



Substrate-dependent signalling success in the wolf spider, *Schizocosa retrorsa*

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Signals used in communication are often hypothesized to be optimally designed for their signalling environment. Here, we explore the importance of signalling substrate on seismic signal efficacy and reproductive behaviour in the wolf spider, *Schizocosa retrorsa*: a species found on multiple signalling substrates (pine litter and/or red clay or sand). In this multimodal signalling species, simultaneous with conspicuous visual displays, males produce percussive seismic signals via an impulse mechanism which tends to excite a substrate evenly across a wide band of frequencies. We first quantified the transmission characteristics of this broadband percussive signal by playing recorded signals back across three naturally occurring substrates, two of which represent substrates upon which *S. retrorsa* is commonly found: leaf litter, pine litter and red clay (the latter two exemplify their natural habitat). The substrates varied in their transmission characteristics with respect to both attenuation (higher on red clay) and filtering. Next, we compared copulation success, courtship behaviour and microhabitat choice among these same substrates. Copulation frequency was higher on the natural substrates of pine litter and red clay as compared with leaf litter. Males took longer to initiate courtship on leaf litter, but once initiated, courtship behaviour did not vary across substrates and we were not able to discern any choice with respect to the first, or the most common, substrate chosen. Our results show that while *S. retrorsa*'s percussive signals may not be matched to the specific properties of any one substrate, copulation success was substrate dependent and we discuss potential explanations for this substrate-dependent signalling success.

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Understanding past as well as present selection pressures that have influenced the origin, evolution and maintenance of existing communication systems presents a considerable challenge to biologists. Among the multitude of factors known to influence signal form, characteristics of the signalling environment play a crucial role. For example, numerous empirical studies have demonstrated a clear effect of signalling habitat on visual signal evolution in fish (Endler 1991, 1992; Boughman 2001; Maan et al. 2006), birds (Marchetti 1993; Endler & Thery 1996;

Cynx et al. 1998; Lengagne et al. 1999; Lengagne & Slater 2002; Heindl & Winkler 2003a, b; Uy & Endler 2004), and lizards (Fleishman & Persons 2001; Macedonia et al. 2003; Peters & Evans 2003; Leal & Fleishman 2004). In addition, evidence that air-borne signal evolution is influenced by habitat characteristics is provided by studies involving singing insects (Michelsen & Larsen 1983; Romer 1990; VanStaaen & Romer 1997; Schul & Patterson 2003), birds (Richards & Wiley 1980; Ryan & Brenowitz 1985; Wiley 1991) and frogs (Ryan et al. 1990; Ryan & Wilczynski 1991). Fewer studies have assessed habitat-specific effects on the evolution of substrate-borne (seismic) signals (Michelsen et al. 1982; Magal et al. 2000; Cokl & Doberlet 2003; Elias et al. 2004; Cocroft & Rodriguez 2005; Cokl

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et al. 2005, 2007; Cocroft et al. 2006). None the less, one such study provides evidence that substrate type has likely influenced the evolution of seismic courtship signals in a jumping spider as both seismic signal transmission characteristics and mating frequency were best matched to the spider's natural substrate (Elias et al. 2004).

Natural selection is expected to favour signals and signalling behaviour that maximize signal reception and minimize signal degradation (Endler 1992, 1993). If senders are faced with a number of possible habitats and/or signalling channels, many potential strategies could emerge. For example, senders could generate signals that were general to all potential signalling channels/environments. This strategy would likely come at the cost of signal reliability and information content. Alternatively, senders could use specialized signals adapted to only one specific signalling channel/environment. Similarly, this strategy would likely come at the cost of limiting effective signalling opportunities. Senders could also add signal components, having one specialized for each signalling channel/environment (see 'Multiple sensory environments', Candolin 2003; Hebets & Papaj 2005). Again, this strategy would presumably entail added costs of signal production and/or increasing eavesdropping, among others. Finally, senders could be plastic in their signalling behaviour, altering signal form depending upon current signalling/environmental conditions (e.g. Patricelli et al. 2002, 2006). Senders using this strategy would incur the costs associated with plasticity (e.g. Snell-Rood 2005; reviews of phenotypic plasticity costs: DeWitt et al. 1998; Relyea 2002).

Within the auditory/seismic signalling domain, broadband signals may exemplify a strategy of 'general signalling' in that these signals encompass a wide range of frequencies. Therefore, at least some signal energy may be successfully transmitted through a diversity of channels/substrates with different properties. For example, transient impulsive or percussive signals have the property of being able to excite the natural frequency response of the substrate (Pierce 1989). These percussive signals are broadband (contain a wide range of frequencies) at the source and the spectral characteristics of the transmitted signal (i.e. as it is propagated through the signalling channel) are due solely to the properties of the substrate. Senders producing percussive signals can thus effectively transmit signals through any substrate without paying potential costs needed to produce signals tuned to a specific substrate. Furthermore, percussive signals are produced by the impact of a body part against another surface, either a substrate in the environment or another body part. Since these signals can be produced with any appendage, no specialized morphological adaptations are required for their production. Putatively for these reasons, percussive signalling is one of the most ubiquitous sound production mechanisms and can be found in the communication systems of many animals (Uetz & Stratton 1982; Markl 1983; Barth 1985; Manson-Barr & Pye 1985; Hill 2001; Narins 2001; Popper et al. 2001; Randall 2001; Yack et al. 2001; Bostwick & Prum 2003, 2005; Stewart & Sandberg 2006).

