The effect of substrate on the efficacy of seismic courtship signal transmission in the jumping spider *Habronattus dossenus* (Araneae: Salticidae)

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Summary

The jumping spider *Habronattus dossenus* Griswold 1987 (Salticidae) communicates using seismic signals during courtship and can be found on rocks, sand and leaf litter. We examined the filtering properties of, and tested the efficacy of male courtship signals on, these natural substrates. These substrates have drastically different filtering properties at the distances at which the males court. Rocks sharply attenuated all frequencies, with considerable variability among different rocks. Desert sand showed band-pass properties, attenuating frequencies contained in the animal's signal. Leaf litter passed all frequencies and was the most favourable signalling environment. In behavioural trials, the proportion of males mating successfully was significantly higher on leaf litter than on rocks or desert sand. Males did not modify their courtship behaviour on different substrates. Therefore, the effectiveness of male courtship seismic signals appears to be strongly constrained by the available substratum resources.

Key words: vibration, jumping spider courtship, seismic communication, multimodal, signal design, signal evolution.

Introduction

A large body of literature encompasses arthropod acoustic communication, including studies on acoustic properties of natural environments (Larsen and Michelsen, 1983; Michelsen, 1978; Romer, 1998, 2001). Most arthropods, however, do not communicate using airborne sounds. Physical constraints on sound production by small animals limit the efficiency of sound communication (Bennet-Clark, 1998; Larsen and Michelsen, 1983). Conversely, seismic signals (self-generated vibrations transmitted through a solid substrate; Narins, 2001) are more appropriate for communication in small arthropods, such as insects, arachnids and crustaceans (Barth, 1985, 1998; Markl, 1983; Michelsen et al., 1982; Popper et al., 2001; Uetz and Stratton, 1982).

The seismic channel has special relevance to spiders as vibrations are the predominant modality in most sensory-guided behaviours (Barth, 1998, 2002; Foelix, 1996; Uetz and Stratton, 1982). Spiders are found in virtually all terrestrial (and some aquatic) habitats and, thus, potentially signal on a diversity of substrates with drastically different physical properties, especially highly mobile cursorial species. Given communication *via* seismic signals, how are signals affected by substrate heterogeneity, and how do senders and receivers of seismic signals deal with the effects that the channel imposes on them?

Males of the jumping spider, *Habronattus dossenus*

(Griswold, 1987), court females using a complex multimodal display consisting of multiple visual and seismic signals (Elias et al., 2003). Previous work has shown that seismic components in courtship are crucial in mate choice (Elias et al., in press). Like many jumping spiders, *H. dossenus* are cursorial and highly ambulatory. They are found predominantly on small rocks, sand and leaf litter in the Sonoran desert. To investigate the seismic channel and the constraints it imposes on *H. dossenus* communication, we characterized the vibrational properties of these natural substrates using laser vibrometry and combined this with behavioural trials that quantified courtship behaviour on the same substrates. We found that the three natural substrates (rocks, sand and leaves) had different filtering properties. In the lab, males reliably courted on all substrates, but females mated more often with males courting on leaves and rejected males on other substrates. These results indicate a potentially large effect of the communication channel on mating success and signal evolution.

Materials and methods

Animals and substrates

Habronattus dossenus (Griswold, 1987) were collected (Atascosa Mountains, Coronado National Park, Santa Cruz

County, AZ, USA) predominantly on three substrates: (1) rocks (igneous tuffs; Chronic, 1983; mass 107.3±178.4 g; length 6.1±2.6 cm; width 3.7±1.2 cm; depth 2.7±1.4 cm; mean ± S.D.; *N*=8); (2) desert sand (a mixture of particles, mean diameter ± S.D. 0.3±0.025 mm; *N*=36; and fine dust, diameter <0.005 mm); and (3) leaf litter (dried Emory Oak, *Quercus emoryi*, and Mexican Blue Oak, *Quercus oblongifolia*; mass 66.42±26.37 mg, length 4.4±1.2 cm; width 1.8±0.3 cm; mean ± S.D.; *N*=10). Spiders were collected with samples of the substrate on which they were found. Spiders are strictly diurnal and active during the hottest parts of the day; therefore, we conducted all experiments in dry conditions. Animals were housed individually in plastic containers on a 12:12 hourly light:dark cycle and fed weekly on fruit flies (*Drosophila melanogaster*) and crickets (*Acheta domesticus*). Immature females were checked daily until they moulted to maturity. Only virgin adult females aged 16–31 days post-maturation (mean 22 days ± 2.5 S.D.) were used in behavioural trials. All spiders were fed 2 days before experiments.

