & Kevan 1983), with some early authors even reporting that the species lacks any specialized sound-generating apparatus (Wood-Mason 1879, Gurney 1951).

Defensive sounds are produced as adult *M. religiosa* flex the abdomen dorsally (the upstroke), and then re-extend it (the downstroke), while maintaining contact between the abdominal pleura (and perhaps cerci) and dorsal surfaces of the elevated metathoracic wings (Simonot-Revol 1891, Stäger 1928, Judd 1950, Beier 1968, Edmunds 1972, Holroyd 1975, Hill pers.obs.); this abdomino-alary mechanism is similar to that responsible for defensive stridulation in *S. biocellata* (Maldonado 1970) and *P. ocellata* (Edmunds 1972).

Although there is little doubt the sibilant noises produced by

displaying adult *M. religiosa* are defensive in function, the intended receiver(s) of such acoustic signals are only generally known. Measurement of the auditory sensitivity of potential receivers is of critical importance in assessing the relevance to them of an acoustic signal. For effective detection, there must be some correspondence between the receiver's auditory sensitivity curve and the acoustic spectrum of the transmitter.

Mantids such as *M. religiosa* are subject to predation by several disparate taxa including birds, reptiles, bats, rodents, and arthropods (including conspecifics): all are potential receivers of the mantids' defensive sounds (Gurney 1951, Durrell 1956, Holroyd 1975, Vickery & Kevan 1985, Yager *et al.* 1990, Hill pers. obs.). The DK (“deep groove with knobs”) metathoracic ear of *M. religiosa* is maximally receptive to frequencies of 25-45 kHz (Yager & Hoy 1986, 1987). In mantids that possess a DK-type ear, audition is minimal below 10 kHz (Yager 1999). The lack of any investigation into the acoustic characteristics of the sounds produced by *M. religiosa* has hindered an understanding of the role these sounds might play in intraspecific communication.

The objectives of the present study were to: 1) describe the stridulatory structures of *M. religiosa*, 2) characterize the physical parameters of its defensive sounds, and 3) infer specific defensive strategies with which this acoustic signal is associated.

Methods

Collection and care of mantids and assessment of female reproductive state.—Adult *M. religiosa* were collected in early successional fields in Mississauga, Caledon, Stoney Creek, and Grimsby (Ontario, Canada) during the months of August–October 2004 and 2005. In the lab, mantids were maintained under a 12h:12h (L:D) photoregime. Once per day, each mantid was misted with water and, depending on the mantid's size and sex, provided with one or two late-instar *Acheta domesticus* L.

Each female mantid's reproductive state was qualitatively assessed by inspection of abdominal girth and categorized as one of the following: 1) nongravid (abdomen lacking distension indicative of egg production), 2) semigravid (some egg production evident; abdomen partially distended but abdominal pleura not visible in dorsal view), or 3) gravid (advanced egg production evident; abdomen fully distended and abdominal pleura visible in dorsal view).

Preparation and viewing of specimens under a scanning electron microscope.—Samples of wing membrane were obtained from mantids recently killed by freezing, after thawing for approximately 0.5 h at 25 °C. For examination under the scanning electron microscope (S.E.M.) small excised pieces of the fore- and hindwings of *M. religiosa*, of the hindwings of the mantid *Tenodera aridifolia sinensis* (included in the study for comparative purposes: *T. a. sinensis* does not have the same stridulatory mechanism as *M. religiosa*), and of the abdominal pleura of *M. religiosa*, were mounted on aluminum stubs. Five small pieces of the anal region of the hindwing of *M. religiosa* were mounted (one from the right hindwing of a male, one from the left hindwing of a different male specimen, one each from the left and right hindwings of a third male, and one from the right hindwing of a female). One piece of a right forewing (derived from a male specimen and encompassing portions of the cubital and anal veins), one piece of the anal region of a left hindwing (derived from a female *T. a. sinensis*), one piece of the abdominal pleura (derived from a male specimen), and one right cercus (derived from a male specimen) were also mounted. Finally, three entire right hindwings (two derived from female specimens and one derived from a male specimen) were mounted (in small excised pieces). Each wing piece was glued with the dorsal surface, that which contacts the abdomen during stridulation, exposed. Specimens were sputter coated with a gold/palladium alloy and subsequently viewed under a Hitachi S-2500 S.E.M.

Staging of displays, recording of defensive sounds and measurement of sound pressure levels.—Mantid–bird behavioral interactions were staged in the lab. A trial commenced when a mantid was placed on a vertical perch, set 7 to 8.5 cm from the bars of a bird cage containing a canary (*Serinus canarius*). Sounds produced by mantids performing defensive displays in response to the visual stimulus of a canary were recorded. In 2004, sound recordings were made at a constant temperature of 25 °C and sound pressure level measurements obtained. In 2005, sound recordings were made at temperatures of 21.5 to 25.5 °C.

In each trial conducted in 2004, a ½" condenser microphone (Bruel & Kjaer 4133) was positioned ~8 cm normal to the surface of a mantid's extended hindwing. The microphone was connected to a sound level meter (B & K 2204) set on linear response and the output high-pass filtered (Krohn-Hite 3382) at 100 Hz. This system was uniformly responsive to frequencies between 100 Hz and 40 kHz.

The signal was then digitized with a PC (12-bit, 100 kHz; System IV Tucker Davis). In 2005, sound recordings were made using a Tascam (DA-P1) digital audio tape recorder (16-bit, 48 kHz) connected to a Sennheiser (ME66) microphone, with a K6 power module hand-held ~24 cm normal to the surface of a mantid's hindwing. This system responded uniformly to frequencies ranging from 700 Hz to just beyond 20 kHz.

A RadioShack (model no. 33-2055) digital sound level meter (most responsive to frequencies of 32–10,000 Hz) was used to take sound pressure level (SPL) measurements (re 20 µPa) of mantid-produced sounds. The sound level meter was set to hold and fast response (response time = 0.2 s) and held 3 cm normal to the elevated hindwings of a mantid during stridulation.

Sound analysis.—The PC-based signal analysis software DADiSP 2002 was employed in sound analysis. High ambient low-frequency noise present in the recording room necessitated a noise reduction measure to enhance the mantids' signals. (The noise reduction procedure closely parallels that used by Masters (1980) in his study of the disturbance sounds of various insects.) Noise levels in a mantid recording (a portion of the acoustic output encompassing the maximum of the amplitude envelope of a sound syllable was chosen for analysis) were reduced by subtracting the spectrum of a nearly coincident equal-time sample of background noise. Each spectrum to be analyzed corresponded to a sample period of 168 ms, was associated with a single motor movement (downstroke), and was initially converted into a smoothed curve (200 data-point moving average). Spectral data were extracted after application of the noise reduction measure (spectra of background noise were also converted into smoothed curves) and conversion of the y-axis to relative dB (a logarithmic scale, expressed in dB relative to the zeroed value corresponding to the maximum-amplitude frequency of the spectrum), and are herein referred to as 'average frequencies' (to emphasize that they are values derived from spectra converted to logarithmic scales and subjected to a moving average transformation versus values from raw, linear power spectra).

The PC-based signal analysis software MATLAB 7.0.1, along with a custom-made computer program, was employed in analyzing the time domain pattern of mantid-produced sounds. To permit sharper temporal resolution of mantid-generated pulses (a pulse is a portion of a syllable), a band pass filter (3 to 16 kHz) was applied to each time-domain sample.

In 2004, both up- and downpulse (the sounds emitted on the abdominal upstroke and downstroke, respectively) durations were measured. Gross pulse (amplitude envelope) shapes were qualitatively assessed in MATLAB 7.0.1 and the custom-made computer program. A comparatively low sampling rate and lower signal-to-noise ratio limited time-domain resolution of the 2005 sound recordings. The durations of just the highest-amplitude components of downpulses (those portions of the signal for which the amplitude envelope well exceeded that of background noise levels) were therefore extracted as measures of pulse length for the second (2005) dataset. The duration of the measurable portion of each defensive sound emission, as determined from 2005 data, is therefore referred to as a 'truncated downpulse' duration.

Setup of trials for investigation of factors influencing the rate of defensive syllable production.—The possibility of a correlation between a mantid's sex (among other factors such as mantid–predator separation distance) and the number of defensive syllables the mantid will generate per unit time in response to the visual stimulus of a