Animals confronted with multiple signalling substrates may therefore be expected to benefit by incorporating broadband percussive displays in their signalling

repertoire. Although seismic signal production mechanisms in wolf spiders encompass the entire diversity of arachnid sound-producing mechanisms and include percussion, stridulation and tremulation/vibration (Uetz & Stratton 1982; Stratton 2005; Elias et al. 2006; D. O. Elias & A. C. Mason, unpublished observations), several species within the genus *Schizocosa* incorporate predominantly percussive seismic signals (Stratton 2005). Among these 'drumming' species (see Stratton 2005), *Schizocosa retrorsa* is known to occur on at least two different substrate types. *Schizocosa retrorsa* is a locally abundant wolf spider found throughout highly exposed red clay, sand, or pine-covered habitats in northern Mississippi (Hebets et al. 1996). While northern Mississippi is home to a plethora of *Schizocosa* species, the habitat of *S. retrorsa* differs notably from the complex leaf litter habitat of many of the other local species (e.g. *Schizocosa ocreata*, *Schizocosa rovneri*, *Schizocosa stridulans*, *Schizocosa uetzi*, E. A. Hebets, personal observation). The male courtship display has been well characterized and incorporates both seismic and visual signals. Visual signals consist of a rapid foreleg wave and associated pigmentation (Hebets et al. 1996). Linked with this foreleg display is a seismic signal produced by drumming of the pedipalps and the forelegs against the ground (D. O. Elias & A. C. Mason, unpublished observation). Furthermore, males periodically raise their entire bodies off the ground in a movement reminiscent of a pushup (Hebets et al. 1996). Associated with this pushup display is a seismic signal produced by drumming of the pedipalps against the ground (Hebets et al. 1996). Given the general nature of percussive signals, we hypothesized that these signals enable male *S. retrorsa* to effectively communicate across multiple substrate types.

The overall aim of this study was to determine if signalling substrate influences seismic signal efficacy and associated receiver responses in the wolf spider *S. retrorsa*. Specifically, our goals were (1) to quantify the seismic signal transmission characteristics of different substrate types using playbacks of natural signals propagated across natural substrates and (2) to determine the extent to which substrate-type influences male and female reproductive behaviour and habitat choice. Combined, our results show that although males use broadband percussive courtship signals, mating success is still substrate dependent with the highest mating frequencies occurring on the natural substrates of pine litter and red clay. We discuss possible explanations for this substrate-dependent signalling success, including the possible importance of substrate-specific visual signal efficacy and the possibility of substrate-matched receiver preferences, perception and/or processing.

METHODS

Spiders

Penultimate males and females and mature males were collected at night from two sites in Lafayette, Co., MS, in June 1994 and May 2001. Each spider was held in the laboratory individually in a cage measuring 8 × 4 cm

(12:12 h light:dark cycle). Water was provided via a cotton wick dipped into a reservoir below the cage. Spiders were fed several small crickets approximately once each week.

Seismic Signal Transmission

We measured seismic signal transmission by playing recorded *S. retrorsa* male seismic signals through different substrates and measuring the propagated signals at different distances. Playback signals were generated with Matlab (The Mathworks, Natick, MA) using a male *S. retrorsa* signal acquired with laser vibrometry (LDV, Polytec OFV 3001 controller, OFV 511 sensor head, Waldbronn, Germany; Fig. 1). The male *S. retrorsa* signal was recorded on a substrate of stretched nylon fabric at a distance of ~ 2 mm from the courting male. Because percussive signals reflect the properties of the recording substrate, we recorded signals on an unnatural substrate that has been shown to minimally affect signals (Elias et al. 2003, 2006; D. O. Elias & A. C. Mason, unpublished data). By

recording signals produced on this ‘unnatural’ substrate at short distances from the male, we hoped to more closely match signals at the sender source. Playback *S. retrorsa* male courtship signals were generated using a minishaker (B&K Type 4810 Minishaker, B&K Type 2706 Power Amplifier) placed in a plastic box ($35 \times 25 \times 14$ cm) filled with the one of the test substrates (leaf litter, pine litter, or red clay). The minishaker was positioned so that the moving element was at the surface of the test substrate. We recorded propagated substrate vibrations with the LDV sensor head attached to a translation stage (Newport Model 421). Pieces of reflective tape (approx. 1 mm^2) were placed on the substrate to serve as measurement points for the LDV. Signal measurements were taken at the following distances from the minishaker: 5, 10, 20, 40, 80, and 160 mm. Transient percussive signals may not be reproduced well by a minishaker, because of the limited high-frequency response of this device (Casas et al. 2007). Nevertheless, we were able to reproduce much of the bandwidth of the original signals. Future work is necessary to evaluate the transmission of extremely high frequencies in wolf spiders as well as the efficacy of natural versus playback signals.

Five replicates were conducted for each substrate type. For each replicate, the substrate was reintroduced and the shaker was repositioned. New exemplars of the various substrate types were used in each replicate and when possible, new substrate material was used. By introducing new exemplars of substrates we thereby incorporated substrate variability into our measurements. Variability in the field should be even greater, however, and the vibratory conditions may vary dramatically through the season as conditions such as humidity and litter composition change. While this variation is undoubtedly important, we attempted to replicate the environmental conditions in our mate choice test substrates. Future work will be conducted on mating behaviour and seismic properties in natural field conditions.

We measured signal attenuation as root mean square (RMS) amplitude of the signal at different distances in dB relative to the signal amplitude at the 5-mm point (0 dB attenuation). To analyse our attenuation data, we used an analysis of covariance (ANCOVA) with substrate as the independent variable, RMS intensity as the dependent variable, and distance as a covariate. If the model was significant, we performed a least squares (LS) means differences Tukey post hoc test.