Properties of natural substrates

Vibrations were generated using an adjustable phonograph tone-arm (Dual 1019 turntable) with a piezoelectric actuator (Type 350/025/0.60 Strip Actuator; APC International, Mackeyville, PA, USA) attached at the end. The actuator was mounted at a shallow angle with its narrow edge (2.5 mm width) contacting the substrate. As loading the substrate affects its vibrational properties, the adjustable tone-arm allowed us to vary the load placed on the substrate to match the mass of a male spider (9.0±1.3 mg, mean ± S.D., *N*=44). The load was calibrated by resting the tone-arm-mounted transducer on a balance (Ohaus E10640; Ohaus, Pine Brook, NJ, USA). The actuator was calibrated using a laser Doppler vibrometer (LDV, Polytec OFV 3001 controller, OFV 511 sensor head; Polytec, Waldbronn, Germany). Test stimuli were synthesized frequency sweeps (System 3; Tucker–Davis Technologies, Alachua, FL, USA) (1–2500 Hz for rocks and sand, 1–1500 Hz for leaf litter). We recorded propagated substrate vibrations with the LDV sensor head attached to a translation stage (Newport Model 421; Newport, Irvine, CA, USA) allowing precise movement of the recording point. The LDV was positioned perpendicular to the substrate surface. Rocks (*N*=8) were partially embedded in a dish of desert sand approximating conditions in the field. Sand recordings were conducted in a large container (21×26×10 cm) and sand was replaced between experiments (mass: 7300 g, *N*=4). For leaf litter, individual leaves (*N*=10) were recorded in a dish containing desert sand. Recordings were taken at 5 mm intervals starting just beyond the actuator tip, five sweeps at each position. Reflective tape (3M, 0.5 mm^2; Scotchlite, Neuss, Germany) was attached to rocks and leaves as measurement points for the LDV. Sand was reflective enough to measure without reflective material. The vibration actuator was applied to a randomly selected position on each sample, with the provision that for smaller samples the point of stimulation was near one end to allow sufficient distance for measurements.
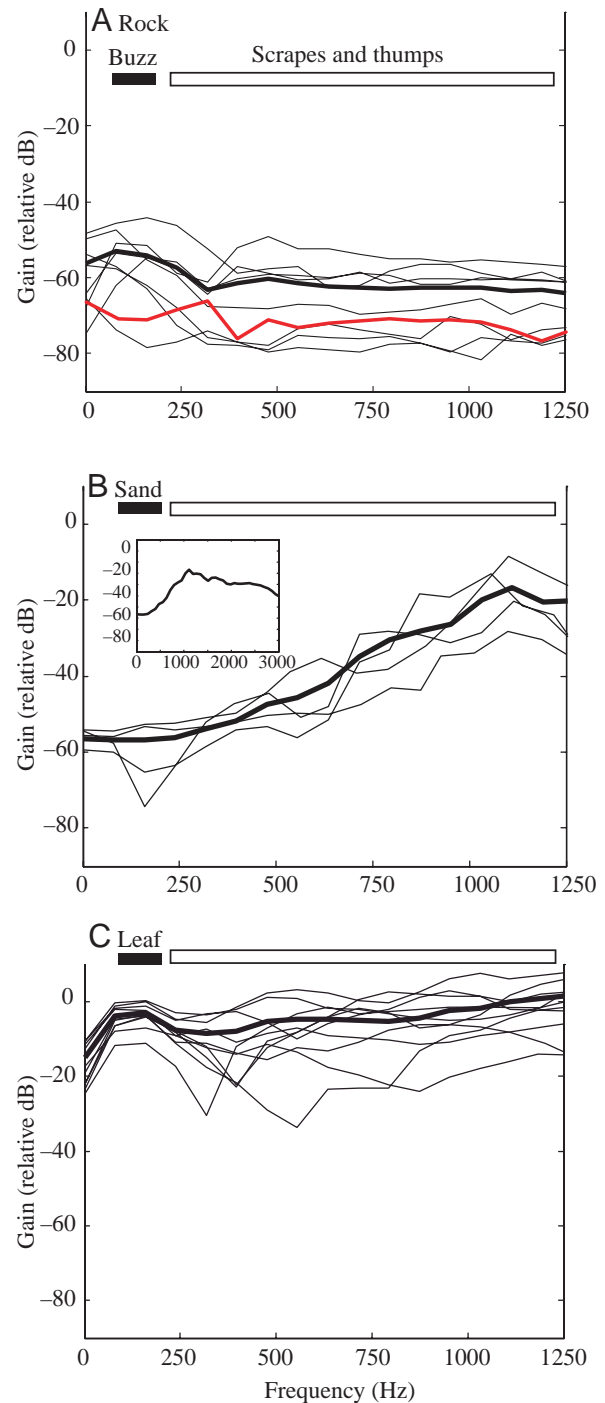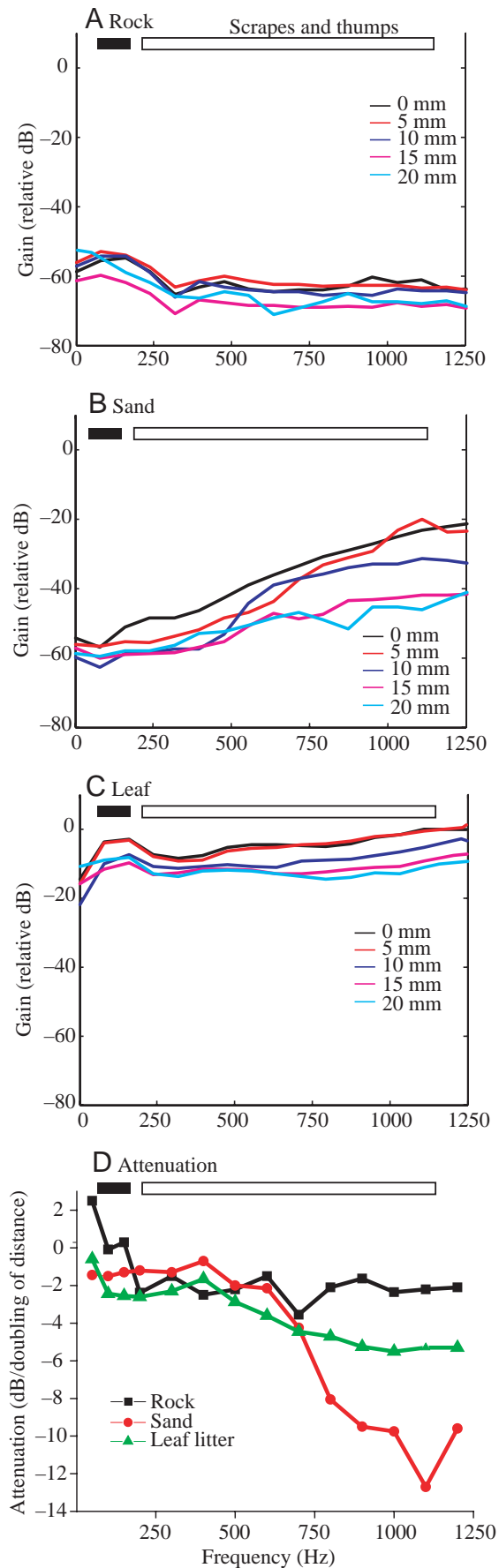

