

Seismic signals in a courting male jumping spider (Araneae: Salticidae)

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Summary

Visual displays in jumping spiders have long been known to be among the most elaborate animal communication behaviours. We now show that one species, *Habronattus dossenus*, also exhibits an unprecedented complexity of signalling behaviour in the vibratory (seismic) modality. We videotaped courtship behaviour and used laser vibrometry to record seismic signals and observed that each prominent visual signal is accompanied by a subsequent seismic component. Three broad categories of seismic signals were observed ('thumps', 'scrapes' and 'buzzes'). To further characterize these signals we used synchronous high-speed video and laser vibrometry and observed that only one seismic signal component was produced concurrently with visual signals. We examined the mechanisms by which seismic signals are produced through a series of signal

ablation experiments. Preventing abdominal movements effectively 'silenced' seismic signals but did not affect any visual component of courtship behaviour. Preventing direct abdominal contact with the cephalothorax, while still allowing abdominal movement, only silenced thump and scrape signals but not buzz signals. Therefore, although there is a precise temporal coordination of visual and seismic signals, this is not due to a common production mechanism. Seismic signals are produced independently of visual signals, and at least three independent mechanisms are used to produce individual seismic signal components.

Key words: seismic signal, courtship, behaviour, visual signal, thump, scrape, buzz, signal ablation, jumping spider, *Habronattus dossenus*, vibration.

Introduction

In the study of animal signals, spiders have emerged as a classic example of signalling using substrate-propagated vibrations (Barth, 1998). The vibrations propagated through the delicate webs of orb-weaving spiders are clear examples of signalling through vibrations (Barth, 1998; Finck, 1981; Frohlich and Buskirk, 1982; Klarner and Barth, 1982; Landolfi and Barth, 1996; Masters, 1984; Masters and Markl, 1981; Vollrath, 1979), but the majority of spiders may also use substrate-propagated vibrations in such varied substrates as water, soil, leaf litter or plants (Barth, 1985, 1998, 2002; Bleckmann and Barth, 1984; Bristowe, 1929; Fernandezmontraveta and Schmitt, 1994; Rovner, 1968; Stratton and Uetz, 1983; Uetz and Stratton, 1982). Three types of substrate-borne vibration-production mechanisms have been described in spiders: percussion, stridulation and vibration (tremulation; Uetz and Stratton, 1982). Percussion is produced by the drumming of body parts against the substrate and has been described in a variety of species (Dierkes and Barth, 1995; Stratton, 1983; Uetz and Stratton, 1982). Stridulation occurs by the rubbing of two rigid body structures relative to each other (Dumortier, 1963) and seems to occur commonly in spiders (Legendre, 1963), particularly in wolf spiders (Family:

Lycosidae; Rovner, 1975; Stratton and Uetz, 1983; Uetz and Stratton, 1982). Tremulation (Morris, 1980) is the third method of substrate-borne vibration production found in spiders (Barth, 2002; Dierkes and Barth, 1995; Rovner, 1980; Uetz and Stratton, 1982) and occurs by the oscillation of body parts, without a frequency multiplier (i.e. stridulation), coupled to the substratum, usually by adhesive hairs on the tips of one or more of the legs. All of these mechanisms can be used to produce substrate-borne (seismic) signals (Aicher et al., 1983; Aicher and Tautz, 1990; Narins, 1990).

Jumping spiders (Family: Salticidae) are unique among spiders in that they are visual 'specialists', having two large, prominent frontal eyes that are specialized for high spatial resolution, as befits their predatory habits as stalker-hunters (Forster, 1982a; Land, 1985). Not surprisingly, vision also plays a prominent role in their signalling behaviour. Males, unlike females, have evolved conspicuously ornamented and coloured appendages that they wave like semaphores during courtship, producing stereotyped, species-specific visual displays that unfold over periods of seconds to minutes (Crane, 1949; Forster, 1982b; Jackson, 1982). These displays function in species isolation, species recognition and female

choice (Clark and Morjan, 2001; Clark and Uetz, 1993; Jackson, 1982) and are specific enough to be useful as taxonomic characters (Richman, 1982). These displays are textbook examples of visual communication (Bradbury and Vehrencamp, 1998). While visual signals are well established, seismic signal production by stridulation (Edwards, 1981; Gwynne and Dadour, 1985; Maddison and Stratton, 1988), percussion (Noordam, 2002) and tremulation (Jackson, 1977, 1982) has been proposed in a few species of jumping spiders.

Within the jumping spiders, members of the genus *Habronattus* are known for extraordinary diversity – especially of the complex, colourful ornaments used in their multifaceted visual displays (Griswold, 1987; Maddison and McMahon, 2000; Peckham and Peckham, 1889, 1890). Over 100 species have been described, with most of them occurring in North America, especially in arid regions of the southwest. Among these species, many exhibit striking morphological and geographical variation (Maddison and McMahon, 2000; Masta, 2000; Masta and Maddison, 2002). We focused on one particular species that has multiple, complex visual ornaments: *Habronattus dossenus*. We recorded male courtship behaviour in *H. dossenus* by using video and laser vibrometry and found that the complex visual displays of signalling males represent only one component of an extremely elaborate multi-modal display. Male *H. dossenus* signal to prospective mates using a repertoire of seismic signals coordinated with specific visual signals. In order to investigate these phenomena, we (1) characterized seismic and visual signals in detail using synchronous high-speed video and laser vibrometry and (2) examined possible seismic signal production mechanisms by performing several experiments where we attempted to manipulate seismic signals. We manipulated abdominal (opisthosoma) movements and contact with the cephalothorax (prosoma) because previous experiments in another *Habronattus* species suggested that seismic signal production originated there (Maddison and Stratton, 1988).

Materials and methods

Courtship behaviour of H. dossenus

Spiders

Male and female *Habronattus dossenus* Griswold were collected in the field between July and September in 2000 and 2001 from the Atascosa Mountains, Coronado National Park, southwestern Arizona (Santa Cruz County). Animals were collected predominantly on leaf litter, rocks or sand. Animals were housed individually and kept in the lab on a 12 h:12 h light:dark cycle. Weekly, spiders were fed a diet of fruit flies (*Drosophila melanogaster*) and crickets (*Acheta domesticus*).