To measure filtering in the different substrates we first calculated transfer functions for each sample at 10, 20, 40, 80 and 160 mm, using Matlab (transfer functions illustrate the input/output relationship between the original signal and the propagated signal). The ‘original signal’ used in the transfer function calculation was acquired by recording the played-back signal at the moving element on the minishaker source.

Next we attempted to measure filtering by characterizing the effects on signal spectral characteristics through each of the substrates at different distances. The spectral content of a signal detected by a female at some distance from a displaying male will be determined by (1) the initial spectrum of vibrational energy imparted to the

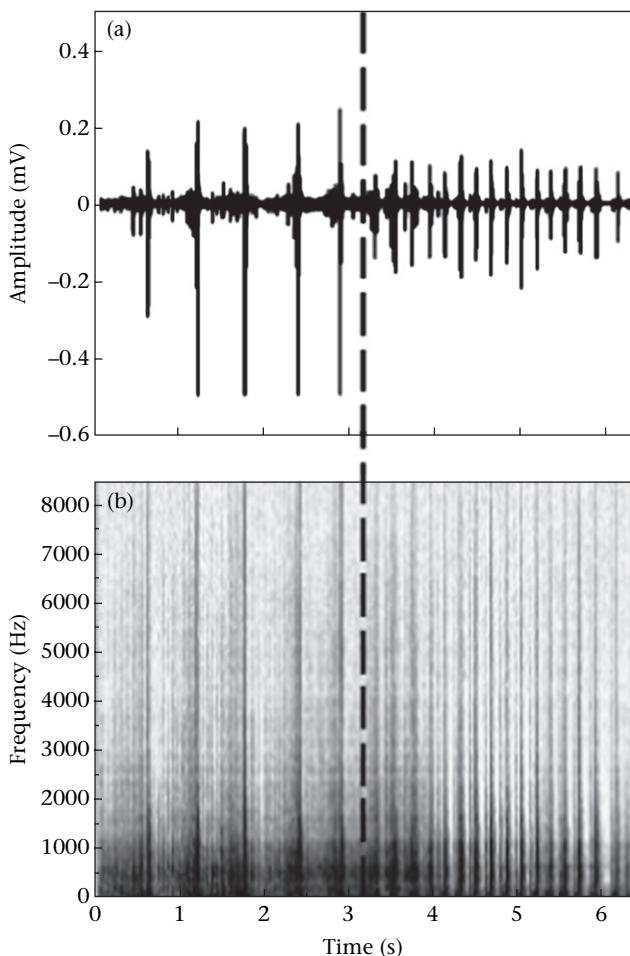


Figure 1. Male *Schizocosa retrorsa* seismic signal recorded using laser vibrometry. (a) Oscillogram of seismic signal; (b) spectrogram of seismic signal. Signals to the left of dashed line are seismic signals produced during ‘pushup’ displays. Signals to the right of the dashed line are seismic signals produced during ‘foreleg wave’ displays. Seismic signals are broadband and include high frequencies.

substrate by the male and (2) frequency-dependent attenuation of that spectrum as the signal propagates between the male and female. To characterize the combined effects of these two factors, we recorded the 10-dB high-frequency cutoff by measuring the point on the spectrum where the signal power dropped 10 dB from the peak transfer function frequency after subtracting DC. The 10-dB cutoff frequency represents a measure of the relative spectral range (or flatness) of the signal spectrum, and was measured at all distances. Accordingly, for signals with a more pronounced peak in the spectrum (i.e. dominated by a narrow range of frequencies) this measure will have a smaller value, whereas larger values represent signals in which a broader range of frequencies are more equally represented. In other words, low relative spectral ranges correspond to transmitted signals with low frequencies dominating while high relative spectral ranges correspond to transmitted signals containing a range of low- and high-frequency components. Changes in the value of this measure with distance reflect the effects of substrate-dependent filtering on the initial signal spectrum. We used a polynomial ANCOVA with substrate as the independent variable, cutoff frequency as the dependent variable, and distance and distance² as covariates. If the model was significant, we conducted pairwise polynomial ANCOVAs to test for pairwise differences. *Schizocosa retrorsa* males are <20 mm in standing legspan (anterior to posterior); so to look at the effects of seismic filtering at distances where tactile and chemosensory cues are likely of less importance, we also performed an ANCOVA on distances greater than 20 mm. If the model was significant, we performed a LS means differences Tukey post hoc test.

All statistical tests were performed using the Systat and JMP analysis packages (SSI, Richmond, CA).

Courtship Behaviour and Mating Success

We examined the influence of microhabitat structure and thus signalling substrate on multimodal courtship behaviour and mating success of *S. retrorsa* by assessing both courtship behaviour and copulation frequency across three naturally occurring substrates, two of which are common substrates for *S. retrorsa*: deciduous leaf litter, pine litter and red clay. In northeastern Mississippi, *S. retrorsa* is locally abundant in open habitats of both pine litter and red clay but is never found in adjacent leaf litter habitats. To examine among-substrate variation in courtship and mating, two sets of three culture dishes (referred to as 'arenas' in the future) measuring 19 cm in diameter and 7 cm high were filled to a depth of ~3 cm with one of the three substrate types. The second set simply enabled running trials simultaneously. Leaf litter, pine litter and red clay were all collected at or near the spider collection locales in Mississippi and were brought back to the laboratory for use in these and the following experiments. Clear acetate was taped around the entire circumference of each arena to prevent spider escape. The three arenas from each set were placed near each other on the table (<5 cm apart) but not touching. In addition, opaque barriers were placed in between each arena to provide visual isolation and

thus, there was no seismic or visual information transfer between arenas. For each set of three arenas, three pairs of males and females were randomly chosen and assigned a substrate type. All females were then placed in their assigned arena and allowed to acclimate for 2 min before their assigned male was introduced. During a trial, each male/female pair was allowed to interact within their assigned arena (leaf litter, pine litter, or red clay). The pairs were left in their arenas for 2 h during which time they were observed every 15 min to see if they were in copula. All individuals were used only once. Copulation generally lasts anywhere from 45 min to more than 2 h (E. A. Heberts, personal observation) and thus, checking every 15 min ensured that we would not miss a copulation.

