Original Article

The effects of microhabitat specialization on mating communication in a wolf spider

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Animal signals experience selection for detectability, which is determined in large part by the signal transmission properties of the habitat. Understanding the ecological context in which communication takes place is therefore critical to understanding selection on the form of communication signals. In order to determine the influence of environmental heterogeneity on signal transmission, we focus on a wolf spider species native to central Florida, *Schizocosa floridana,* in which males court females using a substrate-borne vibratory song. We test the hypothesis that *S. floridana* is a substrate specialist by 1) assessing substrate use by females and males in the field, 2) quantifying substrate-specific vibratory signal transmission in the laboratory, and 3) determining substrate-specific mating success in the laboratory. We predict a priori that 1) *S. floridana* restricts its signaling to oak litter, 2) oak litter best transmits their vibratory signal, and 3) *S. floridana* mates most readily on oak litter. We find that *S. floridana* is almost exclusively found on oak litter, which was found to attenuate vibratory courtship signals the least. Spiders mated with equal frequency on oak and pine, but did not mate at all on sand. Additionally, we describe how *S. floridana* song contains a novel component, chirps, which attenuate more strongly than its other display components on pine and sand, but not on oak, suggesting that the ways in which the environment relaxes restrictions on signal form may be as important as the ways in which it imposes them.

Key words: **sensory drive, vibratory communication, wolf spider**.

INTRODUCTION

Habitat use determines the ecological and environmental conditions that animals experience, thus fundamentally affecting individual fitness, patterns of selection, and interactions between con- and heterospecifics (Rosenzweig 1981; Pulliam and Danielson 1991; Morris 2003). Habitat use also determines the sensory world that animals inhabit, and can therefore impose selection on the sensory system, and on behaviors associated with the use of sensory information, particularly communication. Sensory drive theory (Endler 1992) predicts that selection on signal form favors increased ease of detection, which is determined in large part by the signal transmission properties of the habitat (Morton 1975; Endler 1992; Boughman 2002). As a result, variation in habitats may lead to divergence in signal form (e.g., Maan et al. 2006; Cummings 2007; Tobias et al. 2010), potentially to the point of speciation (Boughman 2002; Seehausen et al. 2008). Because animals can select habitats for use across

a number of spatial and temporal scales (DeCesare et al. 2012; McGarigal et al. 2016), and may experience a broad, or narrow, range of sensory environments as a result, it is critical to assess patterns of habitat use in studies attempting to understand animal communication form and function.

The substrate environment (i.e., the physical surfaces on which individuals may be located) serves as a medium for vibratory communication for many cursorial arthropods. Substrates often change across short distances, and both species diversity and composition can therefore vary across substrates even within a single habitat (Lowrie 1948; Uetz 1975, 1991; Kruys et al. 1999). Substrate-borne vibrations are a critical sensory modality for many arthropods (Barth 1985, 1998; Hill 2001; Virant-Doberlet and Cojl 2004; Elias et al. 2005; Foelix 2011), and sensory drive has thus been implicated in driving the diversification of some arthropod groups (Rodríguez et al. 2004; Cokl et al. 2005; Elias et al. 2010) and has likely contributed to many others. Substrates vary a great deal in how they attenuate and filter acoustic information (Elias et al. 2004; Hebets et al. 2008; Elias et al. 2010), and may differ markedly in how and to what extent they affect signal transmission (Elias and Mason 2011, 2014).

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We aim to address the relationship between substrate use and signal transmission in the wolf spider *Schizocosa floridana*. Wolf spiders in the genus *Schizocosa* are common in leaf litter, grass, and soil environments, and rely heavily on vibratory information for communication (Hebets et al. 2013). Males of every species studied thus far produce substrate-borne vibratory songs to attract mates (Stratton 2005), and the detection of these songs by the female is usually necessary, and often sufficient, for mating (Hebets et al. 2013). In some species (e.g., *Schizocosa stridulans*, Elias et al. 2010), laboratory-based experiments have found that mating rates are highest on substrates that best transmit their songs, while in other species no such match was observed (e.g., *Schizocosa retrorsa*, Hebets et al. 2008). To date, however, no study has simultaneously examined both habitat use in the field and mating across different habitats in any *Schizocosa* species.