Recording procedures

We anaesthetized female *H. dossenus* with CO₂ and tethered them to a wire with low melting point wax. We held females in place with a micromanipulator on a substrate of stretched

nylon fabric (25 cm×30 cm). Males were then dropped onto this substrate 15 cm from the female and allowed to court freely. Females were rotated to face the male until he oriented to her; recordings began when males approached females. We recorded substrate vibrations produced during courtship using a laser Doppler vibrometer (LDV; Polytec OFV 3001 controller, OFV 511 sensor head; Waldbronn, Germany) (Michelsen et al., 1982). Laser Doppler vibrometry is a non-contact method of recording vibrations that measures the velocity of a moving surface by detecting the Doppler shift of a reflected laser beam. Pieces of reflective tape (approximately 1 mm²) were attached to the underside of the courtship substrate 2 mm from the female to serve as measurement points for the LDV. The LDV signal was synchronized with two concurrent methods of video recording: (1) the LDV signal was recorded on the audio track during standard video taping of courtship behaviour (Navitar Zoom 7000 lens; Panasonic GP-KR222; Sony DVCAM DSR-20 digital VCR; 44.1 kHz audio sampling rate) or (2) the LDV signal was digitized (PCI-6023E; National Instruments, Austin, TX, USA; 10 kHz sampling rate) simultaneously with the capture of digital high-speed video (500 frames s⁻¹; PCI 1000; RedLake Motionscope, San Diego, CA, USA; Nieh and Tautz, 2000), using Midas software (Xcitex, Cambridge, MA USA). All recordings were made on a vibration-isolated table. In some recordings, we also captured air-borne sound on a second channel using a probe microphone (B&K Type 4182, B&K Nexus amplifier; Nærum, Denmark).

Sound and video analysis

Complete courtships of 20 different males were recorded. The same tethered female was used for all recordings. Examples were selected for detailed analysis. Body movements were measured frame-by-frame from digital high-speed video using Midas software. We calibrated absolute distances by photographing a 1 mm² grid before each recording. Power spectra of vibratory signals were calculated using Matlab software (The Mathworks, Natick, MA, USA). Spectrograms were made using Canary (Cornell University, Lab of Ornithology).

Seismic signal production mechanisms of H. dossenus

Experimental manipulations

For the signal manipulation experiments, the arena substrate floor for courtship was a sheet of graph paper attached to a square cardboard frame (60 cm×45 cm). Females were tethered as above, and the male's seismic signals recorded using a piezo-electric sensor placed directly underneath the tethered female. We calibrated the response of the piezo-electric sensor using a vibration source (B&K Type 4810 Mini-shaker) and LDV (OFV 3001 controller, OFV 511 sensor head). Although low-frequency responses (<150 Hz) were relatively attenuated by the piezoelectric sensor, the male's signals were not significantly altered (data not shown). All experiments were conducted in a sound-attenuated chamber. Seismic signals were amplified (Nikko NA790) and recorded on the audio track of a

video recording as above (44.1 kHz audio sampling rate). All recordings were also videotaped (Navitar Zoom 7000 lens; Panasonic GP-KR222; Sony DVCAM DSR-20 digital VCR). Recordings of signals were made from each male prior to experimental manipulation. Classical spider anatomy has recognized two body segments in spiders: the prosoma and opisthosoma (Barth, 2002; Foelix, 1996). We use the alternative nomenclature, cephalothorax (prosoma) and abdomen (opisthosoma) to describe the spider's body segments (Maddison and Stratton, 1988). We manipulated males by (1) preventing abdominal movements by attaching the abdomen to the cephalothorax using wax (Kerr Sticky Wax; Cenco Scientific, Chicago, IL, USA; Fig. 3) and (2) preventing contact between the cephalothorax and abdomen by attaching a small piece of aluminium foil to the cephalothorax with wax; this formed a flap that could be inserted at the junction between the abdomen and the cephalothorax (Fig. 5). To ensure that these treatments did not affect normal locomotory activities, we waited two days following these manipulations and observed whether or not the spiders were able to successfully capture prey. Both manipulations were reversible. Two days following reversal by removing the wax or the foil flap, we recorded courtship signals again. We used only males that were able to capture prey during both intervals.

Power spectra analysis

Within a treatment set (control, experimental treatment, recovery) from an individual animal, individual signals (see below) were identified using videotaped data, and a random selection of each seismic signal type acquired. The power spectra of the noise floor, acquired before the start of every recording, was subtracted using Matlab software. Power spectra of different signals were then calculated and averaged using Matlab. This shows how, within an individual, the entire power spectrum of a signal changes according to experimental treatment.

Statistical analysis

For each signal, peak intensities were recorded. For thumps, peak intensities below and above 500 Hz were recorded. For scrapes, the peak intensity was recorded. For buzzes, the intensities of the first three harmonics were recorded. Within treatment sets for each individual, intensities were normalized to the highest intensity produced for all of the signal components. Normalized intensities were then averaged and the relative dB difference between the treatments calculated. The normalized intensities for different individuals were then pooled into their treatment categories and averaged. Differences between treatments were tested for significance ($P < 0.05$) using a repeated-measures analysis of variance (ANOVA) procedure and a *post-hoc* Tukey test with Bonferroni corrections.

Scanning electron microscopy (SEM)

Specimens were fixed, dried and gold coated and then viewed with a Philips SEM 505 microscope.

Results

Courtship behaviour of *H. dosseus*

We divided courtship into four distinct phases based on video data (Fig. 1). Behaviourally, phase 1 consists of sidling movements in which the male approaches in a typical salticid 'zigzag' visual display (Forster, 1982b). During this approach, the male waves his forelegs and spreads his pedipalps in a stereotyped fashion. Phase 2 occurs when the male comes to within approximately one body length (5–8 mm) of the female and produces rapid bouts of visible 'downbeat' gestures as he settles into a typical courtship posture (Fig. 2i). Phase 3 consists of multiple bouts of prolonged signalling. In phase 4, the male attempts to mount the female. Seismic displays occur only in phases 2 to 4 (Fig. 1). Phase 2 is associated with a rapid bout of thumps (see below). Phase 3 consists of multiple bouts of signalling (thumps, buzzes and scrapes; see below). In phase 4, the male accelerates the rate of signals, combining previously separate signals (thumps and buzzes; see below). At least three signal types (thumps, scrapes and buzzes; Fig. 2iii,iv) were evident in all complete courtships, each associated with characteristic stereotyped body postures and unique foreleg movements (Fig. 2i,ii), abdominal movements (Fig. 2i), temporal characteristics (Fig. 2iii) and power spectra (Fig. 2iv). Seismic and visual signal components were only produced during male and female interactions and never in any other context. Analysis of video recordings showed that seismic signals coincide with stereotyped movements of the abdomen and forelegs and both define and account for the three signals described below (Fig. 2).