In 1994, the experimental procedure differed slightly as details of male behaviour were recorded. Since careful observations were often necessary at the start of each pair's interactions, the introduction of males into the three arenas was offset in time by approximately 15 min. For each pair, we measured the latency to male chemoexploration, the latency to male courtship, and the latency to copulation. In addition, upon initiation of male courtship, we recorded the frequency of visual male courtship components: foreleg waves and pushup displays within the first 5 min of courtship for every male.

Habitat Choice

For the habitat choice trials, three experimental set-ups were constructed each with three different habitat types contained in a 19 cm diameter, 7-cm-deep culture dish. Again, multiple experimental set-ups were constructed so that multiple trials could be run simultaneously. The culture dishes each had a piece of cardboard securely placed ~3.5 cm high creating a false floor. The substratum of choice was then placed on top of the cardboard with a depth of ~3.5 cm. Again, the leaf litter, pine litter and red clay were all collected at or near the spider collection locales in Mississippi and were brought back to the laboratory. The three culture dishes per experimental set-up (leaf litter, pine litter and red clay filled) were duct-taped together in a triangular fashion. In the centre of the three culture dishes, a gap was covered with a piece of filter paper that connected all three dishes, thus creating a central platform from which all substrates were accessible. Clear acetate was taped along the outside edges of all three containers to prevent escape and a visual barrier of white paper was placed around the entire set-up.

Penultimate (eight females and 10 males) and mature (18 females and 16 males) individuals of each sex were used in habitat choice trials. For each trial, one individual was placed on the central platform connecting all three habitat types underneath an inverted collecting vial. We waited until the spider was motionless (~1–3 min) and then lifted the vial. We recorded the initial habitat type that the spider was facing, the latency to first movement, and the first substrate type that an individual entered. After an individual made its first microhabitat choice, we recorded the substrate that he/she resided upon every 15 min for 2 h. All individuals were used only once within

their age category, but some penultimate females were tested a second time after reaching sexual maturity. Since there were not enough materials to replace substrates every trial, the same leaf litter, pine litter and red clay was used for all trials. The central platform was wiped down with alcohol in between every trial and we observed no influence of prior substrate use on observed microhabitat choice among our three experimental set-ups. Our experimental design did not control for odour and although it did not appear to pose a problem, future studies should attempt to control this variable.

RESULTS

Substrate Type and Transmission Characteristics

The seismic courtship signal of *S. retrorsa* showed less attenuation on leaf litter and pine litter as compared with red clay (Fig. 2). Using all substrates and all distances in the model, attenuation was dependent on substrate type (substrate: $F_{2,2} = 11.0673$, $P < 0.0001$, substrate*distance: $F_{2,2} = 5.2332$, $P = 0.0072$). Post hoc comparisons revealed no difference between leaf litter and pine litter, but significant differences between leaf litter and red clay, and pine litter and red clay ($P < 0.05$).

The seismic courtship signal of *S. retrorsa* showed differential filtering between substrates (as measured by 10-dB cutoff frequency; $F_{8,66} = 12.7003$, $P < 0.0001$). We found (1) that substrate affected the 10 dB cutoff (main effects: $F_{2,2} = 15.6744$, $P < 0.0001$), (2) that distance affected substrates differently (linear interaction term: substrate*distance, $F_{2,2} = 12.2812$, $P < 0.0001$), and (3) that the 10-dB cutoff changed with distance in a complex way (non-linear interaction: substrate*distance², $F_{2,2} = 8.3105$, $P = 0.0006$). All substrates behaved as low-pass filters,

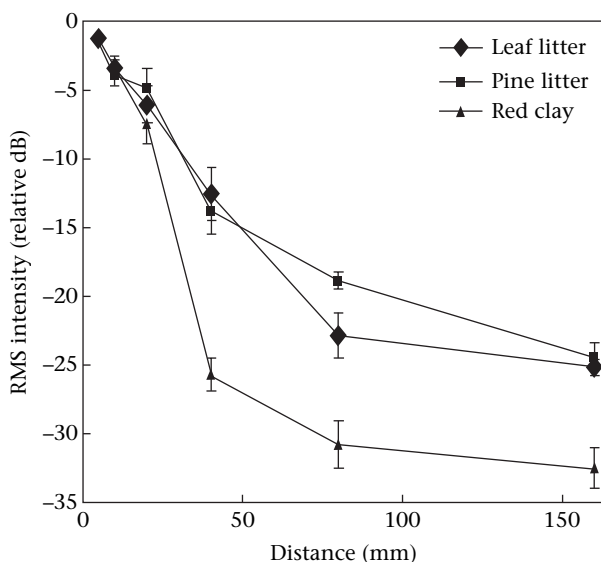


Figure 2. Root mean square attenuation across natural substrates. Relative dB was calculated using the shortest measured point to stimulus (5 mm) as a reference (0 dB). Leaf and pine litter transmit *Schizocosa retrorsa* signals with significantly less attenuation than red clay.

