Current Zoology 56 (3): 370–378, 2010

A signal-substrate match in the substrate-borne component of a multimodal courtship display

Damian O. ELIAS [1], Andrew C. MASON [2], Eileen A. HEBETS [3*]

[1] Department of Environmental Science, Policy and Management, University of California, Berkeley, Berkeley, CA 94720, USA
[2] Integrative Behaviour and Neuroscience Group, University of Toronto Scarborough, Toronto, ON, M1C 1A4, Canada
[3] School of Biological Sciences, University of Nebraska, Lincoln, NE 68588, USA

Abstract The environment can impose strong limitations on the efficacy of signal transmission. In particular, for vibratory communication, the signaling environment is often extremely heterogeneous at small scales. Nevertheless, natural selection is expected to select for signals well-suited for effective transmission. Here, we test for substrate-dependent signal efficacy in the wolf spider *Schizocosa stridulans* Stratton 1991. We first explore the transmission characteristics of this important signaling modality by playing recorded substrate-borne signals through three different substrates (leaf litter, pine litter, and red clay) and measuring the propagated signal. We found that the substrate-borne signal of *S. stridulans* attenuates the least on leaf litter, the substrate upon which the species is naturally found. Next, by assessing mating success with artificially muted and non-muted males across different signaling substrates (leaf litter, pine litter, and sand), we explored the relationship between substrate-borne signaling and signaling substrate for mating success. We found that muted males were unsuccessful in obtaining copulations regardless of substrate, while mating success was dependent on the signaling substrate for non-muted males. For non-muted males, more males copulated on leaf litter than any other substrate. Taken together, these results confirm the importance of substrate-borne signaling in *S. stridulans* and suggest a match between signal properties and signal efficacy – leaf litter transmits the signal most effectively and males are most successful in obtaining copulations on leaf litter [*Current Zoology* 56 (3): 370–378, 2010].

Key words Environmental heterogeneity, Sensory drive, Mate choice, Communication

Attributes of the environment impose constraints on the propagation of signals used in communication (Endler, 1992, 1993; Endler and Basolo, 1998) and as a result, signaling environments can have significant effects on communication behavior, sensory physiology and signal evolution (Endler, 1992; Basolo and Endler, 1995; Boughman, 2002). The medium through which a signal propagates may alter signal properties through a variety of processes including such things as differential propagation (*i.e.* filtering) and/or attenuation. Natural selection is predicted to result in the evolution of signals and signaling behavior that minimize environmental degradation (Endler, 1992). One of the consequences of this process is that signals evolve to match the average transmission characteristics of signaling environments (signal-substrate match) and this has now been demonstrated in a variety of animal systems and across a variety of signaling modalities, e.g., visual signals; Boughman, 2001; Gray et al., 2008; Seehausen et al., 2008 (fish); Nava et al., 2009 (geckos); Shultz et al., 2008 (damselflies): airborne acoustic signals: Brumm and Naguib, 2009; Kirschel et al., 2009; Nemeth et al., 2001; Richards and Wiley, 1980; Ryan and Brenowitz, 1985; Wiley, 1991 (birds); substrate-borne vibratory signals: Elias et al., 2004; Hebets et al., 2008 (spiders).

One particular signaling modality that has recently received much attention is vibration (Michelsen et al., 1982; Markl, 1983; Barth, 1985; Kalmring, 1985; Aicher and Tautz, 1990; Cocroft, 1996; Barth, 1998; Magal et al., 2000; Cocroft, 2001; Fischer et al., 2001; Hill, 2001; Elias et al., 2003; Cokl et al., 2004; Elias et al., 2004; Rodriguez et al., 2004; Virant-Doberlet and Cokl, 2004; Cocroft and Rodriguez, 2005; Elias et al., 2006; Stewart and Sandberg, 2006; Gibson and Uetz, 2008; Hebets et al., 2008; McNett and Cocroft, 2008; Hill, 2009; Uetz et al., 2009). Animals that communicate via substrate-borne vibrations are widespread and arthropods, in particular are renowned for incorporating vibratory signals in their communication repertoire (reviewed in Hill, 2008). The media through which vi-

Received Feb. 10, 2009; accepted Feb. 20, 2010
∗ Corresponding author. E-mail: ehebets2@unl.edu
© 2010 *Current Zoology*

bratory signals travel are often extremely variable and heterogeneous and may change dramatically at relatively small scales (Michelsen et al., 1982; Magal et al., 2000; Elias and Mason, in press). It has been suggested in various taxa (*e.g.* planthoppers, green stink bugs, treehoppers, spiders) that variable filtering and attenuation characteristics of different vibratory signaling substrates have had significant effects on signal evolution (Magal et al., 2000; Elias et al., 2004; Cokl et al., 2005; Casas et al., 2007; Cokl et al., 2007; Hebets et al., 2008) and species diversification (Rodriguez et al., 2004; Cocroft et al., 2006; McNett and Cocroft, 2008; Rodriguez et al., 2006; Rodriguez et al., 2008).