Fig. 1. Seismic transfer functions of natural substrates measured at 5 mm from source: rocks (A); desert sand (B); leaf litter (C). Mean (thick lines) and individual (thin lines) transfer functions are plotted. Boxes show the bandwidth of buzz (black), and thump and scrape (white) seismic signals produced by courting males. Red trace (A) shows transfer function of the rock used in behavioural trials. Inset (B) shows transfer function of desert sand at a different scale to show its band pass property. All dB are gain relative to the input signal.

We calculated transfer functions for each sample, averaging sweeps at each position using Matlab (The Mathworks, Natick, MA, USA) and present gain curves for vibration velocity (dB

Fig. 2. Attenuation on natural substrates. Mean transfer functions at different distances for rocks (A), desert sand (B) and leaf litter (C). Overall attenuation at different frequencies (D).

relative to input signal). Variance between sweeps at each position was low (mean standard deviation: rock 0.0003 dB, $N=20$; sand 0.0032 dB, $N=6$; leaf litter 0.0168 dB, $N=18$). We show average attenuation with distance by calculating the average gain curves at each distance for the same substrate. We also present attenuation by calculating the total attenuation as change in dB per doubling of distance at different frequencies. This was calculated by averaging the change in intensity for each frequency at 5 *vs* 10 mm and 10 *vs* 20 mm.