but the filtering characteristics of the three substrates changed with distance in a complex manner. Pine and leaf litter showed a steadily declining 10-dB cutoff with increasing distance as less of the signal spectrum was transmitted (Fig. 3a, b). For red clay (Fig. 3c), the 10-dB cutoff of the signal was initially low, but as distance increased the relative spectral range increased because of disproportionate attenuation of the low-frequency peak and the consequent flattening of the spectrum. After this period of increased 10-dB cutoff frequency, the cutoff steadily declined at larger distances. These patterns lead to low relative spectral range close to the source and high relative spectral range far from the source (Fig. 3c, d). Previous work examining the seismic characteristics of similar 'sandy' substrates have shown similar filtering curves with resonance peaks centering on 300 Hz (30–300 Hz: Hill & Shadley 2001; 300–400 Hz: Brownell & Van Hemmen 2001; 300–400 Hz: Aicher & Tautz 1990). Pairwise comparisons revealed significant differences between all substrate pairs and significant interactions between substrate and distance, and substrate and distance² (pine and red clay: substrate; $F_{1,1} = 26.5272$, $P < 0.0001$; substrate*distance; $F_{1,1} = 7.9616$, $P = 0.0071$; pine and leaf: substrate; $F_{1,1} = 17.6753$, $P < 0.0001$; substrate*distance²; $F_{1,1} = 4.1567$, $P = 0.0475$; leaf and red clay: substrate*distance; $F_{1,1} = 27.9832$, $P < 0.0001$; substrate*distance²; $F_{1,1} = 19.0468$, $P < 0.0001$).

To observe potential differences between substrates at distances where tactile and chemical cues are absent or reduced, we analysed a subset of the data by including only distances longer than the standing legspan (anterior to posterior) of a male *S. retrorsa* (<20 mm). We observed significant differences between substrates ($F_{5,39} = 13.9065$, $P < 0.0001$) but not distance or distance² ($P > 0.05$). Post hoc tests revealed significant differences between pine and leaf litter, and red clay and leaf litter ($P < 0.05$), but not between pine and red clay (Fig. 3d).

Substrate Type and Male Behaviour

For the substrate-based mate choice trials run in 1994, the presence/absence of male courtship was not dependent on substrate ($N = 33$, $\chi^2 = 0.93$, $P = 0.63$, Fig. 4a). There was also no difference in the latency to male chemoexploration across substrates (ln transformed data, leaf: $N = 5$, mean \pm SE = 2.0 ± 0.7 ; pine: $N = 8$, mean \pm SE = 1.8 ± 0.55 ; red clay: $N = 8$, mean \pm SE = 1.1 ± 0.55 ; $F_{2,18} = 0.69$, $P = 0.52$). However, the latency to male courtship was dependent on substrate type (ln transformed data, leaf: $N = 7$, mean \pm SE = 3.5 ± 0.37 ; pine: $N = 8$, mean \pm SE = 2.7 ± 0.34 ; red clay: $N = 9$, mean \pm SE = 2.1 ± 0.32 ; $F_{2,21} = 4.26$, $P = 0.028$; Fig. 4b). A Tukey–Kramer post hoc comparison of means revealed that males took longer to initiate courtship on leaf litter as compared with red clay ($P < 0.05$; Fig. 4b). Once courtship was initiated, the numbers of male foreleg waves and pushup displays did not differ among substrates (number of foreleg waves, $F_{2,6} = 0.34$, $P = 0.73$; number of pushups, $F_{2,11} = 0.0036$, $P = 1.0$).