Spiders have recently been used as model systems to study substrate-borne (*i.e.* seismic) vibratory communication, in particular wolf spiders of the genus *Schizocosa* (Uetz and Stratton, 1982; Stratton and Uetz, 1983; Hebets and Uetz, 1999; Barth, 2002; Elias et al., 2005; Elias et al., 2008; Gibson and Uetz, 2008; Hebets, 2008; Hebets et al., 2008; Uetz et al., 2009; Elias and Mason, In Press). The wolf spider genus *Schizocosa* consists of 23 described Nearctic species (see Dondale and Redner, 1978; Stratton, 2005) most of which use substrate-borne courtship displays, with some also incorporating visual courtship components. Within *Schizocosa*, species can be categorized into two groups based upon their main method of substrate-borne signal production (Stratton, 2005) - species that produce substrate-borne signals primarily by percussion ("drummers") (e.g. Hebets et al., 2008), and species that produce substrate-borne signals primarily by palpal stridulation, though often in combination with abdominal tremulations and/or percussion ("stridulators") (e.g. Elias et al., 2006). Hebets et al. (2008) proposed that "drummers" may be able to exploit a variety of different signaling habitats, as percussive signals contain broad frequency content allowing at least some signal energy to match a wide range of habitat "filters". To test this idea, they studied the drumming *Schizocosa* wolf spider, *S. retrorsa* (Banks). They quantified substrate-borne signal transmission across different substrates and determined that there was substrate-dependent attenuation and filtering (Hebets et al., 2008). They also documented substrate-dependent mating success in *S. retrorsa*. The substrates upon which pairs were most likely to mate, however, did not match the substrates through which the substrate-borne signal attenuated least (Hebets et al., 2008). Thus, although they found substrate-dependent signaling success, they did not find a signal-substrate match. Ultimately, the substrate-borne courtship component of *S. retrorsa* did not appear to be well matched, in terms of signal transmission, to the natural signaling substrates upon which the species is typically found. Rather, *S. retrorsa* appeared to employ a "generalist" substrate-borne signal and substrate mating preferences were determined by other factors.

In contrast to percussive "drummers" such as *S. retrorsa*, that utilize general morphological features such as pedipalps and and/or forelegs to produce percussive signals, "stridulators" use more specialized structures (*i.e.* stridulatory structures) to produce vibratory signals. These signal-producing structures tend to generate signals with specific frequency characteristics (Dumortier, 1963; Huber et al., 1989; Gerhardt and Huber, 2002), which may limit effective signal transmission in some signaling environments (Elias et al., 2006). Thus, one might predict that the effective transmission of the substrate-borne courtship component of "stridulators" will be more tightly linked to specific signaling substrates than those of "drummers" and that receivers have substrate-dependent responses that match the transmission characteristics. Here, we test this hypothesis using the stridulating wolf spider *S. stridulans*.

Schizocosa stridulans males possess black pigmentation on the foreleg femora and short black hairs ("brushes") on the tibiae (Stratton, 1991, 2005; Hebets, 2008). Male *S. stridulans* courtship consists of both visual and substrate-borne signals. Visual signals involve a "double leg tap" in which the two legs are rapidly tapped on the substrate asynchronously (Stratton, 1991; Stratton, 2005). "Double taps" also have a substrate-borne component resulting from the impact of the legs against the substrate (Elias et al., 2006). In addition to "double taps", *S. stridulans* produce substrate-borne courtship signals involving independently produced palpal stridulations and abdominal tremulations (Elias et al., 2006). In a recent experiment, Hebets (2008) demonstrated that in *S. stridulans*, the substrate-borne courtship signal is most important for mating success and that substrate-borne signals carry both location and identify information.

In order to test for substrate-dependent signal efficacy in *S. stridulans*, we examined both substrate-borne signal transmission characteristics and over-all mating success across multiple signaling substrates. We first examined substrate-borne signal transmission across three different naturally occurring signaling substrates - leaf litter, pine litter, and red clay. Next, we examined the relationship between substrate-borne signal efficacy and mating success by examining copulation frequencies of both muted

and non-muted courting males across signaling substrates of leaf litter, pine litter, and sand. Our results confirm the importance of substrate-borne signaling in *S. stridulans* and demonstrate that the substrate that transmits signals most efficiently is also the substrate where males are most successful in obtaining copulations.

1 Materials and Methods

One hundred and sixteen *S. stridulans* individuals (penultimate males and females and mature males) were collected at night from Panola County in northern Mississippi (near Sardis Reservoir) in the spring of 2004 and 2007. Spiders were housed individually in the laboratory under a 12L:12D light cycle and were provided 2-3 crickets once per week and a constant source of water.

1.1 Substrate-borne signal transmission characteristics

We measured signal transmission by playing *S. stridulans* substrate-borne signals through different signaling substrates gathered from *Schizocosa* collection sites in northern Mississippi (leaf litter, pine litter, and red clay). Playback signals consisted of a male *S. stridulans* signal acquired using laser vibrometry (LDV, Polytec OFV 3001 controller, OFV 511 sensor head, Waldbronn, Germany). The male *S. stridulans* signal was recorded on a substrate of stretched nylon fabric at a distance of >2mm from the courting male. This technique has been successfully used in previous studies as attenuation is minimal at close distances from the sender source (Hebets et al., 2008). Playbacks of *S. stridulans* male courtship signals were generated using a mini-shaker (B&K Type 4810 Mini-shaker, B&K Type 2706 Power Amplifier) placed in a plastic box (35 cm×25 cm ×14 cm) filled with one of the test substrates (leaf litter, pine litter, or red clay) (Hebets et al., 2008). The mini-shaker was positioned so that the moving element was at the surface of each of the test substrates. We recorded propagated vibrations with the LDV sensor head attached to a translation stage (Newport Model 421). Signal measurements were taken at 5 mm, 10 mm, 20 mm, 40 mm, 80mm, and 160mm from the minishaker source.

Five replicates for each substrate-type were measured. For each replicate, the substrate was re-introduced and the mini-shaker source re-positioned. New substrate material was used in each replicate when possible. By introducing new substrate sources we incorporated substrate variability into our measurements (see below). The same male *S. stridulans* recording was used for each substrate replicate.