Schizocosa floridana, a small-bodied wolf spider common to central Florida, is found in in habitats with heterogeneous substrate environments that vary between oak litter, pine litter, sand, grasses, and bare rock, often over distances of a meter or less. Field collections of *S. floridana* have predominantly focused on oak litter microhabitats, which anecdotally appear to have the highest concentrations of individuals. *Schizocosa floridana* males court females with a substrate-borne vibratory song (Rundus et al. 2011; Rosenthal and Hebets 2012), which is both necessary and sufficient to ensure copulation (Hebets et al. 2013; Rosenthal et al. 2018). This song consists of 3 components (Rundus et al. 2011; Rosenthal et al. 2018), each produced by a distinct body part in: percussive "tapping" of the forelegs, stridulatory "thumping" of the pedipalps, and narrow-band high frequency "chirps," produced by movements of the abdomen. While leg taps and palpal stridulation are common across the genus (Stratton 2005), abdominal chirping appears to be unique to *S. floridana*.

Here, we test the hypothesis that *S. floridana* is a substrate specialist, restricting its use of a heterogeneous habitat to oak litter, and we ask whether substrate use is related to its vibratory transmission properties and effective reproduction. To address these questions, we 1) created a map of the substrates at a well-studied *S. floridana* collection site to determine the relative abundances and degree of variability in substrates and surveyed the densities of *S. floridana* and other wolf spiders across the various substrates to gauge microhabitat use, 2) assessed the signal transmission properties of the 3 most common substrates using signal-playback trials to test for a signal–substrate match, and 3) tested for differences in copulation success across the same 3 substrates in lab-based mating trails to determine whether variation in substrates affects the ability of *S. floridana* to mate.

METHODS

Substrate quantification and use

Substrate mapping and collection

We conducted habitat mapping during the day on 4 February 2017 in Alachua County, Florida (29°31′40″N, 82°11′18″W). This site had a mix of surfaces on which spiders were found, primarily leaf litter from oak and pine trees, with areas of sand and grass. We began constructing a substrate map of the field location by subdividing the site into nine 10 × 10 m plots. The layout of these plots (Figure 1) covers a representative sample of the major substrate types present in the area. We were unable to map a contiguous area in a single direction due to the presence of dense
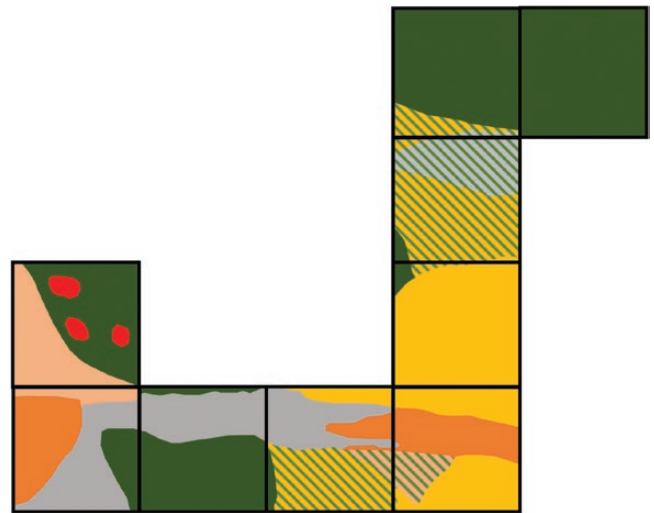

Figure 1

The distribution of substrates across the surveyed site. The surveyed area contained oak (green), pine (yellow), tall grass (orange), short grass (pink), sand (gray), and tree trunks (red). Mixed-color areas represent areas that were equally divided between 2 substrate types. Nearly 90% of the surveyed substrate was made up of oak litter (46%), pine litter (26%), or sand (17%).

stands of palmettos and oak trees, and thus our map is not a symmetrical shape.

Within each of our 10 × 10 m plots, we constructed smaller maps of the substrate layouts and then joined these maps together to generate a map of substrates for the entire site (Figure 1). We assigned areas to a substrate type if that substrate made up more than 75% of the ground cover. If areas were mixed, we marked them as consisting of a mixture of the 2 most common substrates. We marked the location of substrate boundaries using a field tape to measure the distances between those boundaries and the marked edges of the plot. Additionally, we took overhead photographs of each plot, as well as video recordings of walkthroughs of each plot's substrate boundaries. Photographs and video recordings are available in the Supplementary Materials.