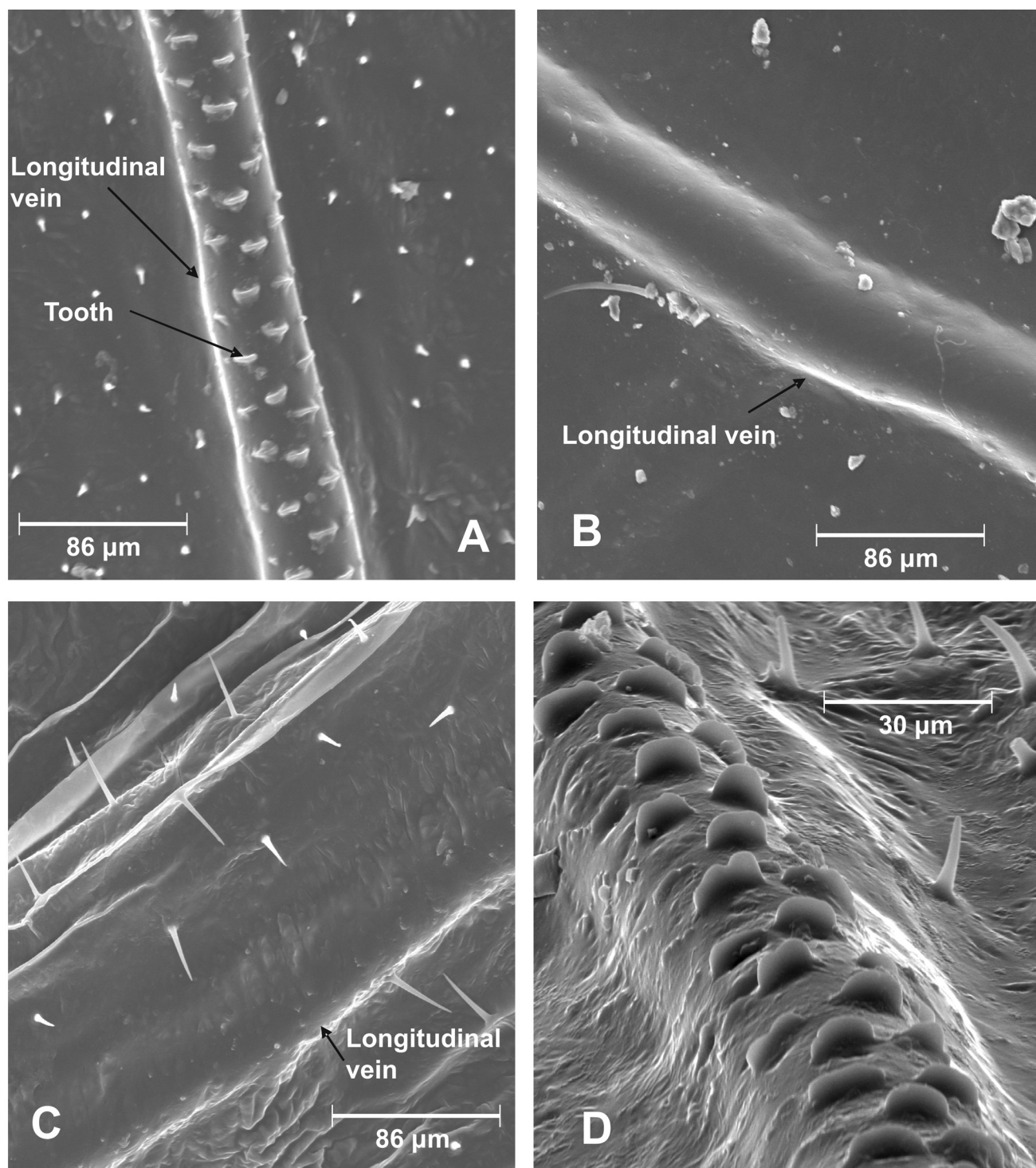


Fig. 1. Stridulatory structures. A. Longitudinal vein of hindwing bearing teeth (dorsal view, *M. religiosa*). B. Longitudinal vein of forewing lacking teeth (dorsal view, *M. religiosa*). C. Longitudinal vein of hindwing lacking teeth (dorsal view, *T. a. sinensis*). D. Oblique view of hindwing vein of *M. religiosa* showing structural irregularity of teeth.

predator was investigated using a multivariate, repeated-measures experimental design.

In each trial ($n = 171$), a mantid was placed on a vertical perch (height = 20.5 cm) positioned 8, 13 or 18 cm from the front bars of a cage containing a canary. The canary was constrained to remain within 6 cm of the front bars of its cage. The number of sequential stridulatory emissions produced in a one minute-long time period

(within the first 2 min following the onset of the mantid's defensive display) was obtained for each mantid ($n = 57$). Each mantid was randomly assigned to one of three different 'test orders' and one of four canary 'predators' and was tested three times (once at each distance from the canary). The first distance at which each mantid was tested corresponded to that specified by its assigned 'test order'. Consecutive trials involving the same mantid were conducted at

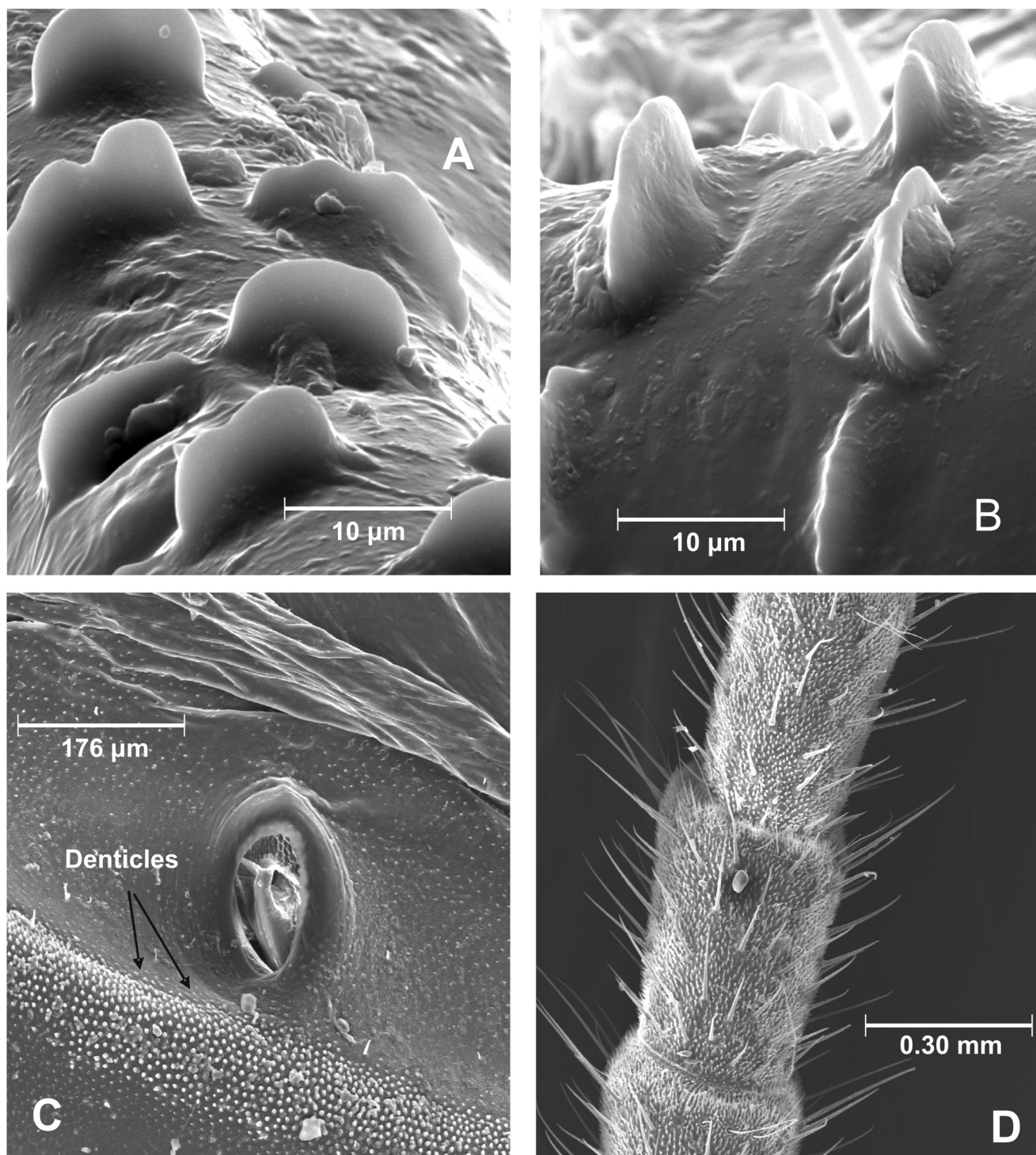


Fig. 2. Stridulatory structures of *M. religiosa*. A. Oblique view of teeth showing apical maxima and furrows. B. Lateral view of teeth showing longitudinal asymmetry. C. Dorsal view of denticulate abdominal pleura. D. Cercus.

least 1 h apart and specific mantid-predator pairings were constant across treatments.

Setup of playback trials.—Playback trials were performed to assess the behavioral responses of adult mantids to the broadcast defensive sounds of a conspecific female. A playback sound file was developed from a recording made under the same conditions as those described above (see Staging of displays, recording of defensive sounds and

measurement of sound pressure levels). A battery-powered car radio amplifier (GM 42A Pioneer) was connected to a leaf tweeter speaker (Panasonic Technics) and PC computer. The sound file was read at a sampling rate of 100 kHz. To reduce ambient noise, all trials were conducted in a sound-attenuating room. It was hypothesized that if adult *M. religiosa* are able to 'hear' the defensive sounds of conspecifics, test mantids would exhibit phonotaxis, or some other perceivable change in behavior (e.g., a head turn towards the speaker,

freezing) in response to exposure to the broadcast sounds.

During most trials ($n=20$), the acoustic output was broadcast at a maximum sound pressure level of 62 to 72 dB (as measured using the RadioShack meter) at a distance of 3 cm from the speaker. These intensities fell within the normal range of SPLs of mantid-generated sounds at the same distance from the sound source (data obtained before playback trials were conducted). At the onset of each trial, an adult female mantid was placed on a vertical perch connected via a horizontal rope to an identical perch located some distance away. The perch on which the mantid was initially placed was positioned 8.5 cm away from the speaker, such that the horizontal cord connecting the two perches ran in a line perpendicular to and away from the center of the vertical face of the speaker. This setup was designed to enable a test mantid's movement away from (and potentially back towards) the source of the broadcast sounds.

During a few trials ($n = 3$), the acoustic output was broadcast at a maximum sound pressure level of 73 to 75 dB at a distance of 3 cm from the speaker; these intensities coincided with the upper limit of the normal range of mantid-generated sounds at the same distance away from the sound source. Adult male *M. religiosa* are more 'restless' than females and consistently flew off the vertical perch before being exposed to broadcast sounds; therefore, in these three trials, the perch-cord-perch apparatus was replaced with a plastic cylinder (height = 19 cm, diameter = 6 cm) into which each adult male mantid was placed. The cylinder was closed at one end (the bottom) and covered at the other with fine mesh netting. The center of the plastic cylinder was set 10.5 cm from the speaker.

The first 2 min of each trial constituted an acclimation period in which the test mantid was not exposed to any broadcast sounds. During the third and final minute of each trial, the playback file was broadcast. Each test mantid's behavior during acclimation was compared to that during exposure to sound.