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 5mm point (0 dB attenuation). To analyze our attenuation data we used a polynomial ANCOVA with substrate as the independent variable, RMS amplitude as the dependent variable, and distance and distance^2 as covariates. If the model was significant, we performed a Least Squares Means Differences Tukey post-hoc test. Distance^2 was used in the model to account for non-linear attenuation of signals.

1.2 Substrate and signaling success

Signaling arenas Three signaling substrates: leaf litter, pine litter, and sand, were gathered from *Schizocosa* collection sites in northern Mississippi. The substrates used for the signal transmission and mating trials were collected in different years and red clay was not available for the mating trials. Regardless, red clay, sand, and pine litter are all naturally occurring substrates upon which *Schizocosa stridulans* is not normally found only leaf litter represented a 'typical' signaling substrate for *S. stridulans.* A stock of each of our three substrates was taken to the laboratory where they were immediately placed in a -20 freezer for a minimum of 3 days prior to initial use. This was done in an attempt to kill any organisms that might have been residing in the naturally collected substrates. Signaling arenas consisted of circular plastic containers measuring 20.3 cm diameter by 7.6 cm height (Pioneer Plastics, Inc.) filled approximately 5 cm deep with one of the three substrates. During the course of a single day, the same substrate materials were used for each treatment (e.g. the same leaves, pine needles, and sand grains). However, between each trial within a day, all materials were removed, the arena was cleaned with alcohol, and the materials were replaced in a haphazard fashion. Thus, the substrate configuration for each trial was different, mimicking natural substrate variation across space and time. At the end of every day, substrate materials were removed and placed in the freezer within the larger stock of substrate material. A mite infestation in a previous year led to this protocol of freezing substrate material day-to-day, in an attempt to reduce the likelihood of spreading mites among our test animals via shared substrates. We did not observe mites on any of the spiders used in this experiment. Between days different amalgamations of substrate materials from the stocks were used. We found no effect of date (a reflection of potential substrate re-use) on the likelihood to copulate ($\chi^2 = 2.63$, $df = 1$, $P = 0.11$) and no interaction between

date and substrate on the likelihood to copulate (substrate × date $\chi^2 = 3.61$, $df = 2$, $P = 0.16$).

Male manipulations Upon maturation, males were randomly assigned a substrate-borne signaling treatment: muted or non-muted. Mature males were muted in a similar fashion as in Elias et al. (2006). Briefly, males were placed in the freezer for several minutes to reduce over-all activity levels. Once motionless, they were situated directly on top of ice chips in a Petri dish under a dissecting scope. Using a piece of wire with a small loop at the tip connected to a soldering iron with an adjustable heat source, we melted drops of a 50/50 mixture of violin rosin (WM Lewis & Son, Elkhard, IN USA) and beeswax onto the motionless animals. For our muted males, we waxed the tibio-cymbial joint to prevent pedipalp stridulation. In addition, we waxed the prosoma (cephalothorax) to the opisthosoma (abdomen) to prevent abdominal movements. These same manipulations have previously been shown to prevent the production of substrate-borne courtship signals while leaving all visual signals unaffected (see Elias et al. 2006). For our non-muted males, we placed a drop of the same wax mixture on the dorsal surface of the prosoma (cephalothorax). Prior to mating trials we verified that males were able to successfully capture prey. Our manipulations did not adversely affect male locomotion or behavior in any qualitatively noticeable fashion.

Mating trials During a single set of observations, a single male and female pair were placed in each of the three signaling arenas (leaf litter, pine litter, and sand) for both the muted and non-muted treatments, resulting in six arenas each with a female-male pair (muted: leaf, pine, and sand; non-muted: leaf, pine, and sand). The arenas were arranged as two sets, each with one representative substrate, forming two triangles on the bench top. Each individual arena was encircled with a skirt of white paper to prevent external visual stimuli. One arm of a fiber optic light source was placed above the center of each set of three arenas and was never moved. Between trials the placement of each signaling substrate was rotated to overcome any effect of light and/or location on mating outcome.

Eighty seven mature virgin females (15–29 days post maturation; mean = 20.4 days post maturation, SE =0.26) were randomly assigned a signaling substrate and male signaling treatment (*i.e.* leaf litter/muted male, $n = 14$; leaf litter /non-muted male, $n = 15$; pine litter/muted male, $n = 14$; pine litter/non-muted male, $n = 15$; sand/muted male, $n = 14$; sand/non-muted male, $n = 15$). We used a repeated measured design where individual males (14 muted, 15 non-muted) were run across all three substrates, but females were used only once. Females were placed in their signaling arena a minimum of one hour prior to the start of the trial so they could both acclimate and lay down silk. Mature males were then introduced and female-male pairs were allowed to interact for 45 minutes. The pairs were observed in real-time throughout the trial and we recorded the time to first courtship (when possible) and copulation. We used a repeated measures design where individual males were run through each of the three substrate types in a haphazard order. The number of days in between trials for males ranged from 1– 6 with an average of 2.2 (SE = 0.15) and there was no difference in the average number of days between trials for muted versus non-muted males (Wilcoxon Test, $\chi^2 = 0.73$, $P = 0.39$). Males that copulated were always given at least 2 days between trials.

A Chi-Square test was used to determine if copulation frequency was dependent on male substrate treatment. A repeated measures Cochran's Q test was then used to test the hypothesis that mating success was independent of substrate. All time data (*e.g.* latency to first courtship) was natural log transformation and a repeated measure ANOVA was used to test for differences in latencies across substrates.