Thumps

Thumps (Fig. 2A) occur at the beginning of a sequence of seismic signals. They can precede a sequence of scrape groups or buzzes in phase 3 of courtship (Fig. 2A; see below) or occur simultaneously with buzzes in phase 4 (Fig. 1). The front legs and abdomen both produce the thump (Fig. 2A). First, the forelegs are raised high above the body and are then rapidly slapped down onto the substrate (1–2 in Fig. 2A), producing a percussive impulse (2 in Fig. 2A). This percussive component was the only display that produced a detectable air-borne component (data not shown). Approximately 8 ms later, the forelegs return to a nearly vertical position (2–3 in Fig. 2A) and the abdomen is pulled back and released (4–5 in Fig. 2A), causing it to 'ring' at a frequency of 58.3 ± 7.5 Hz (mean \pm s.d., $N = 5$; Fig. 2Ai). This movement produces a brief, high-intensity broadband signal (Fig. 2Aiv). Movements of the forelegs and abdomen are highly coordinated, with delays of 86.1 ± 32.0 ms ($N = 27$) for lone thumps and 46.0 ± 8.0 ms ($N = 30$) for thumps preceding buzzes. Both of these categories of thumps also differ in duration and envelope shape (data not shown). Thumps consist of unique foreleg movements (Fig. 2Aii) and two seismic components: a percussive component caused by the front legs contacting the substrate and a more-intense component caused by the oscillation of the abdomen (Fig. 2Aiv).

Scrapes

Scrapes (Fig. 2B) are emitted in groups lasting 5.3 ± 1.1 s ($N=10$) (Sc G in Fig. 1C). Within these groups, scrapes occur at a frequency of 5.7 ± 1.2 Hz ($N=15$ scrape groups; Fig. 2Bi). One to four scrape groups occur between thumps and these occur only in phase 3 of courtship (Fig. 1). Individual scrapes (Sc in Fig. 1C) are associated with movements of the forelegs and abdomen (Fig. 2Bi). An up-and-down movement of the foreleg tips (2–3 in Fig. 2B) is followed by a dorso-ventral oscillation of the abdomen (1–2 in Fig. 2B). This ‘rocking motion’ produces an underlying low-frequency oscillation (5.7 Hz) that is evident in the oscillogram (Fig. 2Biii). Abdominal and foreleg movements are highly coordinated, with

delays of 32.3 ± 7.0 ms ($N=409$). In adjacent scrape groups, the forelegs alternate coming together and moving apart laterally. Two types of movements can occur between scrape groups: (1) when scrape groups follow thumps, the 3rd legs are repositioned against the body as the male moves forward incrementally, and (2) when scrape groups precede a thump, the pedipalps are moved rapidly up and down prior to the thump. Individual scrape seismic signals are produced only during abdominal movements (Fig. 2B) and not during characteristic foreleg movements (Fig. 2Bii). Within groups, individual seismic scrapes are short, broadband signals (Fig. 2Biv). The frequency of abdominal movement is much lower than the frequency of vibrational signal produced (Fig. 2Bi,iv).

Buzzes

Buzzes (Fig. 2C) occur alone in phase 3 of courtship or simultaneously with thumps in phase 4 (Fig. 1). Buzzes in phase 3 are always preceded by 2–5 thumps. The number of thumps occurring increases linearly as courtship progresses (Fig. 1). Both abdominal and leg movements accompany the signal. The front legs come down in a slow continuous movement (1–2 in Fig. 2C), while the abdomen produces a sustained, rapid, low-amplitude oscillation at a frequency of 65.0 Hz (Fig. 2C). Abdominal movements are precisely synchronized with the vibratory signal, while distinctive foreleg movements (Fig. 2Cii) occur at variable delays (180 ± 644 ms, $N=14$; Fig. 2C). Buzz seismic signals are long in duration, with a fundamental frequency of 65.0 ± 2.9 Hz ($N=12$) plus higher harmonics (Fig. 2Civ). Frequencies of seismic buzzes are temperature dependent (data not shown). Abdominal oscillations are at the same 65 Hz frequency as the fundamental frequency of the buzz seismic signal (Fig. 2C).

Seismic signal production mechanisms of *H. dossenus*

Experimental manipulations

Abdominal movement. Analysis of high-speed videos, along with observations suggesting that abdominal movements are not visible to a female while the male is courting, suggests that most seismic signals are produced by abdominal movements and not by movements of the legs. To investigate whether seismic signals are produced by any of the observed body movements, we performed a series of experiments where we tried to eliminate signals. We did this by immobilizing the abdomens of males by fixing them with wax to the cephalothorax (Fig. 3). This

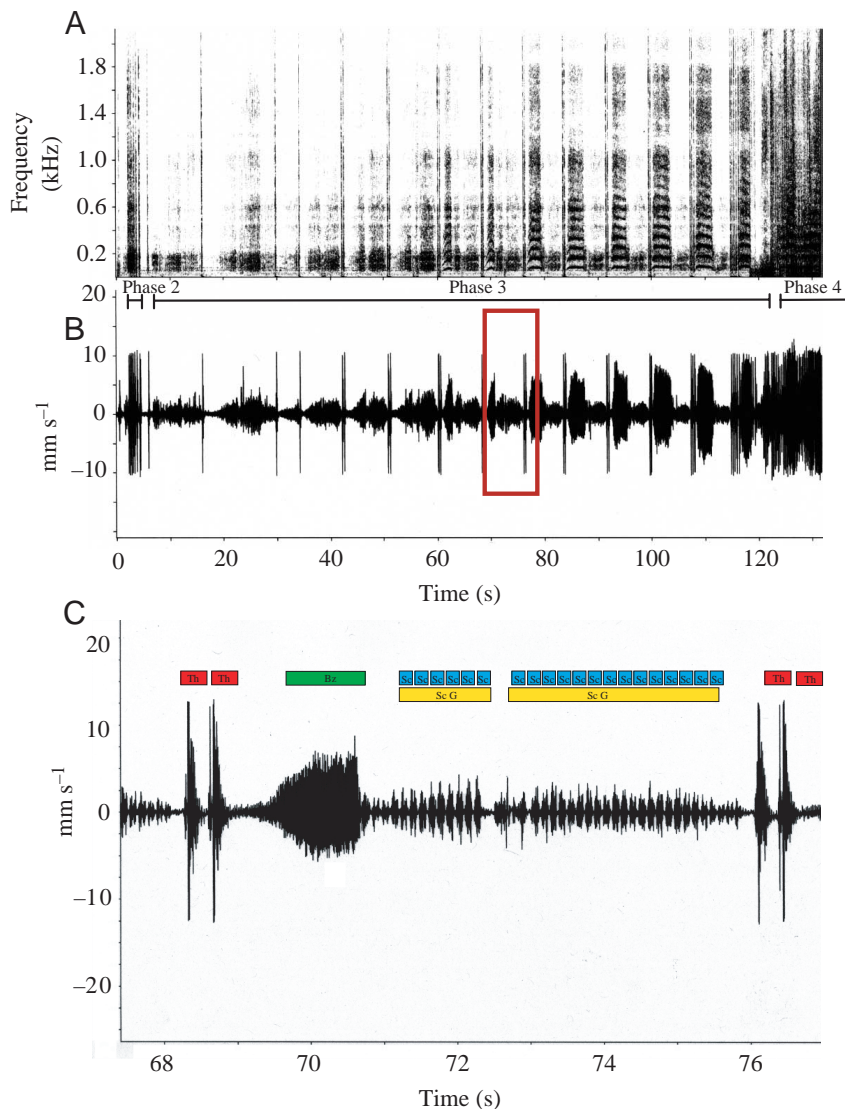


Fig. 1. Seismic signals of courting male jumping spiders. (A) Sonogram of a seismic signal. (B) Oscillogram of seismic signals. Courtship can be divided into four distinct phases, with seismic signals occurring in phases 2–4. (C) Detail of oscillogram marked by the box in B. All three types of seismic signals can be observed: thumps [Th (red)], buzzes [Bz (green)] and scrapes [Sc (blue)]. Individual scrapes occur in groups consisting of multiple repeated scrapes [Sc G (yellow)]. Recordings made using a laser Doppler vibrometer.