Statistical analyses

Spectral and time domain data (2004).—Mann-Whitney, two-sample t-tests and two-sample Kolmogorov-Smirnov tests were performed as appropriate, to investigate whether the following parameters differed between female and male mantids: 1) mean highest amplitude, or peak average frequency of downpulses, 2) mean upper and lower average frequency limits of the downpulse spectral curve at various relative dB values, 3) mean duration of uppulses, and 4) mean duration of downpulses. Kolmogorov-Smirnov tests were performed on both untransformed variables (original measurements) and variables centered about their means; the latter tests were conducted to eliminate the possible influence of shape (as opposed to measure of central tendency) differences between distribution pairs on the returned significance levels.

The duration of an individual mantid's uppulse was taken to be the average of the durations of two separate uppulses generated by that individual; the duration of an individual mantid's downpulse was evaluated the same way.

Two-sample Kolmogorov-Smirnov tests were conducted to investigate whether the distribution of mean differences in peak average frequency between two downpulses produced by the same mantid, differed from the distribution of mean differences in peak average frequency between two downpulses produced by different mantids. The differences in peak average frequency between two downpulses produced by different mantids were obtained by taking the absolute value of the difference between the peak average frequency of a downpulse produced by one mantid and the peak

average frequency of a downpulse produced by another, randomly selected, mantid.

Spectral and time domain data (2005).—One-way analyses of variance and Kruskal-Wallis tests were performed as appropriate, to investigate whether the following parameters differed among male, non gravid female and egg-bearing (including both semigravid and gravid) female mantids: 1) mean highest amplitude, or peak average frequency of downpulses, 2) mean upper and lower average frequency limits of the downpulse spectral curve at various relative dB values, 3) mean peak average frequency of the spectral peak of second-highest amplitude of downpulses, 4) mean intra-individual variability in the peak average frequency of downpulses, 5) mean inter-individual variability in the peak average frequency of downpulses and 6) mean duration of truncated down-pulses. Wherever a significant difference among groups was detected, *post-hoc*, Bonferroni-corrected pair-wise comparisons of means were performed using t- or Mann-Whitney tests. Intra- and inter-individual variabilities were measured as described in the preceding section [Spectral and time domain data (2004)].

Data collected in the repeated measures experiment in which number of defensive syllables produced per minute was the response variable of interest, were analyzed via the multivariate analysis of variance approach. Sex (of a test mantid) was included as a between-subjects factor. All univariate follow-up tests were Bonferroni-corrected.

Sound pressure level data.—A Kruskal-Wallis test, followed by a Dunn's (1964) nonparametric multiple comparison of means test, were performed to investigate whether the mean sound pressure level of defensive sounds differed among non gravid females, gravid females and males. Each observation within a sample (e.g., non gravid females, gravid females, males) of SPL measurements represented the average of three SPL measurements of the sounds produced by one mantid.

Most statistical analyses were performed using the statistical software packages Minitab 13, S-Plus 6.1, SPSS 12.0.1, and SAS 6.12. The Dunn's (1964) nonparametric multiple comparison of means test was performed manually.

Results

Stridulatory structures.—The dorsal surface of each of the five examined tissue pieces derived from the anal region of the hindwings of *M. religiosa* revealed longitudinal venation that was tooth-studded (Figs 1A, D). Inter-tooth spacing is highly irregular. The teeth are roughly semi lunar in shape and asymmetrical at both their apices and bases. The base of each tooth is longest in the direction perpendicular to the long axis of the veins and many teeth exceed their basal width (dimension parallel to the long axis of the veins) in height. Viewed perpendicular to the axis of the longitudinal vein with which they are associated, many teeth appear planar or concave on the side that opposes the direction of abdominal movement during the downstroke, while being convex and strongly buttressed on the other (Fig. 2B). The teeth are characterized by either a gentle upward tapering or by bearing an apex that features a variable number of shallow furrows (Fig. 2A).

Only the longitudinal veins of the anal region [including the second anterior anal vein (AA2) and all longitudinal veins posterior to AA2] bear stridulatory teeth and these teeth are frequently more prominent distad on the wing (Fig. 3). The dorsal surfaces of the

first anterior anal vein (AA1) and all longitudinal veins anterior to AA1, either lack teeth or feature sporadically-distributed shallow humps, the humps conferring a moderately roughened appearance to the veins with which they are associated.

Neither the forewing piece derived from *M. religiosa* (Fig. 1B) nor the hindwing piece derived from *T. a. sinensis* (Fig. 1C) exhibited any teeth or other similar structures. The longitudinal veins of the forewing of *M. religiosa* appeared smooth, while those of the hindwing of *T. a. sinensis* bore sporadically-distributed hair sensillae, similar to those seen on membranous parts of the wings of both species of mantid.

On the abdominal pleura of *M. religiosa* there is a field of short, roughly symmetrical and densely distributed peg-like structures arranged in a band running parallel to the long-axis of the mantid's abdomen (Fig. 2C); these abdominal denticles are much shorter than the teeth observed on the longitudinal veins of the hindwings. The cercus of *M. religiosa* features many hair sensillae, but lacks any modifications suggestive of specialization for sound production (Fig. 2D).

Sound analysis

Qualitative characterization of sound pulses.—The entirety of the sound emission produced by a single cycle of generator (abdominal) movement during stridulation will be referred to as a syllable. The portion of a syllable resulting from the upstroke of a mantid's abdomen against the elevated hindwings will be termed an up-pulse, while that resulting from the downstroke will be called a downpulse. Each up- or downpulse is a sustained complex waveform. In the sound recordings, the uppulse could not always be resolved from background noise, but when evident, was easily distinguished from the downpulse by its more gradually increasing amplitude envelope and substantially lower maximum amplitude. The amplitude envelope of all uppulses examined ($n = 40$; 17 female, 23 male) were strongly left-tailed, showing a very gradual rise with time until a maximum was attained just prior to the onset of the downpulse. The amplitude envelopes of downpulses were more variable in shape. Of the 148 downpulses examined, 137 (73 female, 64 male) had amplitude envelopes that were right-tailed, presenting an abrupt rise to a maximum followed by a more gradual decline, 9 (3 female, 6 male) had amplitude envelopes that were symmetrical about the maximum, and 2 (both male) had amplitude envelopes that were left-tailed. Noticeable disparities in pulse, and thus syllable shapes, both between individuals and between separate sound emissions produced by the same individual, were apparent.

Inter-syllabic intervals and pulse durations (2004 data).—The Kolmogorov-Smirnov Z test statistics and associated significance levels stated below, except for those pertaining to the distributions of intra- vs inter-individual variability in peak frequency, correspond to tests conducted on unmanipulated datasets and yield information about differences between the centers of pairs of distributions. Most Kolmogorov-Smirnov tests performed on centered test variables returned nonsignificant results (thus indicating no significant differences in shape between pairs of distributions); those performed on centered mean intra- and inter-individual differences in peak frequency returned significant results (see Acoustic spectra: 2004 data).

The mean duration of downpulses (195 ± 41 ms, $n = 76$) was greater than that of uppulses (149 ± 57 ms, $n = 40$) (Kolmogorov-Smirnov test statistic: $Z = 2.79$, $P < 0.001$) and the mean duration of downpulses was greater for females (206 ± 38 ms, $n = 38$) than

for males (185 ± 41 ms, $n = 38$) (Mann-Whitney test statistic: $W = 1725.5$, $P = 0.0032$). Females also generate significantly longer up-pulses than males (mean for females = 167 ± 49 ms, $n = 17$; mean for males = 135 ± 61 ms, $n = 23$; $Z = 1.54$, $P = 0.018$).

No apparent pattern emerged for intersyllabic intervals, either between the syllables generated by one mantid during a single episode of sound production, or among individuals (Fig. 5A).

Truncated down-pulse durations (2005 data).—Average durations of truncated downpulses were calculated for five groups, differentiated on the basis of sex and/or reproductive state: males (48.6 ± 13.2 ms, $n = 25$); non gravid females, or those females exhibiting no overt signs of egg production (56.3 ± 12.4 ms, $n = 20$); non gravid + semigravid females pooled, or those females exhibiting no overt signs of *advanced* egg production (53.9 ± 10.7 ms, $n = 37$); semigravid females + gravid females pooled, or those females exhibiting overt signs of egg production (47.5 ± 9.4 ms, $n = 33$); and gravid females, or those females exhibiting overt signs of *advanced* egg production (43.8 ± 9.7 ms, $n = 16$). The dual grouping of semigravid females separately with both non gravid and gravid females is justified, as assessment of reproductive state is very subjective.

An ANOVA, conducted to test for a difference between at least two of the five groups was significant ($F = 4.48$, $P = 0.002$). A follow-up simultaneous, pair-wise comparison of all five mean truncated downpulse durations revealed that non gravid females produced longer truncated downpulses than did gravid females ($T = 3.32$, $P = 0.002$), or gravid and semigravid females pooled, while non gravid and semigravid females considered together as a group, produced longer truncated downpulses than did gravid females.

Factors influencing the rate of defensive syllable production.—The rate of repetition of the acoustic defensive response of a mantid (as measured by mean number of syllables produced per minute in response to the visual stimulus of a canary) was found to depend on the mantid's sex.

There was a significant main effect for 'sex' at all three mantid-predator distances (8, 13 and 18 cm), with female mantids generating, on average, fewer syllables per minute (60.73 ± 19.08 , $n = 28$) than males (74.80 ± 16.81 , $n = 29$) ($F = 17.10$, $P < 0.0001$). The mean numbers of acoustic emissions generated per minute for males and females at each distance from an avian predator are given in Table 4.

Acoustic spectra.—The defensive sounds generated by *M. religiosa* are broadband and contain frequencies concentrated mostly within the audio (< 20 kHz) range. Wide spectral variation in downpulses exists, both within and between individuals. The acoustic spectra of *M. religiosa* most often feature one or two frequency peaks. Harmonic relationships between spectral peaks are not apparent.