2 Results

2.1 Substrate-borne signal transmission characteristics

The substrate-borne courtship signal of *S. stridulans* shows less attenuation on leaf litter as compared to pine litter or red clay. Using all substrates and all distances in the model, attenuation curves were dependent on substrate type (substrate × distance: $F_{2,2} = 16.633$, $P < 0.0001$; substrate × distance^2: $F_{2,2} = 11.563$, $P < 0.0001$; Fig. 1). Post-hoc comparisons revealed significant differences between leaf litter and pine litter ($P < 0.0001$), leaf litter and red clay ($P < 0.0001$), and pine litter and red clay ($P < 0.0001$).

2.2 Substrate and signaling success

Using a repeated measures design, a total of 29 males (14 muted and 15 non-muted) were tested on all three substrate types, resulting in 87 female-male pairings. Only one muted male copulated (on sand) whereas 11 of the non-muted males copulated at least once (Fig. 2A). Copulation frequency was dependent on male substrate treatment – non-muted males were more likely to copulate than muted males ($\chi^2 = 11.73$, $P = 0.0006$; Fig. 2A). A Cochran's Q test run only on non-muted males

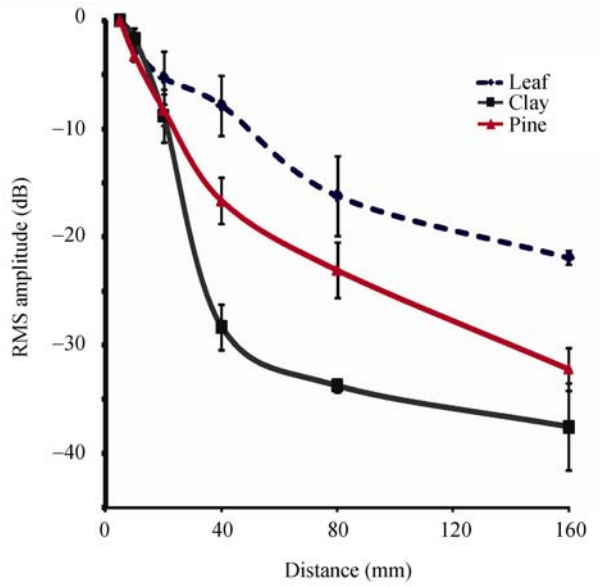

Fig. 1 Root mean square (RMS) attenuation across natural substrates

Relative dB was calculated using the shortest measured point to stimulus (5 mm) as a reference (0 dB). Leaf litter transmit *Schizocosa stridulans* signals with significantly less attenuation than red clay or pinle litter substrates.

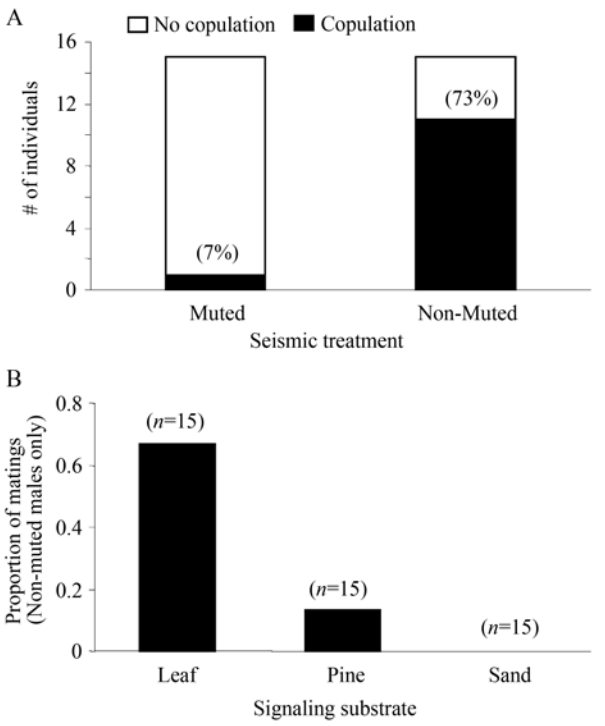

Fig. 2 Copulation success for experimentally manipulated males across natural substrates

A. Across all natural substrates, non-muted males had greater copulation success than muted males. B. For non-muted male treaments, males were more likely to mate on leaf litter than other available natural substrates (sand and pine litter).

revealed that copulation frequency was dependent on signaling substrate (Q = 15.27, P = 0.0005; Fig. 2B). Individual paired comparisons revealed that non-muted males mated more on leaf litter than pine litter (Q = 6.4, P = 0.01) and sand (Q = 10, P = 0.002) but mating frequencies were not different between pine litter and sand (Q = 1, P = 0.16). Only one individual copulated more than once, on both leaf litter and pine litter. Latency to copulation on leaf litter averaged 22 minutes (n = 10; SE = 4.36) and 21.9 minutes on pine litter (n = 2; SE 14.2).

The distribution of first substrates experienced did not differ between muted and non-muted males (muted males: leaf litter 1st = 5, pine litter 1st = 5, sand 1st = 3; non-muted males: leaf litter 1st = 4, pine litter first = 5, sand 1st = 6; χ^2= 0.99, P = 0.61). Two males mated on their first trial, three on their second, and eight on their third. This distribution did not differ from the null expectation of copulation success being independent of mating trials (*i.e.* a null expectation of 33% for each mating trial) (Probability test of 0.33 across trail #, χ^2 = 4.5, P = 0.1). The one male that mated repeatedly, mated on its 2nd and 3rd trial.