treatment was fully reversible. Males were recorded prior to treatment, then with abdomen immobilized and finally after removal of the wax. We could readily identify the occurrence of each signal type by the stereotypic leg movements and postures characteristic of each signal from videotapes (Fig. 2ii). Only the abdominal and not the weak percussive component of the thump was analyzed (Fig. 2A). All three seismic signals were greatly attenuated when the abdomen was immobilized (Figs 3, 4). All frequencies were attenuated in all signal types (Fig. 3). Experimental treatments were significantly different ($P < 0.001$) from both control and recovery treatments (Fig. 4). All signals recovered following removal of the wax, and no significant differences were observed between the control and recovery treatments (Fig. 4). Thus, abdominal movements are necessary for seismic signalling.

Abdomen–cephalothorax contact. Observations using synchronous high-speed video and vibrational recordings revealed that the power spectrum of a buzz exactly matched the oscillation frequency of the abdomen, while the power spectra of thumps and scrapes included much higher frequencies than the oscillation frequency of the abdomen. This hinted that buzz, scrape and thump signals are produced by different mechanisms. Hence, in a second set of experiments, we prevented direct contact between the cephalothorax and abdomen but did not prevent abdominal movements (Fig. 5). We prevented abdomen–cephalothorax contact by placing a small barrier of aluminium foil between the cephalothorax and abdomen. Recovery treatments consisted of removing the barrier (Fig. 5). Buzzes were unaffected at all frequencies (Figs 5A, 6C); no significant differences were observed between the control, experimental

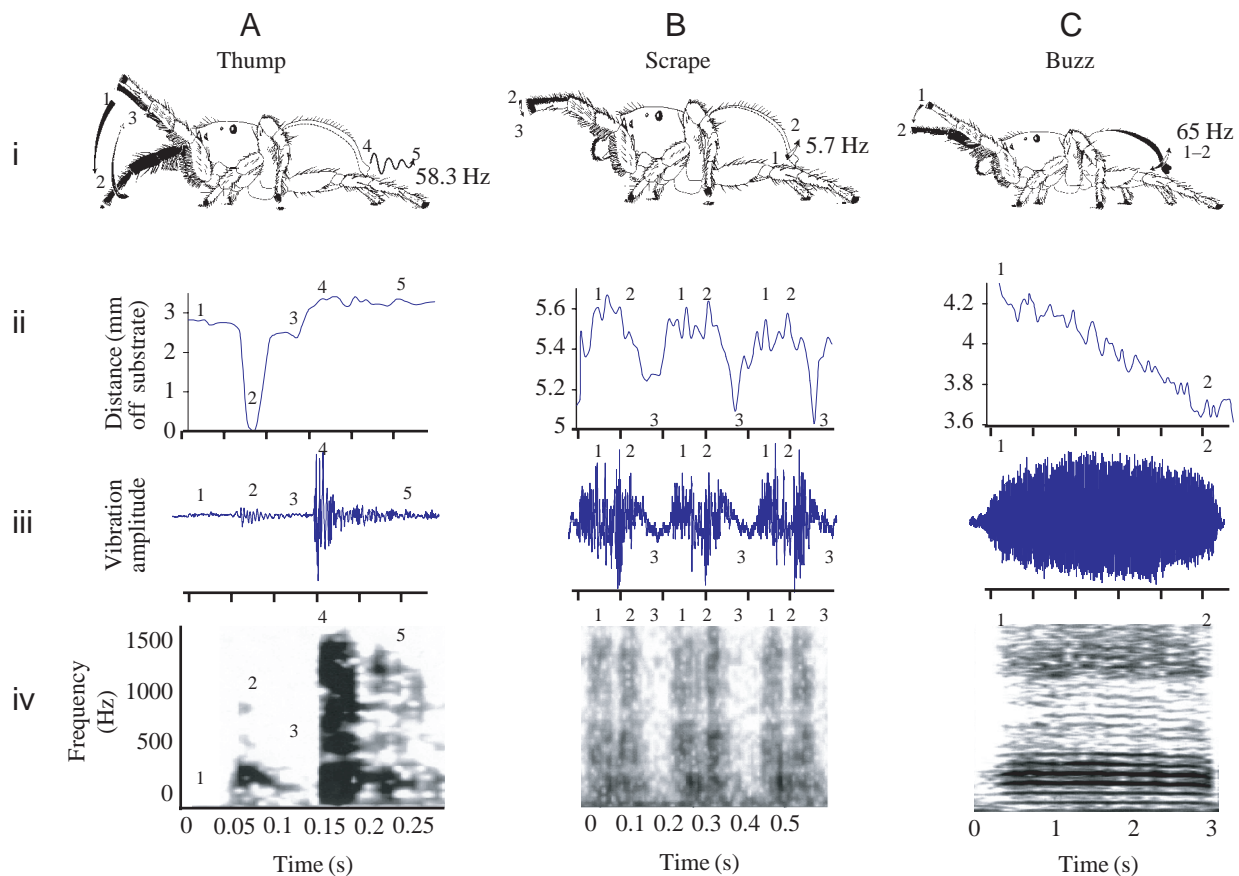


Fig. 2. Types of seismic signals. Top panels (i) show body positions, with numbers (1–5) illustrating movements of the forelegs and abdomen. Middle panels show (ii) the position of one of the forelegs (mm above the substrate) and (iii) the oscillograms of the seismic signals. Bottom panels (iv) show the frequency characteristics of the seismic signals. Panels ii–iv are shown in the same time scale, with numbers (1–5) corresponding to the body movements illustrated in panel i. (A) Thump signal. Front legs come down (1–2), contact the substrate and quickly move back up (2–3). Shortly afterwards the abdomen is pulled back and released, and the abdomen ‘rings’ at 58.3 Hz (4–5). Thumps are broadband signals with peak frequencies at 203 Hz and 1203 Hz. Production of signal corresponds with the percussive contact of the front legs against the substrate (1–2) and movements of the abdomen (4–5). (B) Scrape signal. Abdomen moves up (1–2) and shortly afterwards the front legs come down (2–3). Scrapes occur in groups with a frequency of 5.7 Hz. Scrapes are broadband signals with peak frequencies at 230 Hz and 550 Hz. Production of seismic signal corresponds to movements of the abdomen. (C) Buzz signal. Front legs come down (1–2) as the abdomen oscillates at 65 Hz (1–2). This signal has a fundamental frequency at 65 Hz with several harmonic frequencies (130 Hz, 195 Hz and 260 Hz). Production of seismic signal corresponds with movements of the front legs and abdomen.