2004 Data

The mean overall highest-amplitude (average) frequency (that derived from the dominant spectral peak) for all mantids (males and females pooled) was 7.37 ± 3.44 kHz ($n = 73$); for the spectral subpeak of second-highest amplitude, the mean highest-amplitude (average) frequency was 7.66 ± 3.66 kHz ($n = 53$). The modal peak (average) frequency range was the 1-kHz interval between 11 and 12 kHz (Fig. 4). Of the 73 spectra samples, approximately half ($n = 36$) featured a dominant peak in the 0-7 kHz frequency range, while in the other 37, this peak occurred in the 7-14 kHz frequency range. The mean highest-amplitude (average) frequency was significantly

Table 2. Upper and lower frequency bounds and spectral bandwidths of *M. religiosa* at 3, 6 and 12 dB (re 20 μ Pa) down.

	3L ^a	3U ^b	Δ 3	6L	6U	Δ 6	12L	12U	Δ 12
Mean (kHz)	3.65	12.8	9.50	2.43	16.7	14.5	1.67	26.3	25.2
S.D. ^d (kHz)	1.90	3.00	2.59	1.21	2.57	2.54	0.59	5.15	5.33
n	64	73	64	56	73	56	34	73	34

a= lower bound

b= upper bound

c= frequency bandwidth

d= standard deviation

higher for males (8.20 ± 3.32 kHz, $n = 35$) than for females (6.60 ± 3.41 kHz, $n = 38$) ($Z = 1.70$, $P = 0.006$) and there was a nonsignificant tendency for the spectra of female mantids to exhibit a prominent subpeak more frequently than those of male mantids. A sample spectral curve obtained from a female specimen is presented in Fig. 5D.

Statistical comparisons of the distributions of absolute differences in mean peak average frequency between two downpulses generated by the same individual, versus between two downpulses generated by two different individuals, revealed that the latter distribution was stochastically greater than the former. Inter-individual variability (as measured by absolute differences) in peak average frequency exceeded intra-individual variability in terms of distribution shape and perhaps also in terms of central tendency ($Z = 2.57$, $P < 0.001$; $Z_{\text{centered}} = 2.07$, $P < 0.001$). Kolmogorov-Smirnov tests were significant within males ($Z = 2.03$, $P = 0.001$; $Z_{\text{centered}} = 1.91$, $P = 0.001$), within females ($Z = 1.49$, $P = 0.023$; $Z_{\text{centered}} = 1.61$, $P = 0.012$) and with both sexes pooled. The mean interpulse (intra-individual) and inter-individual absolute differences in peak average frequency for males were 1.80 ± 2.54 kHz and 4.46 ± 3.39 kHz, respectively ($n = 35$); those for females were 1.88 ± 2.10 kHz and 4.02 ± 3.17 kHz, respectively ($n = 38$); and those for the pooled sample were 1.84 ± 2.30 kHz and 3.86 ± 2.90 kHz, respectively ($n = 73$).

Quantitative investigation of possible intersex differences between the mean spectral widths and upper and lower bounds of the mantids' spectral curves (with y-axes converted to logarithmic, relative dB scales) yielded few significant results. The mean average frequency bounds and bandwidths of the spectral profile of *M. religiosa* (both sexes pooled) at 3, 6, and 12 dB down, are given in Table 2. 'Average' spectral curves for female and male *M. religiosa* are presented in Figures 5B and 5C, respectively.

2005 Data

The mean overall highest-amplitude average frequency for all mantids (males, non gravid females and gravid females pooled) was 9.36 ± 1.53 kHz ($n = 78$), while the mean highest-amplitude (average) frequency of the second-highest amplitude subpeak was 8.87 ± 2.39 kHz ($n = 36$). The overall modal peak (average) frequency range was the one-kilohertz interval between 9 and 10 kHz. Statistical comparison of the mean peak average frequencies for males (9.15 ± 0.93 kHz; $n = 25$), non gravid females (9.50 ± 1.51 kHz, $n = 20$) and gravid females (9.41 ± 1.87 kHz, $n = 34$) revealed no significant differences among groups.

The mean intra- and inter-individual variabilities in peak frequency (variability measured as the absolute difference in highest-energy frequency between two downpulses) did not differ significantly among groups (males, non gravid females and gravid females).

Comparisons of mean spectral widths and upper and lower bounds of the mantids' spectral curves revealed some significant intergroup differences. The mean average frequency bounds and bandwidths of the spectral curves of male, non gravid female and gravid female mantids at 3, 6, and 12 dB down are given in Table 3, with statistically significant differences among groups indicated.

Sound pressure levels.—A Kruskal-Wallis test revealed that at least two of the three mean SPL values (non gravid females, gravid females and males) were significantly different ($H = 7.13$, $P = 0.028$). A Dunn's (1964) nonparametric multiple comparisons of means test ($k = 3$, $\alpha = 0.15$) showed no significant difference between the mean SPLs of sounds produced by gravid females (68 ± 3 dB, $n = 61$) and males (68 ± 3 dB, $n = 48$) [Dunn's test statistic, $|T|$ for gravid females *vs* males = 0.515], but a significant difference between the mean SPLs of either of these two groups and that of non gravid females (70 ± 3 dB, $n = 16$; $|T|$ for non gravid females *vs* gravid females = 2.65, $|T|$ for non-gravid females *vs* males = 2.24, where statistical significance was achieved when $|T| \geq 1.96$].

Behavioral analysis.—No mantid ($n = 23$) exhibited any defensive behavior or significant change in its behavior in response to exposure to the broadcast sounds of a female conspecific. All mantids tested showed some combination of behaviors commonly seen in unperturbed mantids [e.g., grooming, resting, peering (side-to-side rocking movements) and extending the prothoracic legs in the direction of nearby objects (including the speaker)] both before and during sound playback.

Table 3. Upper and lower frequency bounds (kHz) and spectral bandwidths (kHz) of male, non gravid female and gravid female *M. religiosa* at 3, 6 and 12 dB (re 20 μ Pa) down. Within a data column, mean values highlighted in dark gray are statistically greater than mean values highlighted in light gray.

	3L ^a	3U ^b	Δ 3	6L	6U	Δ 6	12L	12U	Δ 12
Males	6.38 \pm 0.63 (n=25)	11.8 \pm 1.02 (n=25)	5.41 \pm 1.22 (n=25)	4.88 \pm 1.17 (n=25)	13.9 \pm 0.90 (n=25)	8.98 \pm 1.61 (n=25)	2.07 \pm 0.82 (n=21)	16.6 \pm 1.03 (n=25)	14.6 \pm 1.00 (n=21)
Non gravid females	6.46 \pm 0.91 (n=20)	13.0 \pm 1.31 (n=20)	6.50 \pm 1.25 (n=20)	4.34 \pm 1.45 (n=20)	14.6 \pm 1.36 (n=20)	10.3 \pm 2.00 (n=20)	1.64 \pm 0.61 (n=17)	17.2 \pm 1.46 (n=20)	15.4 \pm 1.57 (n=17)
Gravid females	6.04 \pm 1.49 (n=34)	12.4 \pm 1.65 (n=34)	6.31 \pm 1.15 (n=34)	4.21 \pm 1.66 (n=34)	13.9 \pm 1.29 (n=34)	9.70 \pm 1.64 (n=34)	2.09 \pm 1.05 (n=32)	16.4 \pm 1.25 (n=34)	14.3 \pm 1.40 (n=32)

a=lower bound

b=upper bound

c=frequency bandwidth

Table 4. Intersex comparisons of mean rate of defensive syllable repetition (number of sound emissions per minute) at three different mantid-predator distances.

	Mantid-predator distance		
	8 cm	13 cm	18 cm
Males (n=29)	70.6±19.8	77.6±14.9	76.3±15.2
Females (n=28)	60.7±20.6	63.8±14.9	57.7±21.3

Discussion

Stridulatory Structures.—The motor movements that occur during defensive stridulation in adult *M. religiosa*, coupled with the locations of the stridulatory structures, indicate that in this species sounds are produced by repeated scraping of the denticulate areas of the abdominal pleura against the tooth-studded dorsal surfaces of the longitudinal veins of the hindwings. The specific locations (anal regions) of the teeth on the hindwings coincide with the areas subject to maximal contact during defensive sound production.

The cerci, which bear short densely-distributed sensillae and a protruding edge at each interface between adjacent segments, might also function in stridulation if they come in contact with the longitudinal veins of the hindwings. Beier (1968) attributed mantid-produced sounds to this latter mechanism, without commenting on any specializations of the hindwing venation.

Stridulatory teeth on the hindwings of *M. religiosa* appear to be asymmetrically buttressed against the relatively forceful movement of the abdomen on the downstroke, the loudest portion of each cycle of generator movement. The spacing of the shallow humps located on the anterior longitudinal veins of the hindwings of *M. religiosa* [as well as on many of the longitudinal veins of the hindwings of *T. a. sinensis* (Hill pers. obs.)] is comparable to that of the stridulatory teeth found on the longitudinal veins of the anal region of the hindwings of this mantid. It is easy to imagine how localized, morphological modifications of these shallow humps (which *M. religiosa* may at one time have borne on all the longitudinal veins of the hindwings) could lead to the evolution of stridulatory teeth in this species.

The abdomino-alary mechanism of stridulation in *M. religiosa* is like that of some tettigoniids of the genus *Pantecphylus*, where friction between a broad file present on the abdominal tergites and raised portions of the dorsal surfaces of the hindwings effects defensive sound production (Heller 1996, Schmidt & Stelzer 2004). Heterogeneous stridulatory fields in which the 'teeth' of the effective 'file' are distributed over a wide area, as is seen in *M. religiosa*, are typical of structures responsible for the production of defensive or disturbance sounds across a wide range of taxa, including beetles, wasps and orthopterans (Dumortier 1963, Tschuch & Brothers 1999, Montealegre-Z *et al.* 2003).

The irregular and diffuse field-like nature of the 'file' in *M. religiosa* predicts nonresonant sound generation (Elsner & Popov 1978), and thus an acoustic output that is broadband (Montealegre-Z & Morris 1999, Montealegre-Z *et al.* 2003). This type of stridulatory mechanism is in contrast to the coherent files responsible for the production of calling songs in many ensiferan orthopterans (Bennet-Clark 1999, Montealegre-Z & Morris 1999, Prestwich *et al.* 2000).