Due to the complexity of the substrates, it was often not possible to locate males at all time points during a trial. As a result, we do not have complete data on the likelihood to court among substrates - we often could not confirm the presence/absence of male courtship. However, courtship was confirmed for 67% of trials with muted males (n = 28/42) and 84% of trials with non-muted males (n = 38/45). Courtship was easier to confirm for non-muted males since we could hear a male's courtship even if we could not locate him visually. Across substrates, 79% of males were confirmed to court on leaf litter, 62% on pine litter, and 86% on sand. The lower proportion of males known to court on pine litter reflects the difficulty in both hearing courtship and in visually locating a courting male on pine litter. Essentially, both leaf litter and pine litter proved difficult for observations, but on leaf litter we could frequently confirm courtship simply by listening for the male's substrate-borne signal. The latency to the start of courtship did not differ among males or among substrates (Repeated Measures MANOVA, between males: $F_{1,9}$ = 0.89, P = 0.37; within males: substrate, $F_{2,8}$ = 0.39, P = 0.69, substrate × male, $F_{2,8}$ = 0.24, P = 0.79).

Fifty percent of the males used were collected mature and the distribution of mature males between the muted and non-muted treatments did not differ (muted males: 64% collected mature, non-muted males: 40% collected mature; χ^2 = 1.7, P = 0.19). Of the males that were not

collected mature, there was no difference in average male age between muted and non-muted males ($F_{1, 13}$ = 0.21, P = 0.66). Female age ranged from 15 – 29 days post maturation molt and mean female age did not vary among treatments ($F_{5, 86}$ = 0.34, P = 0.89).

3 Discussion

By combining a quantitative assessment of substrate-borne signal transmission across substrates and mating trials using muted and non-muted males across similar substrates, we were able to demonstrate a match between signal transmission and mating behavior. Specifically, the substrate-borne courtship component of *S. stridulans* was shown to transmit best (*i.e.* attenuate least) on leaf litter as compared to both pine litter and red clay. Additionally, mating trials with muted males confirmed that the substrate-borne courtship component is crucial to mating success, with only 1 out of 42 mating trials with a muted male resulting in copulation. Finally, for non-muted males, copulation success was substrate-dependent, as males were more likely to copulate on leaf litter as compared to either pine litter or sand. *Schizocosa stridulans* is naturally found only in leaf litter habitats, despite their close physical proximity to pine, sand and clay substrates inhabited by other *Schizocosa* species (*e.g. S. retrorsa,* Hebets, pers obs.). Together our results suggest that the signaling environment occupied by *S. stridulans* may provide (have provided) strong selection pressure influencing the evolution and function of their courtship signals.

Our vibratory playback experiment revealed that leaf litter attenuates the substrate-borne courtship signal of *S. stridulans* less than either pine litter or red clay. Similar results were recently obtained using the "drumming" wolf spider *S. retrorsa* (Hebets et al., 2008) – the substrate-borne signal transmitted with least attenuation on leaf litter. In *S. retrorsa* this result was driven by the attenuation properties at low frequencies – leaf litter passes low frequencies with little to no attenuation. Given the properties of our chosen signaling substrates, it is not surprising that leaf litter transmits the vibratory signals of *S. stridulans* most effectively as well — as male *S. stridulans* concentrate signal energy at these lower frequencies (Elias et al., 2006). However, for *S. retrorsa,* signal transmission results did not match the mating success data - pairs copulated more on pine litter and red clay despite the higher signal attenuation, suggesting that females did not select males based on the lower frequency characteristics of their substrate-borne signals (Hebets et al., 2008).While variation in the properties of the signaling substrate has been implicated as an important force driving assortative mating and species evolution in other taxa, the majority of empirical evidence comes from systems where environmental variation occurs in one medium (e.g. water, air) - for example, at extreme differences in water depth among three spine sticklebacks or across different host plant species for planthoppers (Boughman, 2001, 2002; Seehausen, 2002; Cocroft et al., 2006; Rodriguez and Cocroft, 2006; McNett and Cocroft, 2008; Rodriguez et al., 2008; Seehausen et al., 2008; Stelkens and Seehausen, 2009; Elias and Mason, In Press). In many vibratory signaling environments, however, individuals will encounter a variety of signaling substrates (leaf litter vs. sand vs. pine litter) at short distances, each with different physical properties (Elias and Mason, In Press). In jumping spiders, males of some species appear well adapted to particular signaling substrates over others that are equally available (Elias et al., 2004). Similarly, in *S. stridulans*, our results suggest that males are better adapted to signaling via substrates on which the species typically occurs than other available environments.

Having signal components matched precisely to particular signaling environments/substrates may facilitate more effective information transfer (Hill, 2009). For example, with reduced variability in effective signal transmission due to a tight signal-substrate match, selection pressure for increased accuracy or quantity of information may be amplified. In other words, since variability in signal transmission is likely reduced in systems with signal-substrate matches, the variability detectable by receivers may be more likely to reflect attributes of the signaler. In support of this idea, in systems where animals show signal-substrate matches, females appear to use multiple signal properties for mate choice decisions. For example, plant hopper females use both frequency and timing information in signals (Cocroft and Rodriguez, 2005). In contrast, in systems where the signaling environment is more variable, mate choice appears to be solely based on simple temporal characteristics like rate (Parri et al., 1997). While it is unknown what specific substrate-borne signal characteristics females use to choose mates in *S. stridulans*, results from other studies suggest that male signals may carry multiple forms of information. Male *S. stridulans* for example, produce complex substrate-borne signals using percussion, stridulation and tremulation, encompassing the entire known diversity of spider sound production mechanisms (Uetz and Stratton, 1982; Stratton,

2005; Elias et al., 2006). Elias et al. (2006) suggested that different components of the male substrate-borne signal transmit different forms of information ("multiple messages") and behavioral assays have demonstrated that females can obtain both location and identity information from a male's seismic courtship signal (Hebets, 2008). As our study manipulated the presence or absence of substrate-borne signals overall, we unfortunately could not examine the contribution of specific signal components and further research is necessary to explicitly test these ideas.