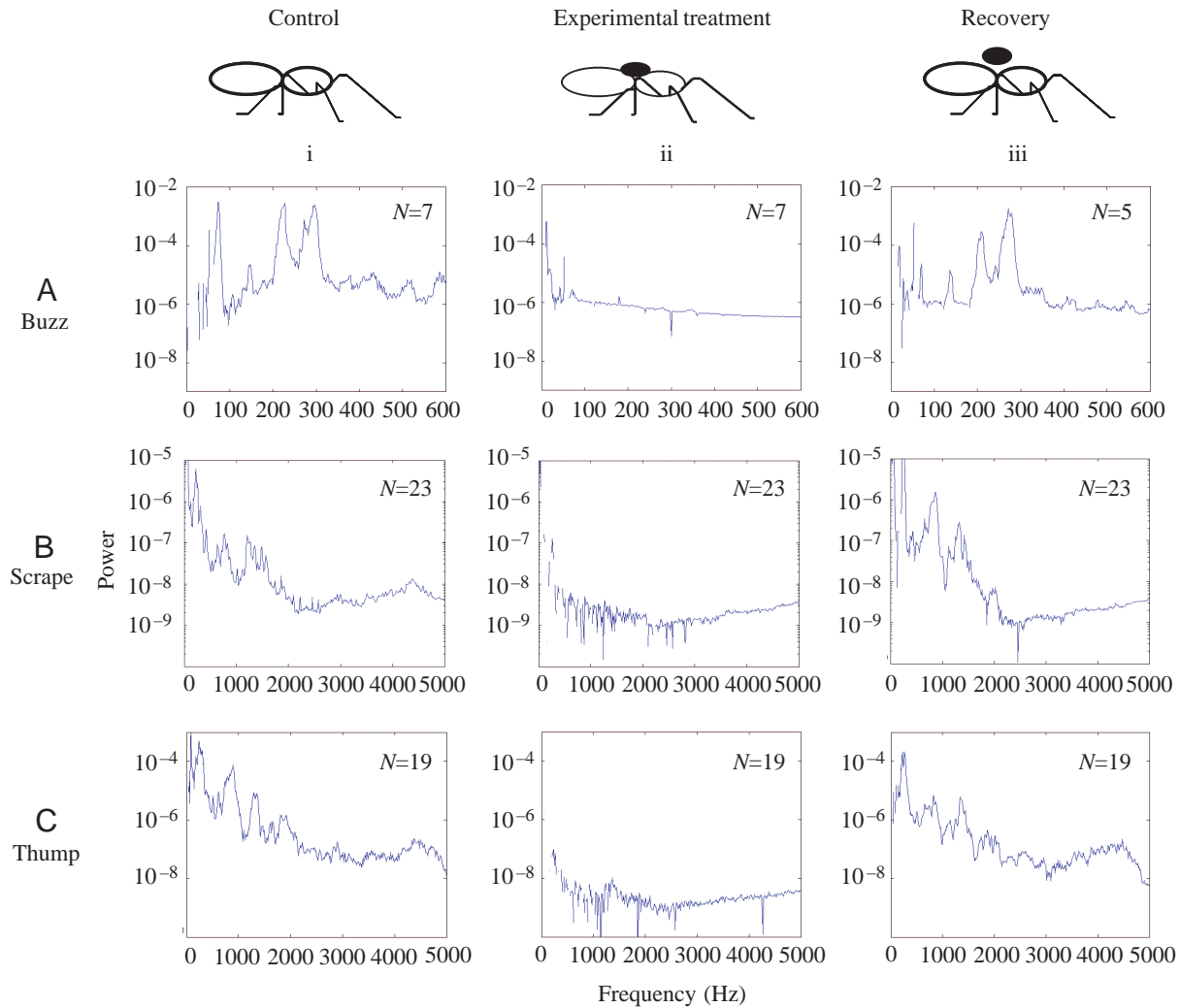
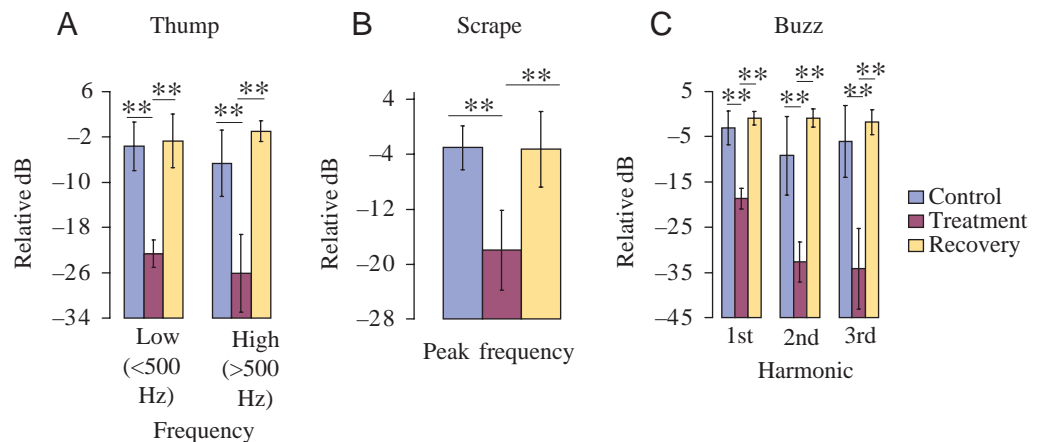


Fig. 3. Effects of male abdominal immobilization on power spectra of different seismic signals. (A) Buzz signal; (B) scrape signal; (C) thump signal. Panels i–iii represent mean power spectra for one individual during the control, experimental and recovery treatments, respectively. Experimental treatment consisted of waxing the cephalothorax to the abdomen, rendering body segments immovable relative to each other. Recovery treatment consisted of removing the wax from the animal.

Fig. 4. Effects of male abdominal immobilization on (A) thump, (B) scrape and (C) buzz seismic signals. Within individuals, peak intensities were normalized to the maximum intensity produced for all of the signal components. Normalized intensities were then averaged, and the relative dB difference between the treatments (control, experimental treatment and recovery) of all the individuals tested \pm S.D. ($N=5$). Experimental treatments attenuated peak frequencies of all signals significantly (** $P<0.001$; Tukey *post-hoc* test with Bonferroni corrections). No significant differences were observed between control and recovery treatments.