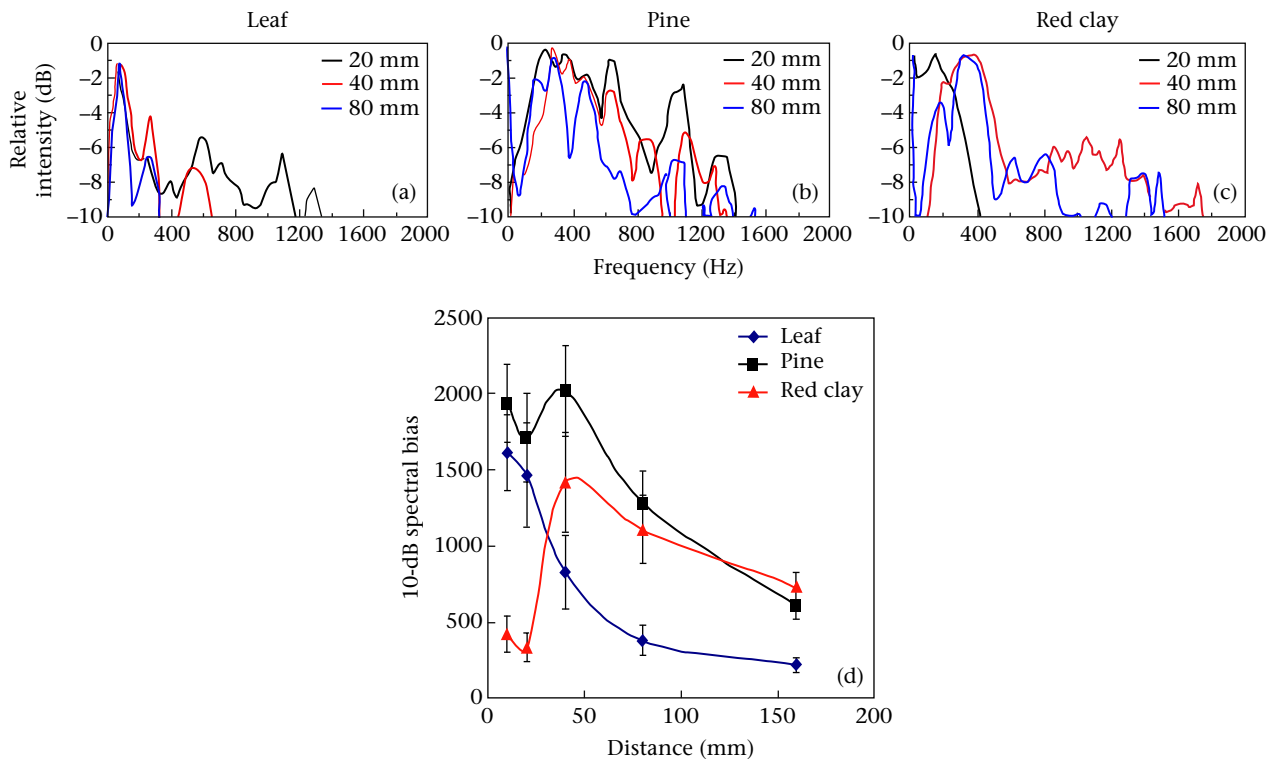


Figure 3. Differential filtering across natural substrates. Average transfer functions ($N = 5$) for (a) leaf litter, (b) pine litter, (c) red clay and (d) the 10-dB high-frequency cutoff for each of the different substrates. The 10-dB cutoff represents a measure of the relative range of the signal spectrum at each distance. Transfer functions are plotted normalized to the peak frequency at each distance (0 dB). Different colours represent transfer functions at different distances (black: 20 mm, red: 40 mm, blue: 80 mm). Pine litter and red clay have a higher relative spectral range than leaf litter.

Substrate Type and Copulation Frequency

Trials in 1994 were conducted before we discovered that female *Schizocosa* are typically not receptive immediately upon maturation (Norton & Uetz 2005) and several of the trials involved a female that was less than 6 days postmaturation moult (leaf: $N = 3$; pine: $N = 5$; red clay: $N = 6$). Thus, our analysis of copulation frequency only includes data on females that are at least 6 days postmaturation moult (the earliest age that a female mated in our experiments) and includes an even distribution of trials from all three substrate types from both 1994 and 2001 (1994: leaf: $N = 8$; pine: $N = 6$; red clay: $N = 5$; 2001: leaf: $N = 6$; pine: $N = 4$; red clay: $N = 7$; $\chi^2 = 0.91$, $P = 0.63$). Copulation frequency was dependent upon substrate type ($\chi^2 = 11.15$, $P = 0.004$; Fig. 5). Pairwise comparisons revealed that pairs were more likely to copulate on both pine litter and red clay than on leaf litter (leaf litter versus pine, $\chi^2 = 8.3$, $P = 0.004$; leaf litter versus red clay, $\chi^2 = 8.6$, $P = 0.003$; pine litter versus red clay, $\chi^2 = 0.006$, $P = 0.94$; Fig. 5). There was no difference in the age distribution of females across substrate types (leaf litter: $N = 14$, mean \pm SE = 13.3 ± 1.6 ; pine litter: $N = 10$, mean \pm SE = 14.6 ± 1.9 ; red clay: $N = 12$, mean \pm SE = 15.5 ± 1.7 ; $F_{2,33} = 0.45$, $P = 0.64$). Males of known age also did not differ across substrate types (leaf litter: $N = 5$, mean \pm SE = 25.2 ± 3.76 ; pine litter: $N = 5$, mean \pm SE = 21.2 ± 3.76 ; red clay: $N = 7$, mean \pm SE = 21 ± 3.17 ; $F_{2,14} = 0.42$, $P = 0.66$). The remaining males were

already mature when they were collected and thus, they were of unknown age. However, there was an even distribution of mature-collected males across all treatments ($\chi^2 = 2.0$, $P = 0.38$).

Substrate Type and Habitat Choice

A total of eight subadult females, 18 adult females, 10 subadult males and 16 adult males were used in the habitat choice trials. Within each age class, individuals were only used once, but four females were used as subadults and then again as adults. The individual's first choice of microhabitat did not depend on the age/sex category of individuals ($\chi^2 = 5.36$, $P = 0.5$; Table 1). When we pooled all individuals, first choice did not depend on age (subadult versus adult, $\chi^2 = 0.64$, $P = 0.72$) or sex (female versus male, $\chi^2 = 2.1$, $P = 0.36$). The microhabitat upon which individuals were observed most often also did not depend on age/sex category ($\chi^2 = 5.86$, $P = 0.44$; Table 1). Again, when all individuals were pooled, the majority choice did not depend on age ($\chi^2 = 2.1$, $P = 0.36$) or sex ($\chi^2 = 3.5$, $P = 0.18$). Of the four females that were used as a subadult and again as an adult, two of them retained the same overall preference (red clay) and all of them showed a different first choice.