Schizocosa stridulans males not only produce complex substrate-borne signals, but also have associated visual displays (motion displays and foreleg ornamentation). Despite this, the substrate-borne signal has been shown to be the most important courtship component – in the absence of the substrate-borne signal, mating frequencies significantly plummet (Hebets, 2008). The results of this study corroborate this previous finding, as muted males were not successful in acquiring copulations, regardless of the signaling substrate. Previous studies on other visually ornamented *Schizocosa* species have suggested that the visual courtship component increases the efficacy of courtship signaling in heterogeneous signaling environments, such as complex leaf litter (Uetz and Stratton, 1982; Stratton and Uetz, 1983; Scheffer et al., 1996; Hebets and Uetz, 1999; Hebets and Uetz, 2000; Uetz et al., 2009). Future studies manipulating visual signals in such complex signaling environments may enable a direct test of this hypothesis.

While the focus thus far has been on substrate-coupled vibratory signals and visual signals, arachnids use a variety of other signaling modalities in communication, for example chemical (Rypstra et al., 2009; Rypstra et al., 2003), olfactory (Gaskett 2007) and near-field sound (Santer and Hebets 2008) signals. While these types of signals have not been ruled out in *S. stridulans,* and may indeed have environment-dependent transmission, numerous studies suggest that substrate-borne (seismic) and visual signals are the predominant modalities used by *Schizocosa* wolf spiders (Scheffer et al., 1996; Hebets and Uetz, 1999; Uetz and Roberts, 2002). Nevertheless, future work examining other sensory modalities is certainly warranted.

Ultimately, properties of the environment influence animals in a variety of ways. Often the environment is described as "constraining" and thus biasing the evolution of signals and sensory systems in particular directions (Endler, 1992). This process of "sensory drive" predicts that not all signals are perceived equally in all environments and that natural selection will drive the evolution of signals and signaling behavior that are best suited to a particular environment (Endler, 1992, 1993). From a female choice perspective, specialization in specific signaling substrates on the part of males (i.e. signal-substrate matching) may increase detectable variation among males due to the increased reliability of signals, which may then lead to an increase in content-based selection. This scenario is predicted to lead to more variable male mating success on specialized substrates, as females are better able to discriminate between potential mates on these substrates. This prediction will be tested in future studies on *Schizocosa* wolf spiders. In the end, depending upon the details of the content-based selection pressure, signal-substrate matching could ultimately facilitate the evolution of complex or multicomponent signals.

In summary, the variation inherent in the signaling environment for vibratory communication is often extreme and thus, a focus on vibratory communication could provide invaluable insights into our general understanding of sensory ecology and its role in signal evolution. As such, spiders provide an ideal taxon within which to test hypotheses on signal evolution and the effects of the environment on sensory and neural processing.

Acknowledgements We would initially like to thank M. Stevens for an invitation to contribute to this special volume. Additionally, we would like to thank Gail Stratton, Pat Miller, Dustin Wilgers, Rodrigo Willemant, Norman Lee, Michael Kasumovic and Dawn Dong-yi Xiao for assistance with spider collection, data collection, and general support. We would also like to thank anonymous referees for helpful and insightful comments. This project was funded by a National Science Foundation International Research Fellowship (0502239) to DOE, NSERC Discovery Grant (238882 241419) to ACM, and a National Science Foundation CAREER award (IOS - 0934990) to EAH.

References

Aicher B, Tautz J, 1990. Vibrational communication in the fiddler crab *Uca pugilator*.1. Signal transmission through the substratum. Journal of Comparative Physiology A. Sensory Neural and Behavioral Physiology 166: 345–353

Barth FG, 2002. A Spider's World: Senses and Behavior. Berlin: Springer-Verlag.

Barth FG, 1985. Neuroethology of the spider vibration sense. In: Barth FG ed. Neurobiology of Arachnids. New York: Springer-Verlag, 203–229.

Barth FG, 1998. The vibrational sense of spiders. In: Hoy RR, Popper AN, Fay RR ed. Comparative Hearing: Insects. New York: Springer, 228–278.

Basolo AL, Endler JA, 1995. Sensory biases and the evolution of sensory systems. Trends in Ecology & Evolution 10: 489–489

Boughman JW, 2001. Divergent sexual selection enhances reproductive isolation in Sticklebacks. Nature 411: 944–948

Boughman JW, 2002. How sensory drive can promote speciation. Trends in Ecology & Evolution 17: 571–577

Brownell P, Farley RD, 1979. Orientation to vibrations in sand by the nocturnal scorpion *Paruroctonus mesaensis*: Mechanism of target localization. Journal of Comparative Physiology 131: 31–38

Brownell PH, 1977. Compressional and surface-waves in sand used by desert scorpions to locate prey. Science 197: 479–482.