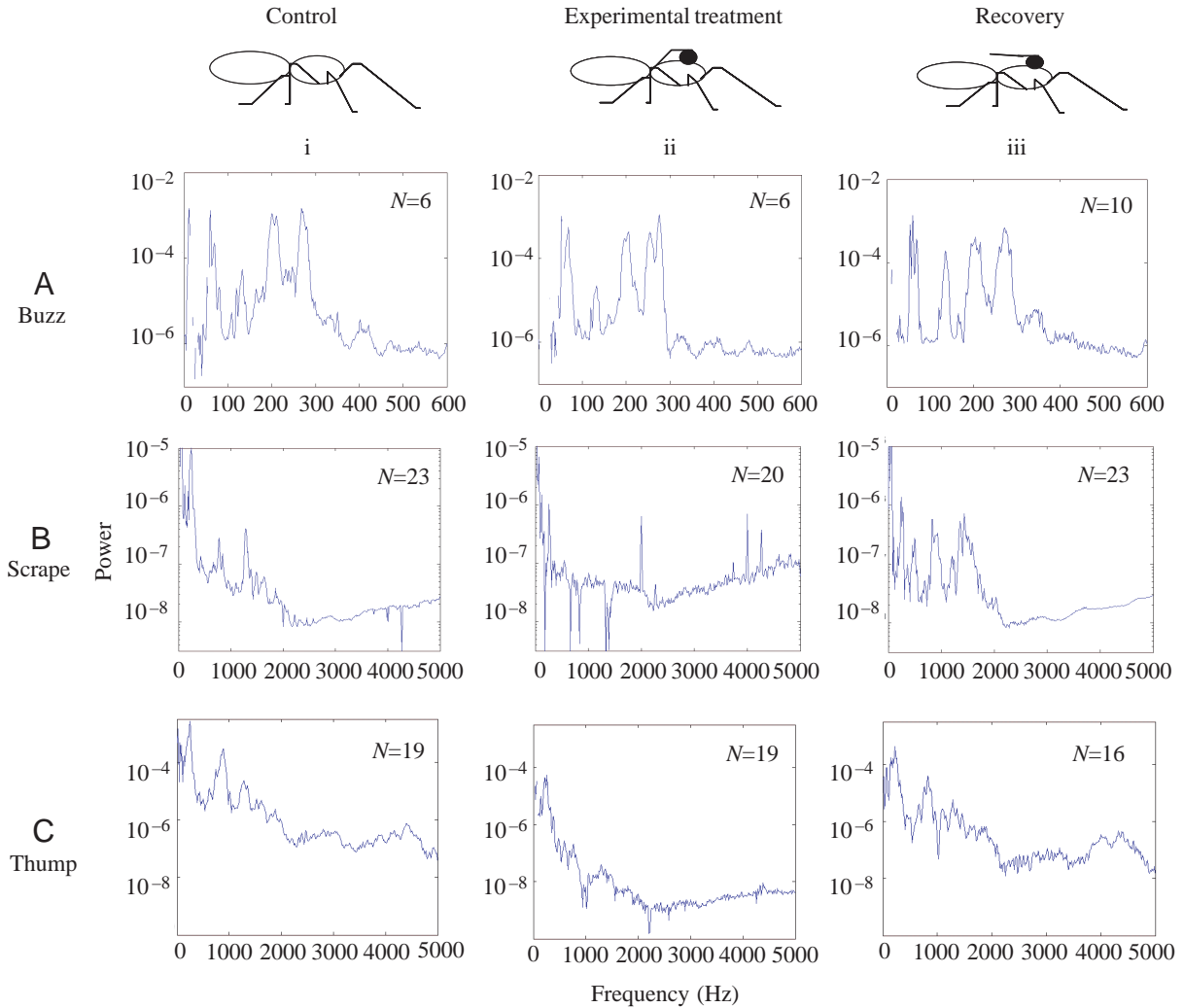
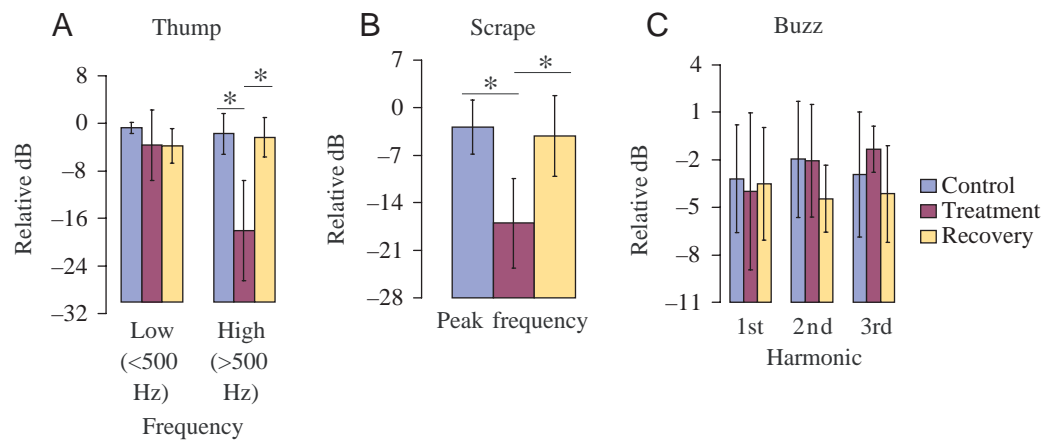


Fig. 5. Effects of preventing male abdominal and cephalothorax contact on the power spectra of different seismic signals. (A) Buzz signal; (B) scrape signal; (C) thump signal. Panels i–iii represent mean power spectra for one individual during the control, experimental and recovery treatments, respectively. Experimental treatment consisted of waxing a piece of flexible foil to the cephalothorax and placing one end of the foil between the cephalothorax and abdomen. Recovery treatment consisted of removing the foil from between the cephalothorax and abdomen.

Fig. 6. Effects of preventing male abdominal and cephalothorax contact on (A) thump, (B) scrape and (C) buzz seismic signals. Within individuals, peak intensities were normalized to the maximum intensity produced for all of the signal components. Normalized intensities were then averaged, and the relative dB difference between the treatments calculated. Graphs show relative dB difference between the treatments (control, experimental treatment and recovery) of all the individuals tested \pm s.d. ($N=5$). Experimental treatments attenuated peak frequencies of scrape and high-frequency (>500 Hz) ranges of thumps significantly ($*P<0.05$; Tukey *post-hoc* test with Bonferonni corrections). No significant differences were observed for buzz and low (<500 Hz)-frequency ranges of thumps. No significant differences were observed between control and recovery treatments.



and recovery treatments (Fig. 6C). Both scrapes and thumps, however, were affected. Scrapes were attenuated significantly at all frequencies (Figs 5B, 6B). For thumps, low-frequency components (<500 Hz) were unaffected but high-frequency components of the thump (>500 Hz) were attenuated (Figs 5C, 6A). Experimental treatments for the scrape and high-frequency components of the thump were significantly different ($P < 0.05$) from both control and recovery treatments (Fig. 6). Control and recovery treatments were similar for all components (Fig. 6). Thus, including the percussive component of thumps, at least three separate mechanisms are used in the production of vibrational signals. Buzz signals are produced by abdominal oscillations and do not require contact between the abdomen and cephalothorax. Scrape and thump signals, on the other hand, require abdomen–cephalothorax contact to produce the high frequencies evident in both of these signals.

