



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

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