Brumm H, Naguib M, 2009. Environmental acoustics and the evolution of bird song. In: Naguib M, Zuberbuumlhler K, Clayton NS, Janik VM ed. Advances in the Study of Behavior. Vol. 40. Elsevier San Diego: Academic Press Inc., 1–33

Casas J, Magal C, Sueur J, 2007. Dispersive and non-dispersive waves through plants: Implications for arthropod vibratory communication. Proceedings of the Royal Society B: Biological Sciences 274: 1087–1092

Cocroft RB, 1996. Insect vibrational defence signals. Nature 382: 679–680

Cocroft RB, 2001. Vibrational communication and the ecology of group-living, herbivorous insects. American Zoologist 41: 1215–1221

Cocroft RB, Rodriguez RL, 2005. The behavioral ecology of insect vibrational communication. Bioscience 55: 323–334

Cocroft RB, Shugart HJ, Konrad KT, Tibbs K, 2006. Variation in plant substrates and its consequences for insect vibrational communication. Ethology 112: 779–789

Cokl A, Presern J, Virant-Doberlet M, Bagwell GJ, Millar JG, 2004. Vibratory signals of the harlequin bug and their transmission through plants. Physiological Entomology 29: 372–380

Cokl A, Zorovic M, Millar JG, 2007. Vibrational communication along plants by the stink bugs *Nezara viridula* and *Murgantia histrionica*. Behavioural Processes 75: 40–54

Cokl A, Zorovic M, Zunic A, Virant-Doberlet M, 2005. Tuning of host plants with vibratory songs of *Nezara viridula* l (heteroptera: Pentatomidae). Journal of Experimental Biology 208: 1481–1488

Dondale CD, Redner JH, 1978. Revision of the Nearctic wolf spider genus *Schizocosa* (Araneida: Lycosidae). Canadian Entomologis*t* 110: 143–181.

Dumortier B, 1963. Sound emissions in Arthropoda. In: Busnel RG ed. Acoustic Behavior of Animals. Amsterdam- ondon-New York: Elsevier, 277–338

Elias DO, Hebets EA, Hoy RR, Mason AC, 2005. Seismic signals are crucial for male mating success in a visual specialist jumping spider (Araneae:Salticidae). Animal Behaviour 69: 931–938.

Elias DO, Kasumovic MM, Punzalan D, Andrade MCB, Mason AC, 2008. Assessment during aggressive contests between male jumping spiders. Animal Behaviour 76: 901–910.

Elias DO, Lee N, Hebets EA, Mason AC, 2006. Seismic signal production in a wolf spider: Parallel versus serial multi-component signals. Journalof Experimental Biology 209: 1074–1084.

Elias DO, Mason AC, In Press. Signaling in variable environments: Substrate-borne signaling mechanisms and communication behavior in spiders. In: O'Connel-Rodwell C ed. The Use of Vibrations in Communication: Properties, Mechanisms and Function across Taxa. Kerala: Research Signpost.

Elias DO, Mason AC, Hoy RR, 2004. The effect of substrate on the efficacy of seismic courtship signal transmission in the jumping spider *Habronattus dossenus* (Araneae: Salticidae). Journal of Experimental Biology 207: 4105–4110.

Elias DO, Mason AC, Maddison WP, Hoy RR, 2003. Seismic signals in a courting male jumping spider (Araneae: Salticidae). Journal of Experimental Biology 206: 4029–4039.

Endler JA, 1992. Signals, signal conditions, and the direction of evolution. American Naturalist 139: S125–S153.

Endler JA, 1993. Some general comments on the evolution and design of animal communication systems. Philosophical Transactions of the Royal Society of London Series B-Biological Sciences 340: 215–225.

Endler JA, Basolo A, 1998. Sensory ecology, receiver biases and sexual selection. Trends in Ecology & Evolution 13: 415–420.

Fischer S, Samietz J, Wackers FL, Dorn S, 2001. Interaction of vibrational and visual cues in parasitoid host location. Journal of Comparative Physiology A. Sensory Neural and Behavioral Physiology 187: 785–791

Gaskett AC, 2007. Spider sex pheromones: emission, reception, structures, and functions. Biological Reviews 82: 26–48.

Gerhardt HC, Huber F, 2002. Acoustic Communication in Insects and Anurans. Chicago, London: The University of Chicago Press.

Gibson JS, Uetz GW, 2008. Seismic borne communication and mate choice in wolf spiders: Components of male seismic signals and mating success. Animal Behaviour 75: 1253–1262

Gray SM, Dill LM, Tantu FY, Loew ER, Herder F et al., 2008. Environment-contingent sexual selection in a colour polymorphic fish. Proceedings of the Royal Society B-Biological Sciences 275: 1785–1791.

Hebets E, A., Uetz GW, 2000. Leg ornamentation and the efficacy of courtship display in four species of wolf spider (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 47: 280–286.

Hebets EA, 2008. Seismic signal dominance in the multimodal courtship display of the wolf spider *Schizocosa stridulans* Stratton 1991. Behavioral Ecology 19: 1250–1257.

Hebets EA, Elias DO, Mason AC, Miller GL, Stratton GE, 2008. Substrate-dependent signalling success in the wolf spider *Schizocosa retrorsa*. Animal Behaviour 75: 605–615.

Hebets EA, Uetz GW, 1999. Female responses to isolated signals from multimodal male courtship displays in the wolf spider genus *Schizocosa* (aranerae: Lycosidae). Animal Behaviour 57: 865–872.

Hill PSM, 2001. Vibration and animal communication: A review. American Zoologist 41: 1135–1142.

Hill PSM, 2008. Vibrational Communication in Animals. Cambridge, MA: Harvard University Press.

Hill PSM, 2009. How do animals use substrate-borne vibrations as an information source? Naturwissenschaften 96: 1355–1371.

Huber F, Moore TE, Loher W, 1989. Cricket Behavior and Neurobiology. Ithaca: Cornell University Press.

Kalmring K, 1985. Vibrational communication in insects (reception and integration of vibratory information). In: Kalmring K, Elsner N ed. Acoustic and Vibrational Communication in Insects. Berlin: Paul Parey, 127–134.