Scanning electron microscopy

The observation that high-frequency signal components require direct contact between body parts that move relative to each other suggests a stridulatory mechanism (Dumortier, 1963). Therefore, we examined, using SEM, the cephalothorax–abdomen junction of both male and female *H. dossenus* for evidence of a stridulatory apparatus, as observed in males of another *Habronattus* species (Maddison and

Stratton, 1988). Female *H. dossenus* do not produce seismic signals in any context. SEMs revealed the presence of a file on the male cephalothorax (Fig. 7Bi) but not on the female (Fig. 7Ai). In the apposing abdominal areas, we noted the presence of hardened sclerotized scrapers on the male (Fig. 7Bii) but not on the female (Fig. 7Aii). Thus, scrape and thump signals appear to be produced by stridulation.

Discussion

Our results show that male *H. dossenus* use seismic signals together with their visual displays and that male *H. dossenus* courtship signals consist of complex visual signals co-occurring with multiple seismic signals. Based on high-speed video and synchronous laser vibrometer recordings, seismic signals correspond to movements of the male's abdomen but not of his forelegs (with the exception of the initial percussive component of thumps). Furthermore, preventing abdominal movements by fixing the abdomen relative to the cephalothorax 'silenced' males but did not affect visual or percussive display components. Hence, visual and seismic signals are produced by anatomically different neuromuscular mechanisms, visual signals by muscles controlling foreleg movement and vibratory signals by muscles controlling abdominal movement, yet both signals are coordinated with delays of 30–60 ms for scrapes and thumps and 300 ms for

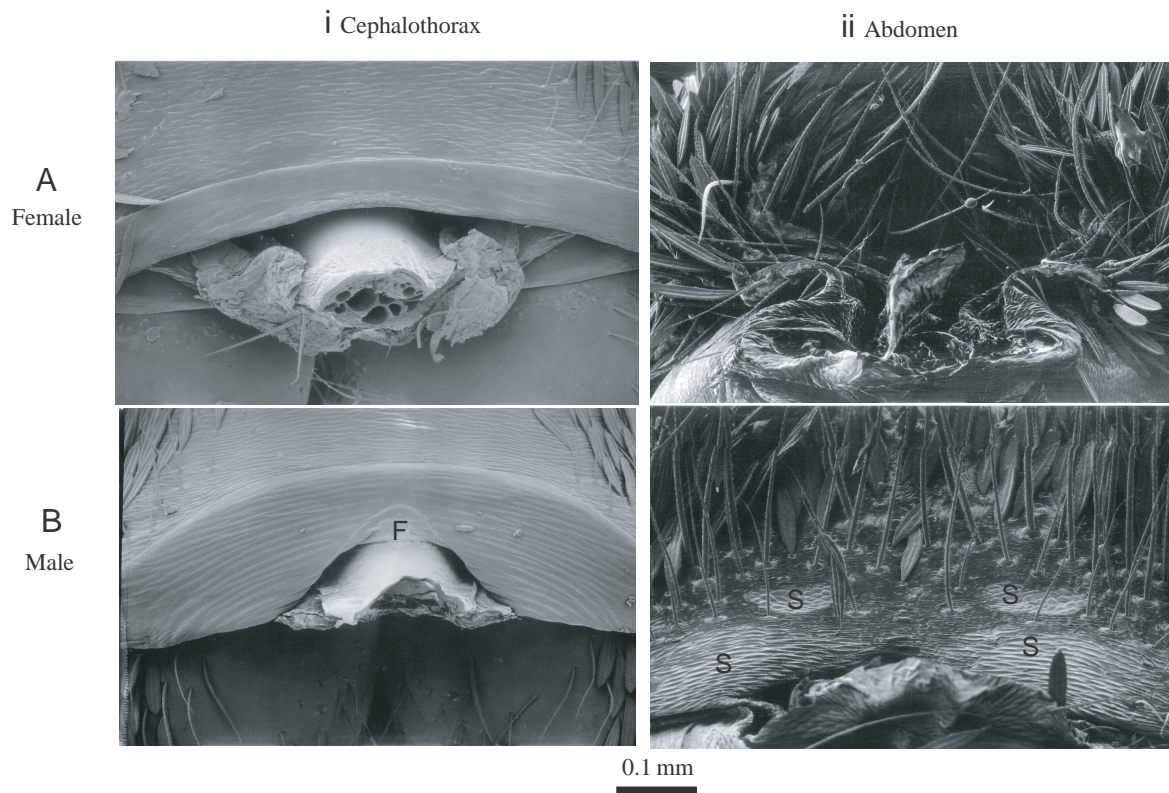


Fig. 7. Scanning electron micrograph (SEM) of cephalothorax and abdomen junction on (A) female and (B) male *H. dossenus*. (i) SEM of the posterior end of the head; (ii) SEM of the anterior end of the abdomen. F represents the ridged file found on male *H. dossenus*. S shows the location of the scrapers on the male.

buzzes. Abdominal movements exactly match the frequency characteristics of the buzz signal but not the thump or scrape signal. In addition, preventing contact between the abdomen and the cephalothorax attenuated thump and scrape signals but not buzz signals. SEMs of the cephalothorax–abdomen junction revealed the presence of a scraper and file; thus, scrapes and thumps are produced through stridulation while buzzes are not.

Three different mechanisms are responsible for the different signals: (1) the first thump component is produced from percussion with the forelegs and the ground, (2) scrapes and the second thump component are produced from abdominal movements coupled to a frequency multiplier (stridulation) and (3) buzzes are produced from abdominal oscillations alone (tremulation). Selective elimination of only the high frequencies of thump signals suggests that both vibratory mechanisms (stridulation and tremulation) contribute to thumps or possibly that low frequencies in thumps are produced using a different area on the scraper, one where contact was not prevented. The entire diversity of substrate-borne vibration-production mechanisms described to date in spiders (Uetz and Stratton, 1982) is seen here in one species: *H. dossenus*. To our knowledge, no other spider described exhibits such complexity in seismic signal production. This is surprising since it occurs in a family in which signalling is thought to be predominantly visual (Foelix, 1996). This raises the question of why *H. dossenus* has evolved multiple seismic signals in addition to its repertoire of visual signals.