Behavioural trials

Spiders were randomly assigned to one of three treatments: (1) rock, (2) sand or (3) leaf litter. Males were randomly paired with a female, and each individual was only used once.

For rock trials, a large rock (granite, 23×20×7 cm) was used as the behavioural arena to provide sufficient area while limiting courtship to the rock surface. While *H. dossenus* was not found on this particular rock, its transmission properties are similar to rocks on which the animal was found (Fig. 1, red). An acetate cylinder (12.5 cm diameter, 13.5 cm height) was glued to this rock. For sand and leaf litter trials, a similar sized plastic cylinder was used as the courting arena with either sand (7 cm in depth) or leaf litter atop a small amount of sand (2 cm in depth). An opaque paper cylinder around each setup prevented visual distractions. Surfaces were cleaned with ethanol and the sand stirred between trials to remove chemical cues.

Females were placed into the arena first. Trials lasted 30 min and were only included if males courted. *Habronattus dossenus* courtship comprises four phases identifiable by stereotyped postures and movements (Elias et al., 2003). Phase 1 includes only visual signals (Elias et al., 2003). Multimodal courtship (phases 2–4) begins when males are within approximately one body length of the female, and includes multiple bouts of prolonged seismic and visual signalling. Three different seismic signals are identified: narrow-band buzzes (65 Hz + harmonics); broadband thumps (200–1200 Hz); and scrapes (200–550 Hz) (Elias et al., 2003). We obtained several measures of courtship (1) copulation success, (2) phase 1 duration and (3) multimodal duration. Results were analyzed with ANOVA (analysis of variance) and Bonferonni-corrected Tukey *post hoc* tests, using Systat (SSI, Richmond, CA, USA).

Results
Properties of substrates

Transfer functions for samples of rock ($N=8$), desert sand ($N=4$) and leaf litter ($N=10$) were calculated at a distance of 5 mm from the stimulator, representing the distance where multimodal courtship usually starts (Fig. 1). While there is

variation between different samples for all substrates, e.g. at 100 Hz, –45 to –75 dB for rocks, –55 to –65 dB for sand, and –0.5 to –11.5 dB for leaf litter, both leaf litter and sand (at lower frequencies) are more consistent than rocks (Fig. 1). Rock is an inelastic medium and at the intensities produced by our stimulator (and the animal), vibration was highly attenuated and low-pass filtered (Fig. 1A). Desert sand acted as a band pass filter (Fig. 1B, inset), passing frequencies around 1 kHz and attenuating frequencies in the animal's signal bandwidth (Fig. 1B). Leaf litter passed all frequencies approximately equally (Fig. 1C).

Average transfer functions were calculated at different distances for each substrate to determine their attenuation characteristics (Fig. 2). On rocks, we sometimes observed an amplification of very low frequencies (>50 Hz), potentially an artefact caused by the rocking of the entire substrate (Fig. 2A,D). Attenuation was frequency dependent with overall attenuation increasing at higher frequencies for all substratum types (Fig. 2). Attenuation was similar for all types at low frequencies (>700 Hz). For rocks and leaf litter, the overall form of the gain curves did not change with distance (Fig. 2A,C) although there was a moderate increase in attenuation with frequency in leaf litter (Fig. 2D). Attenuation in sand was strongly frequency dependent and increased with frequency (Fig. 2B,D).

Courtship on natural substrates

The proportion of pairs that mated was significantly higher on leaf litter (N=15) compared with either rocks (N=14) or sand (N=14) ($F_{2,41}$=5.945, P=0.005; Tukey *post hoc*, leaf litter *vs* rock, P=0.025; leaf litter *vs* sand, P=0.009; Fig. 3). The proportion of males copulating with females was not statistically different between rocks and sand (P=1; Fig. 3).