We estimated the relative areas our collection site covered by each substrate by measuring the pixel area of each substrate type on our illustrated map. For areas that were a mixture of 2 substrates, we assigned 50% of the pixel area to each substrate. For analytical purposes, we measured the areas covered by the 3 most common substrate types (oak litter, pine litter, and sand), and grouped all other substrates (bare rock, trees and bushes, short and tall grass, fallen logs, moss) into an "other" category. Substrates likely differ in terms of available surface area as a factor of the structural complexity of the substrate, or the depth of available habitat. It is therefore possible that our measurements of surface area are underestimates in some habitats (i.e., leaf and pine litter). However, we consider these measurements to be the best broad representation of the relative areas covered by each substrate type.

Species composition and distribution

To estimate patterns of substrate use by *S. floridana* as well as other heterospecifics on the various substrate types, we performed timed spider collections in each of the 9 plots, with the order of collection randomized. Collections lasted 20 min in each plot, with 3 min' break between each plot and were carried out by 2 researchers

(M.F.R. and B.K.), for a total of 40 person-minutes per plot (and 320 person-minutes of total collection across all substrates). Both researchers had experience in identifying and collecting wolf spiders.

Wolf spiders (Family Lycosidae) possess a tapetum, a reflective structure at the back of the eyes that reflects light (Foelix 2011). This structure facilitates the spider's detection by humans using a headlamp, as the visible eye-shine makes the locations of spiders easy to pinpoint. To survey spiders in the field, we therefore collected spiders by their eye-shine. We began the first collection at 20:00, as that is the earliest time at which the sky is dark enough for eye-shines to be easily visible. Previous collection experience with *S. floridana* (e.g., Rundus et al. 2011; Rosenthal and Hebets 2012; Rosenthal et al. 2018) suggests they are active from the evening into the night. We collected all spiders in the family Lycosidae, recording the substrate on which each spider was collected; if a spider was straddling multiple substrates, we recorded all substrates touched by at least one leg. Additionally, we collected a further 200 *S. floridana*, along with 5 gallon-bags of each of the 3 most common substrates (oak litter, pine litter, and sand) for use in vibratory transmission experiments and substrate mating rate experiments.

All spiders collected during the timed collections were sacrificed and preserved in ethanol. We examined these spiders under a dissecting microscope and assigned a species, where possible. Many of the collected spiders were small-sized juveniles, or otherwise difficult to assign to a species. We (M.F.R. and 2 undergraduate assistants) thus categorized these into morphospecies. The researchers agreed on the assignment of a category for all but 5 of the collected spiders, which we henceforth excluded from any species-specific analyses.

Statistical analysis

All statistical analyses were performed in R v3.5.1 (R Core team 2018). We performed chi-square tests to assess whether *S. floridana* was distributed randomly across substrates, and whether its distribution differed significantly from other Lycosids. For the first test, we compared the distribution of *S. floridana* across 4 major substrate types (oak litter, pine litter, sand, other) to expected variables calculated using the relative areas covered by those 4 substrates. For the second test, we compared the distribution of *S. floridana* across the substrates to the distribution of all other lycosids across those substrates.

Substrate-specific transmission

We assessed the effect of substrate type on signal transmission by playing back *S. floridana* courtship through the 3 most common substrates (oak litter, pine litter, and sand). Substrate playback trials followed the methods of Hebets et al. (2008). Briefly, we induced 3 male *S. floridana* to court by placing them on a stretched nylon substrate that was impregnated with female silk (female silk contains pheromones that induce male courtship, Kaston 1936; Rovner 1968; Roberts and Uetz 2005). We then recorded their songs using a scanning laser vibrometer (Polytec PSV-400), with the laser point situated on the nylon within 1mm of the male's body. We next measured the transmission of the 3 courtship components (thumps, taps, chirps), using playbacks of these components from the 3 exemplar males. Courtship recordings often included a number of songs, and signal components for playback were selected based on recording quality (i.e., lowest levels of background noise). We conducted 3 replicates for each substrate type, and between replicates, we

rearranged the substrate. Thus, we ultimately had playbacks of songs from 3 individuals across 3 replicates of 3 substrate types. We performed playbacks using a 10 mm Samsung linear resonant vibration actuator, with the actuator output calibrated using a digital equalization filter (Cocroft et al. 2014). For the oak litter and pine litter treatments, the actuator was attached to the substrate with low-temperature hot glue. For the sand treatment, the actuator was pressed gently into the sand.