The absence of predictable subpeaks in the spectral profile of *M. religiosa* is not surprising, given the heterogeneity of the sound generator morphology in this species. Yet this lack of stereotypy in spectral subpeaks stands in interesting contrast to the condition observed in some acoustic Ensifera producing sound via nonreso-

nant mechanisms (Elsner & Popov 1978, Meyer & Elsner 1996).

Acoustic profile.—Defensive sounds produced by adult *M. religiosa* are broadband, of relatively low intensity and contain frequencies mainly in the audio (<20 kHz) portion of the spectrum, but extending into the ultrasonic (up to about 26.3 kHz at 12 dB down, according to 2004 data). Within spectra, harmonics are not evident, although one or two prominent subpeaks (in addition to the dominant peak) are common. In general, the loudest sound within a syllable occurs on the downstroke, which results in the production of a sound emission of relatively short duration and impulsive onset. Intersyllabic intervals are irregular, but on average, of greater duration for females. There is evidence to suggest that the rate of defensive sound production decreases as a mantid's separation distance from an avian threat increases. Characteristics of the defensive sounds of *M. religiosa* are highly variable in both the frequency and time domains.

Temporal characteristics.—Both Haskell (1964) and Masters (1980) noted that the defensive sounds of insects lack a stereotyped time interval between acoustic emissions: this is the condition seen in *M. religiosa*. Intersyllabic duration and thus, the rate of production of defensive syllables are affected by a mantid's sex, with males having higher rates of sound production than females.

In most instances, the downpulse of *M. religiosa* features an impulsive onset, whereby the maximum energy (loudness) is reached before the midpoint of the syllable's duration; this feature is shared by the hisses of *G. portentosa* (Nelson & Fraser 1980) and appears to be widespread among defensive sounds in insects (Masters 1980).

Spectral characteristics.—As predicted by the architecture of the stridulatory apparatus, the frequency spectrum of *M. religiosa* is broadband and variable; these features may imply the absence of selection for the coding of higher information content as in the social signals of acoustic Ensifera (Morris pers. comm.). At a relative amplitude level of 6 dB below that of the frequency of maximum energy, the mean spectrum included frequencies ranging from about 2.4–16.8 kHz (2004 data); this band of frequencies is similar to that (2–20 kHz) which characterizes the defensive hisses of the cockroach *Gromphadorhina portentosa* Schaum (Nelson 1979). Broadband output is a widely-shared feature of defensive or disturbance sounds in insects (Haskell 1961, 1964; Masters 1980; Tschuch & Brothers 1999; Naskrecki 2000).

Individuals of *M. religiosa* appear to vary in their capacity to produce ultrasound. Although the upper frequency limit of the mean spectrum at 12 dB down was ~26.3 kHz (2004 data), this value exceeded 30 kHz in the analyzed spectra of 13 of 35 males and 3 of 38 females. Males of the katydid *Panoploscelis specularis* Beier also incorporate ultrasonic components up to 35 kHz in their defensive sounds (Montealegre-Z *et al.* 2003).

The peak frequency of *M. religiosa* is so variable that a true central frequency is apparently absent. A broadband disturbance spectrum without any consistent frequency peaks has also been described for the cricket *Brachytrupes tropicus* Gorochoy (Desutter-Grandcolas 1998b). The overall modal range for the dominant average frequency of *M. religiosa* is approximately 9–12 kHz, while the spectral interval into which the second highest proportion of analyzed peak average frequencies falls, is 8 to 11 kHz. Thus, the range of frequencies between 8 and 12 kHz may constitute a more informative measure of the central tendency of the dominant

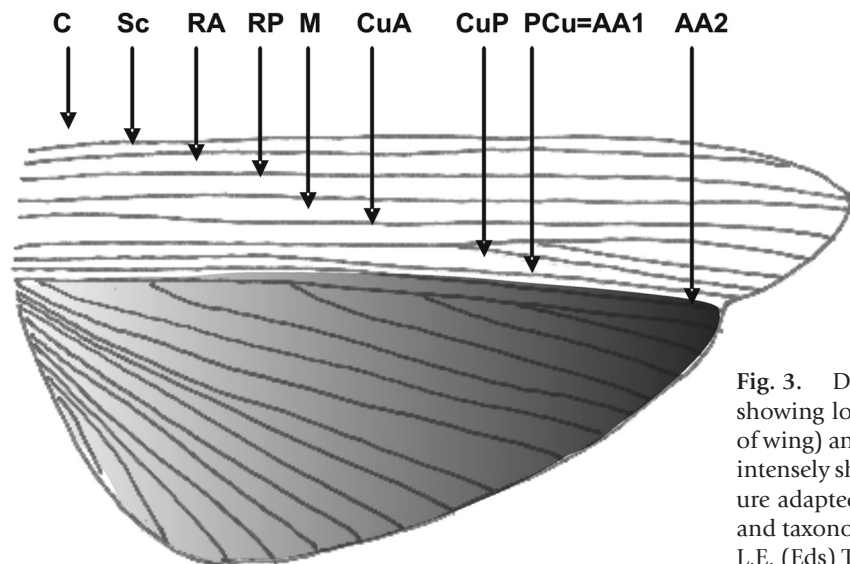


Fig. 3. Dorsal view of right metathoracic wing of *M. religiosa* showing location of teeth (longitudinal veins in shaded region of wing) and their relative prominence distad on the wing (more intensely shaded wing regions bear more prominent teeth). (Figure adapted from Fig. 2.13, p. 31 of Roy, R. 1999. Morphology and taxonomy, pp.19-40. In: Prete F., Wells H., Wells P.H., Hurd L.E. (Eds) *The Praying Mantids*. Johns Hopkins University Press, Baltimore.)

frequency of *M. religiosa* than the mean. Peak frequencies which lie in the 4 kHz-wide modal range observed for *M. religiosa* have been described for the defensive or disturbance sounds of another dictyopteran [e.g., ~10 kHz in the cockroach *G. portentosa* (Nelson & Fraser 1980)] and for those of other orthopteroid insects [e.g., 10 kHz in the katydid *Pantecphylus* sp. (Heller 1996) and 11.2 kHz in males of the katydid *P. specularis* (Montealegre-Z *et al.* 2003)].

While frequency maxima in the midaudio portion of the spectrum may be relatively common among orthopteroids, the disturbance sounds of other insect taxa often feature much lower peak frequencies: e.g., 152-209 Hz in *Sphecius speciosus* Drury wasps (Coelho 1998); 2,000 Hz in five reduviid species (Schilman *et al.* 2001); 384 Hz in *Apis florea* Fabricius (Sen Sarma *et al.* 2002)], or higher [e.g., ~25 kHz for various insects surveyed by Masters (1980)]. If, in *M. religiosa*, inter-individual variability in dominant frequency exceeds intra-individual variability (as suggested by some of my results) then strong morphological peculiarities may be associated with the stridulatory structures of individual mantids.

Although the spectra of *M. religiosa* can feature subpeaks, the relationship between the highest-energy average frequencies of the dominant peak and second-highest amplitude subpeak is not harmonic. If the structural properties (e.g., thickness) of the hindwing membranes (the surfaces that may serve as sound radiators in *M. religiosa*) vary sufficiently across their areas, so too may the optimal vibrational frequencies of the different wing regions, thus potentially interfering with the production of harmonics (Montealegre-Z *et al.* 2003, Morris pers. comm.).

Sound pressure level.—Katydid calls commonly occur at intensities of >90-100 dB at distances of 10 cm (Morris 1999). The contrasting comparatively low intensity of the acoustic output of *M. religiosa* is a hallmark of many insect defensive sounds (Masters 1980, Desutter-Grandcolas 1998b; but see Haskell 1964). At just 3 cm normal to the sound-radiating surfaces, these sounds range from about 68 to 70 dB in *M. religiosa*. Defensive buzzing in the wasp *S. speciosus* occurs at comparably low intensities (70-72.6 dB) at the same dis-

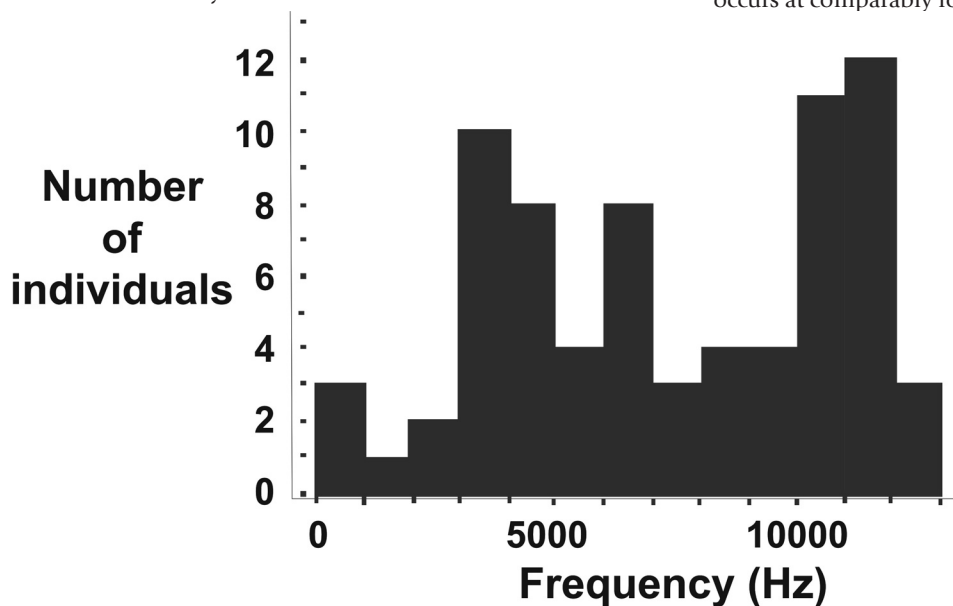


Fig. 4. Distribution of highest-amplitude average frequencies among *M. religiosa* (2004 data).