Courtship duration did not differ between treatments for either phase 1 (visual only; $F_{2,41}$=1.640, P=0.206; Fig. 4) or multimodal (phases 2–4; $F_{2,41}$=2.866, P=0.068; Fig. 4) courtship. Males did not change their signalling behaviour according to substrate, although there was a non-significant tendency to court less on sand.

Discussion

H. dossenus's habitat is highly patchy and heterogeneous. In this study, we chose to look at rocks, sand and leaf litter, which represent the most common substrates in their natural habitat (Elias et al., 2003). Because seismic components of courtship are critical to male success (Elias et al., 2004), it follows that the transmission properties of the substrata are crucial, hence we examined the transmission properties of substrates to determine (1) filtering characteristics, (2) variation in these characteristics and (3) average attenuation.

At distances where courtship naturally occurs, the filtering characteristics of each substrate were different. Rocks passed low frequencies but because rocks are inelastic, little energy was transferred from the stimulator to rocks. The intensity of our stimulator approximated courting males hence initial

attenuation approximates natural conditions. Sand had band pass properties, attenuating relevant frequencies (especially buzz signals). Aicher and Tautz (1990) reported similar characteristics for sand but with a different pass band. This difference may result from differences in stimulation methods or sand characteristics – particle size and sand composition differ between beach and Sonoran desert habitats. Leaf litter had a flat frequency response, although there was considerable variation. Some of this variability may have been due to heterogeneities in the structure of the leaf, such as veins (Magal et al., 2000). We did not systematically test such effects, but they are likely to be less pronounced in our system as desert leaf litter is thoroughly desiccated and leaves were uniformly stiff. In general, previous studies of vibrations in leaves on plants show similar all-pass filtering properties (Barth, 2002; Magal et al., 2000; Michelsen et al., 1982).

Environmental filtering has important effects on signal design (Endler, 1992; Larsen and Michelsen, 1983; Romer,
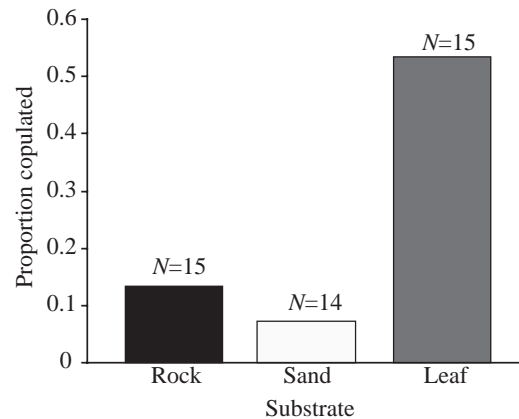
Fig. 3. Female *H. dossenus* courtship responses on natural substrates. Male copulation success was used as a measure of female choice on rocks, desert sand and leaf litter.
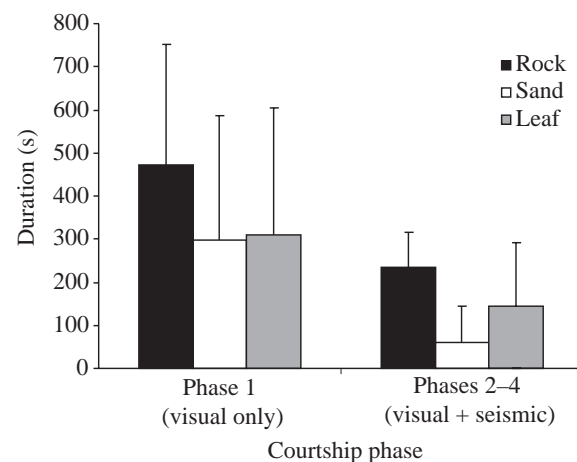
Fig. 4. Male *H. dossenus* courtship on natural substrates. Time spent courting females was used as a measure of male behaviour on rocks, desert sand and leaf litter. Visual only (phase 1) and multimodal (visual + seismic; phase 2) courtship was observed.

2001). Considering the animal's signal bandwidth, rocks (albeit with low amplitude) and leaf litter are best suited to transmit frequency information while signals on sand would be transmitted with significant distortion. Therefore, if frequency information is important, males should signal (and females accept males) on leaf litter or rocks.

Because the shape and mass of solids affects vibrational properties, we estimated the predictability of seismic transmission as an animal encounters different rocks, leaves or patches of sand. Vibration characteristics were more consistent on sand and leaf litter than rocks. Therefore, these substrates should allow more consistent signal characteristics from one location to the next and, if predictable signal quality is important, sand or leaf litter should be preferred.