The distribution of an individual's initial choice of microhabitat was not significantly different from random,

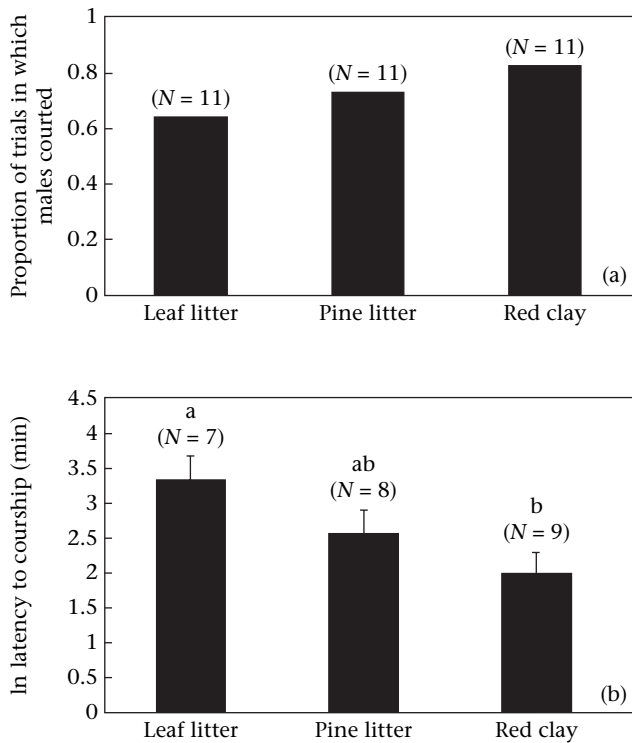


Figure 4. Male *Schizocosa retrorsa* courtship behaviour across three natural substrates. (a) The presence/absence of male courtship did not vary among substrate type. (b) Males took longer to initiate courtship on leaf litter as compared with red clay. Shared letters indicate no statistical difference ($P > 0.05$).

although individuals tended to choose leaf litter on average twice as often as either pine litter or red clay (leaf observed = 49%; pine observed = 26%; red clay observed = 26%; all expected = 33%; $\chi^2 = 4.4$, $P = 0.11$). 'Majority habitat choice' was also random, again with more individuals tending to reside on leaf litter more than the other two substrates (leaf observed = 45%; pine observed = 20%; red clay observed = 35%; all expected = 33%; $\chi^2 = 4.6$, $P = 0.10$).

When including all four age/sex categories, the number of times an individual moved between habitats was

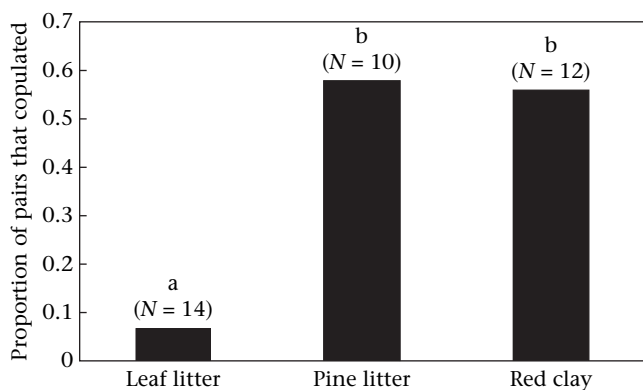


Figure 5. Among-substrate differences in copulation success. Pairs were significantly more likely to copulate on pine litter and red clay as compared with leaf litter. Shared letters indicate no statistical difference ($P > 0.05$).

Table 1. Substrate type and individual movement pattern (proportion of individuals on each substrate type)

Individual's substrate choice	Age/sex category	N (no. of individuals)	Leaf litter	Pine litter	Red clay
First choice	Subadult female	8	0.63	0.13	0.25
	Adult female	18	0.28	0.22	0.5
	Subadult male	10	0.3	0.4	0.3
	Adult male	16	0.44	0.31	0.25
Majority choice	Subadult female	8	0.5	0.13	0.38
	Adult female	18	0.22	0.22	0.56
	Subadult male	10	0.6	0.2	0.2
	Adult male	16	0.5	0.19	0.31

independent of their category (subadult female, mean \pm SE = 0.13 ± 0.72 ; adult female = 2.0 ± 0.48 ; subadult male = 1.5 ± 0.64 ; adult male = 2.4 ± 0.51 ; $F_{3,48} = 2.34$, $P = 0.08$). When all individuals were pooled, the number of times an individual moved between microhabitats did not depend on sex ($F_{1,50} = 1.1$, $P = 0.3$), but it did depend on age, with adult individuals moving more frequently than subadults (subadult individuals, $N = 18$, mean \pm SE = 0.89 ± 0.48 ; adult individuals, $N = 34$, mean \pm SE = 2.18 ± 0.35 ; $F_{1,50} = 4.67$, $P = 0.035$).

DISCUSSION

Results from the multiple independent experiments presented here suggest that substrate-type influences reproductive communication and associated behaviours in the wolf spider *S. retrorsa*. Despite the fact that males produce percussive broadband seismic signals that excite the natural frequency response of any substrate (Pierce 1989) and thus are likely not matched to any specific microhabitat characteristics, we found mating frequency to be highest on *S. retrorsa*'s natural substrates of pine litter and red clay. Males courted more quickly upon these natural substrates as compared with leaf litter, yet once initiated, courtship behaviour was not substrate dependent, indicating that our observed pattern of copulation success is not likely attributable to differences in male behaviour among substrates. Seismic signal playbacks show that *S. retrorsa*'s seismic signal transmits best in terms of attenuation on leaf litter and pine litter and attenuates the most on red clay. As such, it seems unlikely that differential seismic signal attenuation is responsible for our observed substrate-dependent mating success. Regardless, in combination, our results show a close connection between the substrates upon which *S. retrorsa* is naturally found (pine litter and red clay) and female receptivity as measured by copulation frequency.