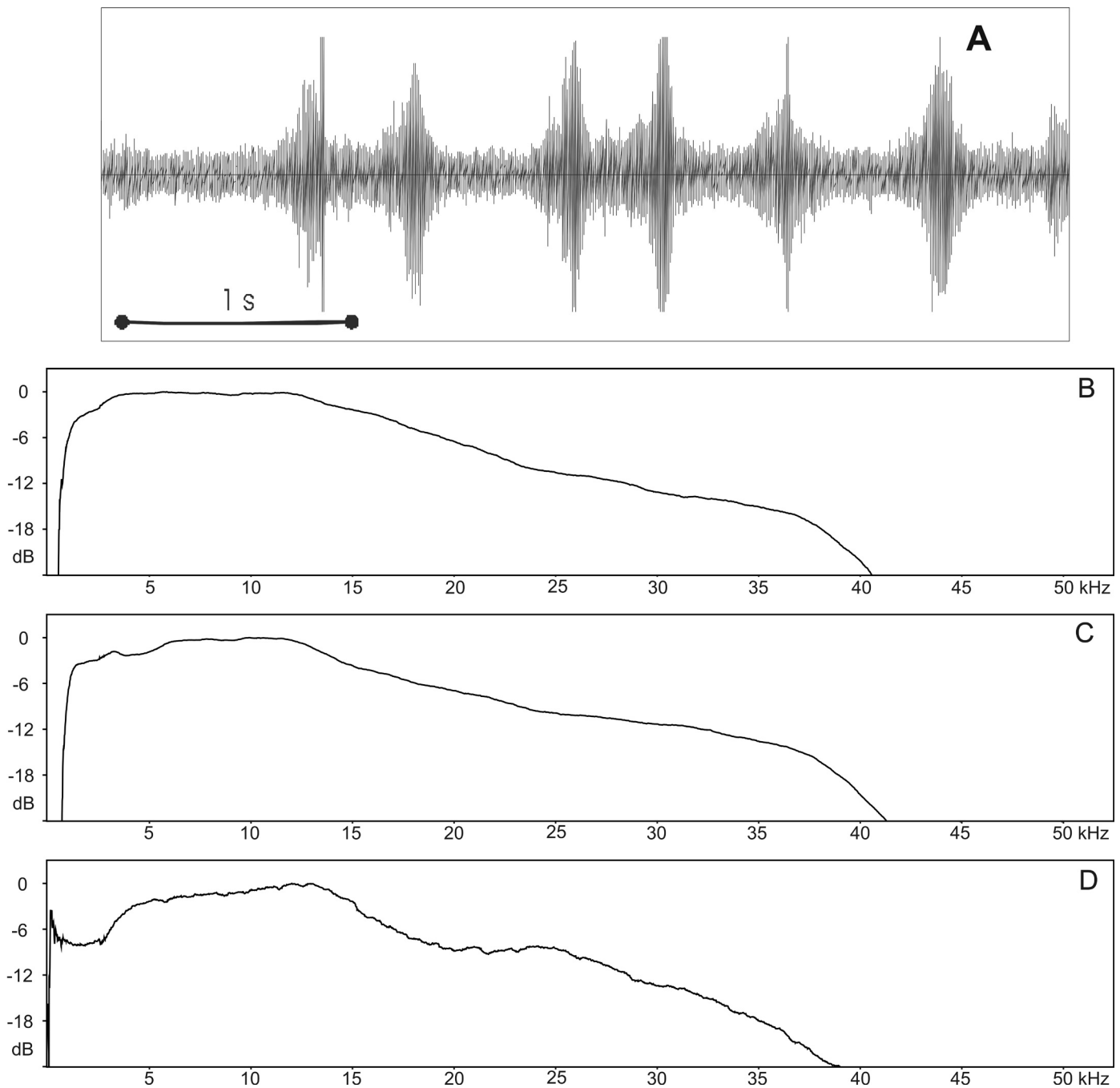


Fig. 5. Defensive sounds of *M. religiosa*. A. Sequence of six complete sound emissions (syllables) by an adult female in background noise, showing variable inter-syllabic intervals. B. Average female spectral curve. C. Average male spectral curve. To derive the average female spectral curve, the smoothed curve (moving average) resulting from the averaging of 17 samples of background noise, was subtracted from the smoothed curve resulting from averaging 17 samples (each of equal sample period to that of the noise samples) of female-produced downpulses superimposed on background noise. The y-axis of the resulting spectrum was then converted to the logarithmic relative dB scale. The average male spectral curve was obtained in a similar manner. D. Sample spectral curve obtained from a single (female) mantid.

tance from the insect (Coelho 1998), while the defensive sounds of *G. portentosa* and another cockroach, *Henschoutedenia epilamproides* Shelford, are louder [70-87 dB at 5 cm from the insect (Nelson & Fraser 1980)] and softer [70 dB at 1 cm from the insect (Guthrie 1966)] respectively. The acoustic component of the defensive display in *M. religiosa* would presumably be effective only at close ranges. Perhaps some threshold loudness is achieved that represents a bal-

ance between effectively deterring an alerted predator and attracting the unwanted attention of more distant potential receivers.

Sex differences.—Overall, defensive sounds vary little between the sexes in *M. religiosa*; this parallels the situation for at least one other insect group that stridulates defensively, the Triatominae (Reduviidae) (Schilman *et al.* 2001). Among most sound-producing in-

sects [e.g., *S. speciosus* (Coelho 1998)], smaller stridulatory organs are associated with the generation of higher frequency and lower intensity acoustic outputs (Bennet-Clark 1998). The observed sex differences in the acoustic profile of *M. religiosa* may arise from the overall sexual size dimorphism and probable concomitant relative inter sex size differences in sound-producing structures, in this species. For example, the tendency for adult female mantids (especially those not showing overt signs of egg production) to produce spectra which are shifted slightly below those of males (see Figs 5B, C) might result from size increases in sound-producing structures associated with selection for greater overall body size in females (for a similar argument see Carisio *et al.* 2004).

Egg-bearing is associated with a decrease in the flexibility of the abdomen in female mantids and abdominal stridulatory movements appear more restricted and less forceful in gravid versus nongravid females. If, as was suggested by the 2005 data, there is a tendency for the acoustic spectra of nongravid female *M. religiosa* to include higher frequencies than those of egg-laden females (or even males), the effect may arise from the supposed greater force and flexibility with which the abdomen contacts the hindwings in the former group. The relatively more vigorous stridulatory movements of nongravid females might also account for the greater mean SPL (~70 dB versus ~68 dB for either gravid females or males) of the defensive sounds generated by this group.

One insect group in which temporal characteristics of generated sounds are influenced by the size of the stridulatory organs is dung beetles: in this taxon, the pulse durations of defensive sounds increase with the length of the stridulatory structures (Carisio *et al.* 2004). It is plausible that a similar relationship holds in *M. religiosa* since females apparently produce both longer down and up pulses than males (2004 data).

Evolution and maintenance of the defensive acoustic signal in M. religiosa.—The broadband nature of the defensive sounds generated by *M. religiosa* may, as some authors have proposed for disturbance sounds in other taxa, be adaptive in ensuring that the spectral output of the signal overlaps with the varied ranges of auditory sensitivity of a wide assemblage of predators, thus serving as a highly generalized antipredator device (Masters 1979, 1980; Tschuch & Brothers 1999).

The effectiveness of the acoustic element of the defensive display of *M. religiosa* in various contexts and against various predators has never been systematically investigated. The adult deimatic reactions (including both visual and acoustic components) of *M. religiosa* and *S. biocellata*, apparently can deter avian predators (Maldonado 1970, Holroyd 1975, Hill pers. obs.). Holroyd (1975) has shown that the adult display of *M. religiosa* has some effectiveness against conspecifics, rodents and reptiles. A confounding factor in attempting to separate the antipredator effects of the acoustic vs visual parts of the defensive display in *M. religiosa*, is the consistent coincidence of these two components in unmanipulated adult displays. The composition and breadth of the spectrum of *M. religiosa*, however, qualify the sound element of the display as at least a plausible contributor to whatever overall protection the display may confer against many birds and mammals. Although *M. religiosa* is predominantly a diurnal species, it is easy to imagine that in the event of nocturnal encounters with predators (e.g., rodents), visual displays by the mantid will be rendered ineffective, with stridulation taking over as the dominant operating defense (see Masters 1979).

Of particular interest is the strong likelihood that *M. religiosa* is itself not receptive to the acoustic portion of the display except

perhaps over very short transmission distances (a few centimetres). The behavioral playback experiments conducted in this study, taken together with the mismatch between the tuning curve of the meta-thoracic ear [threshold sensitivities of 55–60 dB SPL between 25–45 kHz (Yager & Hoy 1986; 1987)] and the acoustic properties of the sounds produced by *M. religiosa*, argue strongly against the possibility of intraspecific communication (particularly over longer distances) in these mantids. My own experience observing nonsexual encounters between adult *M. religiosa* indicates a tendency for individuals of this species to display relatively rarely at conspecifics, and then, only at very short intermantid distances (again, a few centimetres). Perhaps in *M. religiosa*, as has been proposed for snakes and some fishes (Ladich 1999, Young 2003), the first appearances of sound generation and sound perception were removed from each other in evolutionary time.

Two main, nonmutually exclusive defensive functions have been championed for disturbance sounds in insects: startle or confusion mechanisms, and advertisement (honest or dishonest) of aposematic features (Haskell 1961; Masters 1979, 1980; Schmidt 1994; Tschuch & Brothers 1999; Schilman *et al.* 2001). The latter hypothesis has been most readily adopted to explain the functional significance of defensive sound production in mantids. In particular, authors dating back as far as Fabre (1897) have suggested that mantid defensive sounds mimic snake hisses (Maldonado 1970, Preston-Mafham 1990, Edmunds & Brunner 1999). Snake hissing and rattling are both aposematic behaviors that occur in defensive contexts (Klauber 1956, Greene 1988, Young 2003).