Attenuation determines the range of signal transmission. Attenuation in rocks was steep at all frequencies; was more complex in sand, with a steep increase in the overall attenuation with higher frequencies; and was moderate with some increase at higher frequencies in leaf litter. Attenuation was similar at low frequencies for all substratum types. Rocks, however, showed the least overall attenuation with distance but were initially highly attenuated, especially compared with leaves. Therefore, if signal range is important, leaf litter should be preferred.

Successful mating was three times more likely on leaf litter. This is consistent with our observations that leaf litter transmits signals most effectively, reliably and extensively. No significant differences were observed in male courtship effort on different substrates. As males were confined to a particular substrate in these experiments, however, they do not address the question of whether males in the field may adopt strategies favouring courtship opportunities on particular substrates. Alternatively, the fact that males produce seismic signals only at short distances (Elias et al., 2003) may itself be a strategy to compensate for substrate heterogeneity and attenuation. Future work will address this possibility.

Based on the physical properties of rocks, sand and leaf litter, and the behaviour of spiders on these substrates, we can make inferences as to the salient properties of courtship signals. Frequency content, especially of buzz components, may be particularly important. Broad-band signals (thumps and scrapes) occur at greater distances than do narrow-band signals (buzzes), suggesting that a clear assessment of buzzes is important in mate choice. Furthermore, we can infer from the predictability of transmission properties and female mate-choice behaviour on leaf litter that the reliability (consistency) of the frequency components in signals is important.

Natural selection should optimize signal transmission and reception, and both signalling behaviour and the receivers' sensory systems should evolve to match the characteristics of the environment (Endler, 1992, 1993). Habitat-specific effects on signal evolution have been studied predominantly in visual signals in fish (Boughman, 2001; Endler, 1991, 1992; Seehausen et al., 1997) and birds (Marchetti, 1993), and in the acoustic (air-borne) signals in insects (Larsen and Michelsen, 1983; Romer, 1998), birds (Richards and Wiley, 1980; Ryan

and Brenowitz, 1985; Wiley, 1991), and frogs (Ryan et al., 1990; Ryan and Wilczynski, 1991). Signals in most modalities, such as visual and auditory, are adapted to a single medium (e.g. air or water). While signalling conditions may be highly complex in these modalities, the overall characteristics of the transmission medium are relatively homogeneous. Animals using seismic signals may regularly traverse substrates with widely varying physical properties (e.g. rock and vegetation) each of which could be a potential signalling channel. Seismic signal evolution may thus be constrained by such low predictability of the signalling environment. Several strategies are possible. Generalist signals could be designed to function in all available channels. This 'lowest common denominator' strategy would limit both reliability and information content. A second strategy would be to specialize in a subset of available channels – increasing signal reliability at the cost of signalling opportunity. Our data suggest that *H. dossenus* signals are well-suited to the leaf litter microhabitat and that males should prefer to signal on leaves. We detected no pattern in the locations of males and females in the field, but we cannot control for differences in detectability of animals (to humans) on different substrates.

Substrate variability and consequent signal specialization may account for the diversity of seismic signalling behaviour in different *Habronattus* species (Elias et al., 2003, 2004; Maddison and Stratton, 1988). Members of the *agilis* species group, often found on beaches, signal with higher intensity and larger bandwidth than *H. dossenus* (Maddison and Stratton 1988; D.O.E., A.C.M., W. Maddison and R.R.H., manuscript in preparation) – characteristics that are better matched to sand environments particularly if the temporal properties of signals are important (Aicher and Tautz, 1990; present study). Several *Habronattus* species can be found in the same location and each may use signalling channel 'resources' differently. This could explain the large diversity observed in seismic signals and signalling mechanisms. Such 'signalling microhabitat' partitioning could also be a mechanism underlying the intense speciation observed in the *Habronattus* genus (Griswold, 1987; Maddison and Hedin, 2003; Masta and Maddison, 2002). In addition, because courtship in these animals is multimodal and there is a high degree of coordination between visual and seismic signals (Elias et al., 2003), the interaction between signal components in different modalities may be important in microhabitat use and signal design. Optimal habitats for these two signal modalities may not be identical. Future work will examine the possibility that substrate effects on signal use are modified by interactions between visual and seismic modalities.

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