Although our results show substrate-dependent signalling success, with our available sample sizes, we were

unable to find statistical evidence for substrate-specific habitat choice. Individuals tended to prefer leaf litter, the only substrate upon which they are not normally found in the field, over pine litter and red clay. However, in assessing individual movement patterns among the substrates of leaf litter, pine litter and red clay, regardless of age or sex, we found that individuals did not show microhabitat choice with respect to either the substrate upon which they were found most often or the substrate that they chose to enter first. Thus, although our data are not sufficient to rule out some level of substrate preference, they are sufficient to rule out a preference for the two naturally used substrates (pine litter and red clay) over leaf litter. The only observed difference in movement pattern was between immature individuals and adults. Adults moved between habitat types more frequently than immature individuals, but we found no difference between the sexes. This difference in locomotor activity between age groups could potentially result from differential motivation between the groups regarding foraging or even mate searching. Under more natural conditions, there are likely to be many other environmental factors that influence microhabitat choice and movement patterns such as the presence/abundance of prey, predators and conspecifics, moisture levels and light levels.

Because of the broadband nature of percussive signals and the observation that this species is often found on at least two differing substrates, we originally hypothesized that the percussive seismic signal used by *S. retrorsa* males enabled them to signal effectively across diverse substrates. As we show here, pine litter, leaf litter and red clay have very different transmission properties. Our playback experiments show that signalling environment significantly influences both attenuation and filtering of *S. retrorsa* males' seismic signals. The attenuation data reveal that red clay, at all frequency ranges, attenuates the signal significantly more than either leaf litter or pine litter. Taken in combination with our mate choice data, differential attenuation between substrates is likely not a principal factor underlying our observed mating differences, as leaf litter and pine litter appear to transmit the signal best. In contrast, our frequency filtering analysis sorts the substrates in a way that could be consistent with our mate choice data. While we found all substrates to differ in their frequency filtering, at longer distances both pine litter and red clay transmitted signals of higher relative spectral range than leaf litter. Overall, red clay transmitted signals more poorly than either of the other substrates, but when comparing the spectra of the best transmitted frequencies, red clay was more similar to pine litter than leaf litter. This pattern could be consistent with our mate choice results under a scenario where female receptivity is dependent on the relative spectral properties of courtship signals, specifically high-frequency content and not overall signal intensity. Although potentially consistent with our results, frequency-specific female preferences, perception and/or processing clearly require further examination. For example, evidence that females are preferentially 'tuned' to perceive higher bandwidth/high-frequency signals, or evidence suggesting that female mate choice decisions are based solely upon the relative presence or proportion of

high-frequency seismic components would provide strong evidence of a substrate-preference match. Work on the wandering spider, *Cupiennius salei*, has demonstrated that female spider interneurons can indeed be tuned to different frequency ranges present in male communication signals and that these signals can be detected at extremely low intensities (Speck-Hergenroeder & Barth 1987; Barth 1998, 2002). Such evidence in *S. retrorsa* would again highlight the need to consider receiver psychology when contemplating questions of signal evolution (Guilford & Dawkins 1991; Rowe 1999; Hebets & Papaj 2005).

Although this study focused specifically on seismic signal transmission, our observed pattern of copulation frequency across substrates may be the result of substrate-specific visual signal efficacy, as visual signals have been observed to be important in many aspects of *Schizocosa* sexual communication (Stratton & Uetz 1981, 1983, 1986; Hebets et al. 1996, 2006; McClintock & Uetz 1996; Scheffer et al. 1996; Hebets & Uetz 1999, 2000; Uetz & Roberts 2002; Hebets 2003, 2005; Stratton 2005; Taylor et al. 2005). Differences likely exist in structural visual complexity across our different substrates with red clay for example introducing fewer visual obstacles than leaf litter. Measuring substrate influences on visual signal efficacy and its relationship to female mate choice was beyond the scope of this study. However, mate choice trials conducted in the light versus the dark suggest that the visual signal is not necessary for successful copulation in *S. retrorsa* (E. A. Hebets, unpublished data). Future work is clearly needed to tease apart the putative importance of seismic components versus visual signal efficacy, or some combination of the two, on the reproductive behaviour of this species.

The percussive seismic signal production in *S. retrorsa* is in stark contrast to the sound production mechanisms of another locally abundant *Schizocosa* species in Mississippi, *S. stridulans* (Elias et al. 2006). While *S. stridulans* is found in the same general geographical area as *S. retrorsa*, their signalling substrates differ greatly as *S. stridulans* is found predominantly on leaf litter (E. A. Hebets, personal observation). The seismic signals of *S. stridulans* are produced using a combination of pedipalpal stridulation and abdominal vibrations (tremulations; Elias et al. 2006). Seismic signals in this species have stronger low-frequency components than *S. retrorsa*: a pattern predicted if signals were matched to leaf litter microhabitats. Data from both *S. retrorsa* and *S. stridulans* suggest that while communication in these two *Schizocosa* species is matched to their natural habitats, the mechanisms underlying this pattern may be very different between the two species. *Schizocosa stridulans* potentially shows a seismic signal-substrate match, where signals are matched to the average transmission characteristics of their signalling environment. In contrast, *S. retrorsa* may show a substrate preference or tuning match, with receiver perception/processing/decision-making matched to the average transmission characteristics of their signalling environment.

In summary, animal displays have been hypothesized to be optimally designed for their particular signalling environments. This match has been implicated as a major force driving signal evolution and species diversification

(for review see Boughman 2002). Up until now, this match has been demonstrated mostly in studies showing adaptations of senders to increase signal efficacy across particular substrates (signal-substrate match). Receiver roles in these studies have generally been overlooked or assumed to be in congruence with sender behaviour. Sender and receiver behaviour, however, need not be in agreement and such antagonistic coevolution is a major factor driving mating systems (for overview see Arnqvist & Rowe 2005). As suggested in our discussion, receiver behaviour can be adapted to particular substrates regardless of male behaviour (substrate-preference match). To understand mating systems and sender–receiver coevolution, it may be important to understand not only sender, but also receiver adaptations to local signalling environments.

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