The present study has, for the first time, permitted comparison of the acoustic characteristics of the defensive sounds of *M. religiosa* with those of snakes and thus, partial corroboration of the previously-proposed aposematic function for the defensive sounds of this mantid. Young (2003) gives a detailed summary of snake bioacoustics. Snake hissing and rattling are noisy sounds that incorporate wide frequency bands [~3–13 kHz for hissing (Young 1991); 2–20 kHz for rattling (Fenton & Licht 1990; Young & Brown 1993, 1995); summarized in Young 2003], both of which closely coincide with the average spectrum of *M. religiosa* at 6 dB down (~2.4–16.8 kHz according to 2004 data).

Further similarities between the defensive sounds of *M. religiosa* and those of snakes are also evident. For example, the mean peak frequency of snake rattling is about 10 kHz [(Fenton & Licht 1990; Young & Brown 1993, 1995); summarized in Young 2003]: this value lies within the modal dominant frequency range of the spectrum of *M. religiosa*. Snake hissing lacks simple harmonics (Young 1991) which are also apparently absent in the defensive sounds of *M. religiosa*. Hissing via spiracular air expulsion is known to serve a defensive function in the blattid genus *Gromphadorhina* (Nelson 1979, Nelson & Fraser 1980) and at least one organism outside of snakes, the burrowing owl, incorporates mimicry of snake rattling in its defensive repertoire (Rowe *et al.* 1986, Owings *et al.* 2002).

A problem with the hypothesis that sounds generated by *M. religiosa* mimic those of snakes is that the defense would presumably be ineffective against experienced predators, since mantid displays are bluffs (Maldonado 1970, Edmunds & Brunner 1999, Hill pers. obs.). However, the incidence, in nature, of *M. religiosa* displaying and stridulating in response to any one predator species may be sufficiently low as to thwart learning by individual predators and thus permit perpetuation of the bluff as a viable defense of this mantid.

The second function proposed for insect disturbance stridulation, that it serves as a startle mechanism and elicits hesitation and/or

confusion in a potential predator, also appears tenable when applied to *M. religiosa*. Edmunds and Brunner (1999) have commented that the variation which characterizes mantid defensive displays may thwart predator attempts to form 'search images' for these behaviors. One expects that a highly variable, or unpredictable signal should be optimally effective in startling a receiver. The defensive sounds generated by *M. religiosa* conform to this recipe of high evitability (Roeder 1975). The extreme variability of the signal is apparent in both its spectral composition (e.g., the standard deviation of the mean peak average frequency may be as high as 47% of the mean) and temporal pattern (irregular intersyllabic intervals). The abrupt rise to maximum amplitude that is typically featured in the down-pulse is an additional likely contributor to the 'surprise' element of the sound. The relatively low intensity of the defensive sounds of *M. religiosa* is perhaps the single characteristic that argues against the signal's "startle" function.

Both explanations for the mechanism of predator deterrence effected by defensive stridulation may converge. If insect disturbance sounds do indeed mimic the noises generated by snakes, they are mimicking sounds that are themselves characterized by a high degree of randomness, and thus low capacity for specific information content (Young 1991, 2003). This third, hybrid hypothesis may, in fact, best represent the situation in nature, whereby defensive sounds protect by eliciting a startle reaction in a receiver, but exhibit elements of broad homogeneity (e.g., broadbandedness) across taxa and thus form the basis for a web of Batesian mimicry associations (Masters 1980, Young & Brown 1993, Young *et al.* 1999, Montealegre-Z *et al.* 2003). Vibrational movements of the pronotum against the tegmina in *H. epilamproides* generate sounds resembling those of various of the cockroach's mammalian predators and are thus believed to serve a protective function (Guthrie 1966). Adult *M. religiosa* may be one of many insect and noninsect species able to generate a variable and broadband defensive acoustic signal (which may be an honest warning of danger in some taxa, while a bluff in others), the spectral composition of which ensures perception by several phylogenetically disparate predators (Masters 1980).

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References

Alexander R.D. 1960. Sound communication in Orthoptera and Cicadidae, pp.38-92. In: Lanyon W.E., Tavolga W.N. (Eds) *Animal Sounds and Communication*. American Institute of Biological Sciences, Washington.

Beier M. 1968. Mantodea (Fangheuschrecken). *Handbuch der Zoologie* 4: 1-47.

Belwood J.J. 1990. Anti-predator defences and ecology of neotropical forest katydids, especially the Pseudophyllinae, pp.8-26. In: Bailey W.J., Rentz D.C.F. (Eds) *The Tettigoniidae, Biology, Systematics and Evolution*. Crawford House Press, Bathurst.

Bennet-Clark H.C. 1998. Size and scale effects as constraints in insect sound communication. *Philosophical Transactions of the Royal Society of London B Biological Sciences* 353: 407-419.

Bennet-Clark H.C. 1999. Resonators in insect sound production: how insects produce loud pure-tone songs. *Journal of Experimental Biology* 202: 3347-3357.

Carisio L., Palestini C., Rolando A. 2004. Stridulation variability and morphology: an examination in dung beetles of the genus *Trypocopris* (Coleoptera, Geotrupidae). *Population Ecology* 46: 27-37.

Carlberg U. 1989. Defensive stridulation in *Heteropteryx dilatata* Parkinson (Insecta, Phasmida). *Zoologischer Anzeiger* 223: 165-173.

Carpenter D.M. 1921. Experiments on the relative edibility of insects, with special reference to their coloration. *Transactions of the Entomological Society of London* 1921: 1-105.

Chopard L. 1938. La Biologie des Orthoptères. *Encyclopédie entomologique, série A XX*. Paul Lechevalier, Paris.

Coelho J.R. 1998. An acoustical and physiological analysis of buzzing in cicada killer wasps (*Sphecius speciosus*). *Journal of Comparative Physiology A* 183: 745-751.

Coupin H. 1899. Histoire naturelle de la mantis religieuse. *Revue des Sciences (Paris)* 4: 16-19.

Desutter-Grandcolas L. 1998b. First analysis of a disturbance stridulation in crickets, *Brachytrupes tropicus* (Orthoptera: Grylloidea: Gryllidae). *Journal of Insect Behavior* 11: 149-158.

Dufour L. 1841. Recherches anatomiques et physiologiques sur les Orthoptères, et les Hyménoptères et les Neuroptères. Mémoires présentés par divers Savans à l'Académie Royale des Sciences de l'Institut de France, Sciences Mathématiques et Physiques (ou Collection des Mémoires des Savans Etrangers) 7: 265-647.

Dumortier B. 1963. The physical characteristics of sound emissions in Arthropoda, pp.346-373. In: Busnel R.-G. (Ed) *Acoustic Behavior of Animals*. Elsevier, New York.

Dumortier B. 1965. L'émission sonore dans le genre *Gromphadorhina* Brunner (Blattodea, Perisphaeriidae), étude morphologique et biologique. *Bulletin de la Société Zoologique de France* 90: 89-101.

Dunn O.J. 1964. Multiple comparisons using rank sums. *Technometrics* 6: 241-252.

Durrell G. 1956. *My Family and Other Animals*. Rupert Hart-Davis, London.

Edmunds M. 1972. Defensive behaviour in Ghanaian praying mantids. *Zoological Journal of the Linnean Society* 51: 1-32.

Edmunds M. 1976. The defensive behaviour of Ghanaian praying mantids with a discussion of territoriality. *Zoological Journal of the Linnean Society* 58: 1-37.

Edmunds M., Brunner D. 1999. Ethology of defenses against predators, pp.276-299. In: Prete F., Wells H., Wells P.H., Hurd L.E. (Eds) *The Praying Mantids*. Johns Hopkins University Press, Baltimore.

Elsner N., Popov A. 1978. Neuroethology of acoustic communication. *Advances in Insect Physiology* 13: 229-355.

Fabre J.H. 1897. Souvenirs entomologiques (cinquième série): études sur l'instinct et les moeurs des insectes. Librairie ch. Delagrave, Paris.

Fenton M.B., Licht L.E. 1990. Why rattle snake? *Journal of Herpetology* 24: 274-279.

Field L.H., Bailey W.J. 1997. Sound production in primitive Orthoptera from Western Australia: sounds used in defence and social communication in *Ametrus* sp. and *Hadrogryllacris* sp. (Gryllacrididae: Orthoptera). *Journal of Natural History* 31: 1127-1141.

Fullard J.H., Simmons J.A., Saillant P.A. 1994. Jamming bat echolocation—the dogbane tiger moth *Cycnia tenera* times its clicks to the terminal attack calls of the big brown bat *Eptesicus fuscus*. *Journal of Experimental Biology* 194: 285-298.

Goureau C. 1841. Bulletin entomologique. Année 1841. Premier trimestre. Séances de la Société Entomologique de France. *Annales de la Société Entomologique de France* 10: xvii-xviii.

Greene H.W. 1988. Antipredator mechanisms in reptiles, pp.1-152. In: Gans C., Huey R.B. (Eds) *Biology of the Reptilia*. Vol.16. Alan R. Liss, New York.

Gurney A.B. 1951. Praying mantids of the United States, native and introduced. *Annual Report of the Smithsonian Institution* 1950: 339-362.