Two major ‘quality-based’ hypotheses have been proposed for the evolution of multiple signals: ‘backup signals’ and ‘multiple messages’ (Johnstone, 1996; Moller and Pomiankowski, 1993). The backup signals hypothesis states that different signals provide the same information about a sender but allow for a more accurate assessment of condition, while the multiple messages hypothesis states that different signals code for different aspects of a senders condition. The backup hypothesis, in this context, would predict that visual and seismic signals are alternative media for the same signal information and that seismic signals may be most important when visual signals are obscured. This seems unlikely for several reasons. *H. dossenus* courtship only occurs diurnally. Visual courtship starts at ranges up to 60 mm away while seismic courtship signals only occur at close ranges (5–8 mm). The start of courtship appears to be visually mediated since males orient and court to tethered females in the absence of any chemical cues produced, for example, by the female’s drag line. Sometimes, however, males will display when the female is looking in the opposite direction. Regardless, courting males are usually in the female’s line of sight and in close proximity when seismic signals are produced. This still leaves the question of whether the three different seismic signals are acting as ‘backups’ to each other. *H. dossenus* can be collected on various substrates; leaf litter, sandy soil or rocks. Each of the different substrates has very different transmission properties (D. O. Elias, R. R. Hoy and A. C. Mason, manuscript in preparation) and it is possible that some signals propagate

better in some substrates than others. The difference at short distances is minimal however. Also, the most common substrate (leaf litter) transmits all signals equally well. Again, because all signals are produced at very close distances, where signal attenuation is presumably negligible, it seems unlikely that the three signals are redundant backups. Another possibility is that the different seismic signal production mechanisms may act to backup one another. This is unlikely due to the large temporal and spectral differences between the signals.

A better alternative is that seismic signals are used as multiple messages for sender condition. Male *H. dossenus* have multiple visual ornaments. Males, but not females, are strikingly ornamented, especially the body parts that are used in courtship. The forelegs, for example, are bright green with a dark brown border and a fringe of white hair, while the tips of the legs are a deep black. The pedipalps, third pair of legs and face are also ornamented (Griswold, 1987). One problem that may be encountered by having multiple signals in a single modality is the amount of information that can be effectively detected and discriminated (Rowe, 1999). Within a discrete signal modality, habituation, adaptation and transduction mechanisms in sensory neurons, as well as memory capabilities of receivers, may set limits to signals that animals are able to effectively detect and process. Complex signals with many different characteristics in a single modality, for example, are often perceived as one unified stimulus (Honey and Hall, 1989; Rowe, 1999), while information transmitted in multiple modalities is not (Hillis et al., 2002). The evolution of seismic signals could therefore be a way to add multiple messages when there is selection for multiple avenues of information for females and the evolution of further signals in the visual modality is limited by physiological or economic constraints. The three different seismic signals could also be used to relay multiple messages. The occurrence of three different seismic signal production mechanisms that involve different motions and anatomical structures suggests the possibility that each different signal could relay very different information about the male’s condition.

Alternatives to these two quality-based hypotheses have been proposed in models of the evolution of multiple sexual preferences and ornaments (Iwasa and Pomiankowski, 1994; Pomiankowski and Iwasa, 1993, 1998). These models are not necessarily based on mate quality assessment but are instead based on Fisherian ‘runaway selection’ (Fischer, 1930) and their interplay with other Fisherian and handicap traits (Zahavi, 1975). In these models, female preferences lead to the elaboration of male display traits, and multiple male ornaments evolve in spite of the increased cost to males.

Regardless of the evolutionary process that has led to signal elaboration in this species, a further question is how the addition of a second stimulus modality contributes to signal content and efficacy. Spiders in the *Habronattus* group are known for the complexity of visual displays as well as their visual ornaments. *Habronattus dossenus* is no exception to this pattern. How then does *H. dossenus* incorporate two separate

but precisely coordinated sets of complex signals? One possibility is that it is the coordination of visual and seismic signals that relays information. Especially with thumps preceding buzzes and scrape signals, the coordination of visual and seismic signals can be very precise and it is possible that females are using this tight temporal coordination as a measure of male quality. Another possibility is that either vibratory or visual signals carry information, and the tight coordination of the alternative modality directs attention to subsequent signals. In animal signals, signal components that precede focal informative signals have often been shown to improve signal efficacy and efficiency by directing attention (Fleishman, 1988; Rowe, 1999). Jumping spiders' well-developed sense of vision (Blest et al., 1981; Eakin and Brandenburger, 1971; Forster, 1982a,b; Jackson, 1982; Land, 1969, 1985) could possibly be a good mechanism to draw attention to seismic signals that may be more difficult to detect than visual signals. Alternatively, experiments in humans have shown that when sound stimuli are matched with a corresponding visual stimulus, the perception of visual temporal rate is improved (Recanzone, 2003). A similar process may be at work in these animals, particularly in the short-duration thump and scrape signals, where seismic signals could improve the detection of rapidly occurring visual signals. Similar arguments have been made regarding the evolution of visual ornaments and visual motion displays in jumping spiders (Peckham and Peckham, 1889, 1890). If visual form and motion pathways are considered separately (Barth, 2002; Forster, 1982b; Strausfeld et al., 1993), then it is possible that visual ornaments can focus attention on motions or *vice versa* (Hasson, 1991), hence the tight correlation between ornaments and the body parts used in displays (Peckham and Peckham, 1889, 1890). Attention focusing *via* the combinatorial possibilities created by the combination of multiple modalities or components could therefore be a powerful force driving the evolution of complex signals.

While much recent work has documented the occurrence of multi-modal signals in a variety of animals (Fusani et al., 1997; Hoelldobler, 1999; Hughes, 1996; McGurk and MacDonald, 1976; Partan and Marler, 1999; Rowe and Guilford, 1999), including spiders (Hebets and Uetz, 1999; Scheffer et al., 1996; Uetz and Roberts, 2002), the complexity found in *H. dosseus* is impressive. Multiple visual ornaments and visual displays exist together with a complexity of seismic signals that is unprecedented in spiders. *H. dosseus* uses three independent mechanisms to produce three types of signals, which can further be divided into at least seven categories based on the power spectra, envelope shape and temporal structure of the signals (D. O. Elias, A. C. Mason, W. P. Maddison and R. R. Hoy, unpublished observations). Each of these seismic signals is precisely coordinated with a unique visual display, and some visual signals (i.e. pedipalp signals) have no corresponding seismic component. We feel that this signal complexity represents a good system in which to test competing models of signal evolution. Future studies will examine female responses to manipulated and control males in an attempt to elucidate the

function of different aspects of the male's complex, multi-modal multi-component courtship signals.

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