Kirschel ANG, Blumstein DT, Cohen RE, Buermann W, Smith TB et al., 2009. Birdsong tuned to the environment: Green Hylia song varies with elevation, tree cover, and noise. Behavioral Ecology 20: 1089–1095.

Magal C, Scholler M, Tautz J, Casas J, 2000. The role of leaf structure in vibration propagation. Journal of the Acoustical Society of

America 108: 2412–2418.

Markl H, 1983. Vibrational communication. In: Huber F, Markl H ed. Neuroethology and Behavioral Physiology. Berlin: Springer-Verlag, 332–354.

McNett GD, Cocroft RB, 2008. Host shifts favor vibrational signal divergence in Enchenopa binotata treehoppers. Behavioral Ecology 19: 650–656.

Michelsen A, Fink F, Gogala M, Traue D, 1982. Plants as transmission channels for insect vibrational songs. Behavioral Ecology and Sociobiology 11: 269–281.

Nava SS, Conway MA, Martins EP, 2009. Divergence of visual motion detection in diurnal geckos that inhabit bright and dark habitats. Functional Ecology 23: 794–799

Nemeth E, Winkler H, Dabelsteen T, 2001. Differential degradation of antbird songs in a neotropical rainforest: Adaptation to perch height? Journal of the Acoustical Society of America 110: 3263–3274.

Parri S, Alatalo RV, Kotiaho JS, Mappes J, 1997. Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata*. Animal Behaviour 53: 305–312.

Richards DG, Wiley RH, 1980. Reverberations and amplitude fluctuations in the propagation of sound in a forest: Implications for animal communication. American Naturalist 115: 381–399.

Rodriguez RL, Cocroft RB, 2006. Divergence in female duetting signals in the enchenopa binotata species complex of treehoppers (Hemiptera : Membracidae). Ethology 112: 1231–1238.

Rodriguez RL, Ramaswamy K, Cocroft RB, 2006. Evidence that female preferences have shaped male signal evolution in a clade of specialized plant-feeding insects. Proceedings of the Royal Society B-Biological Sciences 273: 2585–2593.

Rodriguez RL, Sullivan LE, Cocroft RB, 2004. Vibrational communication and reproductive isolation in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). Evolution 58: 571–578.

Rodriguez RL, Sullivan LM, Snyder RL, Cocroft RB, 2008. Host shifts and the beginning of signal divergence. Evolution 62: 12–20.

Ryan MJ, Brenowitz EA, 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. American Naturalist 126: 87–100.

Rypstra AL, Schlosser AM, Sutton PL, Persons MH, 2009. Multimodal signalling: The relative importance of chemical and visual cues from females to the behaviour of male wolf spiders (Lycosidae). Animal Behaviour 77: 937–947.

Rypstra AL, Wieg C, Walker SE, Persons MH, 2003. Mutual mate assessment in wolf spiders: Differences in the cues used by males and females. *Ethology* 109: 315–325.

Santer RD, Hebets EA, 2008. Agonistic signals received by an arthropod filiform hair allude to the prevalence of near-field sound communication. Proceedings of the Royal Society B-Biological Sciences 275: 363–368.

Scheffer SJ, Uetz GW, Stratton GE, 1996. Sexual selection, male morphology, and the efficacy of courtship signalling in two wolf spiders (Araneae: Lycosidae). Behavioral Ecology and Sociobiology 38: 17–23.

Schultz TD, Anderson CN, Symes LB, 2008. The conspicuousness of colour cues in male pond damselflies depends on ambient light and visual system. Animal Behaviour 76: 1357–1364.

Seehausen O, 2002. Patterns in fish radiation are compatible with Pleistocene desiccation of Lake Victoria and 14 600 year history for its cichlid species flock. Proceedings of the Royal Society of London Series B-Biological Sciences 269: 491–497.

Seehausen O, Terai Y, Magalhaes IS, Carleton KL, Mrosso HDJ et al., 2008. Speciation through sensory drive in cichlid fish. Nature 455: 620–626.

Stelkens RB, Seehausen O, 2009. Phenotypic divergence but not genetic distance predicts assortative mating among species of a Cichlid fish radiation. Journal of Evolutionary Biology 22: 1679–1694.

Stewart KW, Sandberg JB, 2006. Vibrational communication and mate searching behavior in stoneflies. In: Drosopoulos S, Claridge M ed. Insect Sounds and Communication: Physiology, Behavior, Ecology and Evolution. Boca Raton/London/New York: CRC Press, 179–186.

Stratton GE, 1991. A new species of wolf spider *Schizocosa stridulans* (Araneae, lycosidae). Journal of Arachnology 19: 29–39.

Stratton GE, 2005. Evolution of ornamentation and courtship behavior in schizocosa: Insights from a phylogeny based on morphology (Araneae, Lycosidae). Journal of Arachnology 33: 347–376.

Stratton GE, Uetz GW, 1983. Communication via substrate-coupled stridulation and reproductive isolation in wolf spiders (Araneae: Lycosidae). Animal Behaviour 31: 164–172.

Uetz GW, Roberts JA, Taylor PW, 2009. Multimodal communication and mate choice in wolf spiders: Female response to multimodal versus unimodal signals. Animal Behaviour 78: 299–305.

Uetz GW, Stratton GE, 1982. Acoustic communication and reproductive isolation in spiders. In: Witt PN, Rovner JS ed. Spider Communication: Mechanisms and Ecological Significance. Princeton, NJ: Princeton University Press, 123–129.

Virant-Doberlet M, Cokl A, 2004. Vibrational communication in insects. Neotropical Entomology 33: 121–134.

Wiley RH, 1991. Associations of song properties with habitats for territorial oscine birds of eastern north America. American Naturalist 138: 973–993.