- Guthrie D.M. 1966. Sound production and reception in a cockroach. *Journal of Experimental Biology* 45: 321-328.
- Haskell P.T. 1961. *Insect Sounds*. Quadrangle Books, Chicago.
- Haskell P.T. 1964. Sound production, pp.563-608. In: Rockstein M. (Ed) *The Physiology of Insecta*. Academic Press, New York.
- Heller K-G. 1996. Unusual abdomino-alary, defensive stridulatory mechanism in the bushcricket *Pantecphylus cerambycinus* (Orthoptera, Tettigoniodea, Pseudophyllidae). *Journal of Morphology* 227: 81-86.
- Holroyd E.M. 1975. The ontogeny and function of the display in the praying mantis, *Mantis religiosa*. M.Sc. Dissertation, University of Toronto.
- Judd W.W. 1950. Further records of the occurrence of the European praying mantis (*Mantis religiosa* L.) in southern Ontario (Orthoptera). *Entomological News* 61: 205-207.
- Klauber L.M. 1956. *Rattlesnakes: their habits, life histories, and influence on mankind*. University of California Press, Berkeley.
- Ladich F. 1999. Did auditory sensitivity and vocalization evolve independently in otophysan fishes? *Brain Behavior and Evolution* 53: 288-304.
- Liske E. 1999. The hierarchical organization of mantid behavior, pp.224-250. In: Prete F., Wells H., Wells P.H., Hurd L.E. (Eds) *The Praying Mantids*. Johns Hopkins University Press, Baltimore.
- Maldonado H. 1970. The deimatic reaction in the praying mantis *Stagmatoptera biocellata*. *Zeitschrift fuer Vergleichende Physiologie* 68: 60-71.
- Masters W.M. 1979. Insect disturbance stridulation: its defensive role. *Behavioral Ecology and Sociobiology* 5: 187-200.
- Masters W.M. 1980. Insect disturbance stridulation: characterization of airborne and vibrational components of the sound. *Journal of Comparative Physiology A* 135: 259-268.
- Meyer J., Elsner N. 1996. How well are frequency sensitivities of grasshopper ears tuned to species-specific song spectra? *Journal of Experimental Biology* 199: 1631-1642.
- Montealegre-Z F., Morris G.K. 1999. Sound and systematics of some Tettigoniidae from Colombia and Ecuador, Part I. Pseudophyllinae. *Journal of Orthoptera Research* 9: 163-237.
- Montealegre-Z F., Guerra P.A., Morris G.K. 2003. *Panoploscelis specularis* (Orthoptera: Tettigoniidae: Pseudophyllinae): extraordinary female sound generator, male description, male protest and calling signals. *Journal of Orthoptera Research* 12: 173-181.
- Morris G.K. 1999. Song in arthropods, pp.508-517. In: Davey K.G. (Ed) *Encyclopedia of Reproduction Vol. 4*. Academic Press, New York.
- Naskrecki P. 2000. The phylogeny of katydids (Insecta: Orthoptera: Tettigoniidae) and the evolution of their acoustic behavior. Ph.D. Dissertation, University of Connecticut.
- Nelson M.C. 1979. Sound production in the cockroach *Gromphadorhina portentosa*: the sound-producing apparatus. *Journal of Comparative Physiology* 132: 27-38.
- Nelson M.C., Fraser J. 1980. Sound production in the cockroach *Gromphadorhina portentosa*: evidence for communication by hissing. *Behavioral Ecology and Sociobiology* 6: 305-314.
- Owings D.H., Rowe M.P., Rundus A.S. 2002. The rattling sound of rattlesnakes (*Crotalus viridis*) as a communicative resource for ground squirrels (*Spermophilus beecheyi*) and burrowing owls (*Athene cunicularia*). *Journal of Comparative Psychology* 116: 197-205.
- Preston-Mafham K. 1990. *Grasshoppers and Mantids of the World*. Blandford, London.
- Prestwich K.N., Lenihan M.K., Martin D.M. 2000. The control of the carrier frequency in cricket calls: a refutation of the subalar-tegmina resonance/auditory feedback model. *Journal of Experimental Biology* 203: 585-596.
- Ramsay G.W. 1990. *Mantodea (Insecta), with a review of aspects of functional morphology and biology*. DSIR Publishing, Wellington.
- Riede K., Kroker A. 1995. Bioacoustics and niche differentiation in two cicada species from Bornean lowland forest. *Zoologischer Anzeiger* 234: 43-51.
- Robinson M.H. 1969a. Defenses against visually hunting predators, pp.225-259. In: Dobzhansky T., Hecht M.T., Steere W.C. (Eds) *Evolutionary Biology* 3. Meredith Corporation, New York.
- Robinson M.H. 1969b. The defensive behaviour of some orthopteroid insects from Panama. *Transactions of the Royal Entomological Society of London* 121: 281-303.
- Roeder K.D. 1975. Neural factors and evitability in insect behavior. *Journal of Experimental Zoology* 194: 75-88.
- Römer H. 1993. Environmental and biological constraints for the evolution of long range signalling and hearing in acoustic insects. *Philosophical Transactions of the Royal Society of London, B. Biological Sciences* 340: 179-185.
- Rowe M.P., Coss R.G., Owings D.H. 1986. Rattlesnake rattles and burrowing owl hisses: a case of acoustic Batesian mimicry. *Ethology* 72: 53-71.
- Roy R. 1999. Morphology and taxonomy, pp.19-40. In: Prete F., Wells H., Wells P.H., Hurd L.E. (Eds) *The Praying Mantids*. Johns Hopkins University Press, Baltimore.
- Schal C., Fraser J., Bell W.J. 1982. Disturbance stridulation and chemical defence in nymphs of the tropical cockroach *Megaloblatta blaberoides*. *Journal of Insect Physiology* 28: 541-552.
- Schilman P.E., Lazzari C.R., Manrique G. 2001. Comparison of disturbance stridulations in five species of triatominae bugs. *Acta Tropica* 79: 171-178.
- Schmidt G.H., Stelzer R. 2004. Characterization of male structures, and the stridulatory organs of *Pantecphylus cerambycinus* (Ensifera: Tettigoniodea: Pseudophyllidae). *Entomologia Generalis* 27: 143-154.
- Schmidt J.M. 1994. Encounters between adult spined assassin bugs, *Sinea diadema* (F) (Hemiptera, Reduviidae)—the occurrence and consequences of stridulation. *Journal of Insect Behavior* 7: 811-828.
- Schmitt M., Traue D. 1990. Morphological and bioacoustic aspects of stridulation in Criocerinae (Coleoptera, Chrysomelidae). *Zoologischer Anzeiger* 225: 225-240.
- Sen Sarma M., Fuchs S., Werber C., Tautz R. 2002. Worker piping triggers hissing for coordinated colony defence in the dwarf honeybee *Apis florea*. *Zoology* 105: 215-223.
- Shelford R. 1903. Bionomical notes on some Bornean Mantidae. *Zoologist* 4: 293-304.
- Simmons R.B., Connor W.E. 1996. Ultrasonic signals in the defense and courtship of *Euchaetes egle* Drury and *E. bolteri* Stretch (Lepidoptera: Arctiidae). *Journal of Insect Behavior* 9: 909-919.
- Simonot-Revol 1891. De la phonation chez la *Mantis religiosa*. *Revue d'Entomologie* 10: 11-13, 128, 129.
- Slingerland M.V. 1900. A new beneficial insect in America. The common European praying mantis, *Mantis religiosa* Linnaeus. Order Orthoptera; family Mantidae. Cornell University Agricultural Experiment Station Bulletin 185: 35-47.
- Stäger R. 1928. *Mantis religiosa* L. als Musikerin. *Zeitschrift für wissenschaftl. Insektenbiologie* 23: 162-164.
- Tschuch G., Brothers D.J. 1999. Modeling vibration and sound production in insects with nonresonant stridulatory organs. *Journal of the Acoustical Society of America* 106: 3706-3710.
- Varley G.C. 1939. Frightening attitudes and floral simulation in praying mantids. *Proceedings of the Royal Entomological Society of London Series A General Entomology* 14: 91-96.
- Vickery V.R., Kevan D.K.M. 1983. A monograph of the Orthopteroid insects of Canada and adjacent regions. Lyman Entomological Museum, Memoir 13 Vol. 1, Ste Anne de Bellevue, Que.
- Vickery V.R., Kevan D.K.M. 1985. *The Grasshoppers, Crickets, and Related Insects of Canada and Adjacent Regions*. Agriculture Canada publication 1777.
- Willey A. 1918. Popular and practical entomology. *Insect tropisms*. Canadian Entomologist 50: 357-360.
- Williams C.E. 1904. Notes on the life history of *Gongylus gongyloides*, a mantis of the tribe Empusides and a floral simulator. *Transactions of the Entomological Society of London* 1904: 125-137.
- Wood-Mason J. 1878. On the presence of a stridulating apparatus in certain Mantidae. *Transactions of the Entomological Society of London* 1878: 263-267.
- Wood-Mason J. 1879. Exhibitions, &c. *Transactions of the Entomological Society of London* 1879: iii-v.
- Yager D.D. 1999. Hearing, pp.93-113. In: Prete F.R., Wells H., Wells P.H., Hurd L.E. (Eds) *The Praying Mantids*. Johns Hopkins University Press, Baltimore.
- Yager D.D., Hoy R.R. 1986. The cyclopean ear: a new sense for the praying mantis. *Science* 231: 727-729.

- Yager D.D., Hoy R.R. 1987. The midline metathoracic ear of the praying mantis, *Mantis religiosa*. Cell and Tissue Research 250: 531-541.
- Yager D.D., May M.L., Fenton M.B. 1990. Ultrasound-triggered, flight-gated evasive maneuvers in the praying mantis *Parasphendale agrionina*. II. Tethered flight. Journal of Experimental Biology 152: 41-58.
- Young B.A. 1991. Morphological basis of "growling" in the king cobra, *Ophiophagus hannah*. Journal of Experimental Zoology 260: 275-287.
- Young B.A. 2003. Snake bioacoustics: toward a richer understanding of the behavioral ecology of snakes. Quarterly Review of Biology 78: 303-325.
- Young B.A., Brown I.P. 1993. On the acoustic profile of the rattlesnake rattle. Amphibia-Reptilia 14: 373-380.
- Young B.A., Brown I.P. 1995. The physical basis of the rattling sound in the rattlesnake *Crotalus viridis oreganus*. Journal of Herpetology 29: 80-85.
- Young B.A., Nejman N., Meltzer K., Marvin J. 1999. The mechanics of sound production in the puff adder *Bitis arietans* (Serpentes: Viperidae) and the information content of the snake hiss. Journal of Experimental Biology 202: 2281-2289.