To quantify signal attenuation, we measured the root mean square (RMS) amplitude of the playback with laser recordings of substrate-borne vibrations at 6 distances (5, 10, 20, 40, 80, and 160 mm) from the source. We calculated amplitude as dB relative to the amplitude of the playback recorded at the source, which was the loudest of all recorded measurements.

Statistical analysis

To assess substrate-specific transmission, we performed a linear mixed effects model with courtship RMS as the dependent variable, substrate type, distance from the source, courtship component type, and all their 2- and 3-way interactions as independent variables, and individual identity a random effect.

Mating across substrate types

To assess variation in mating success across substrate types, we ran mating trials in which we allowed female–male pairs to interact freely for 20 min, and visually assessed copulation success. We ran trials under full-spectrum light in 30 cm diameter arenas, walled with 50 cm tall acetate, and wrapped in brown paper on the outside to visually isolate the arenas. We filled the bottom of each arena in a layer of sand ~2 cm thick. From these, we constructed 3 treatments: one arena with oak litter on sand, one arena with pine litter on sand, and one arena with sand only. These arrangements mimicked the layout of substrates in the field, as leaf litter of all types sat on a layer of sand. We constructed oak and pine litter arenas with the litter collected from the field, filling each arena to a depth of 10 cm with haphazardly placed litter. Between each trial, we removed the litter and replaced it into an adjacent arena. We ran 20 male–female pairs per substrate, for 60 pairs total.

Statistical analysis

To assess the effects of substrate on mating behavior, we performed a Fisher's Exact test to assess whether the number of pairs that mated was significantly different across the 3 substrate type treatments.

RESULTS

Substrate quantification and use

Substrate mapping

The 90 m² surveyed area contained a heterogeneous mixture of substrates including oak litter, short and tall grass, slash pine litter, tall shrubbery, sand, fallen trees, and moss (Figure 1). Close to 90% of the site, however, was composed of 3 substrate types: oak litter (46%), pine litter (26%), and sand (17%). Although the collection site was chosen primarily because previous work has identified it as a location at which *S. floridana* is particularly dense, this mixture of oak, pine, and sand is common for central Florida. Because the layout of the collection plots avoided areas where thick shrubbery or tree growth made spider collection impossible, there are several

substrates (bushes and trees) that are under-represented in our map. However, *S. floridana* were never found in grass, shrubbery, trees, or moss during our collections.

Species composition and distribution

We collected 427 wolf spiders during our timed collections. Two species, *S. floridana* ($n = 263$) and *Rabidosa hentzi* ($n = 107$) accounted for 87% of these individuals. We also collected *Hogna carolinensis* ($n = 4$), and other spiders ($n = 57$) that were later categorized into 8 morphospecies, most of which were small, immature individuals (Table 1).

The number of *S. floridana* varied significantly across substrates, with significantly more collected on oak litter (248 out of 263; Figure 2) than expected given the area of the collection site covered by oak litter ($X^2_3 = 253.61$, $P < 0.0001$). The distribution of *S. floridana* across the various substrates also differed significantly from the distribution of the other Lycosids at the collection site ($X^2_3 = 513.70$, $P < 0.0001$; Figure 2). All *S. floridana* were found to be penultimate juveniles at the time of capture.

Substrate-specific transmission

Courtship RMS amplitude was significantly predicted by the interaction between the distance from the playback source and the substrate type, and by the interaction between substrate type and courtship component type (Table 2). RMS amplitude dropped as distance from the source increased, and did so most strongly on sand, and least strongly on oak (Figure 3). Chirp RMS amplitude was lower on average than thump and tap RMS amplitude on pine and sand substrates, but was not significantly different on oak (Figure 4).

Substrate-specific mating success

Mating rates differed significantly across the substrates (Fisher's Exact test, $P < 0.001$). No pairs mated on sand, whereas 19 of 20 pairs mated on oak litter, and 18 of 20 pairs mated on pine litter (Figure 5). While mating rates on sand were significantly lower than on both oak and pine (Fisher's Exact test, $P < 0.001$ in both cases), there was no statistical difference between mating rates on oak litter versus pine litter ($X^2_1 = 0.360$, $P = 0.548$).

DISCUSSION

Despite living in an environment with ready access to heterogeneous substrate types, *S. floridana* is almost exclusively found on oak litter, which was also found to attenuate *S. floridana*'s courtship the least. Residence on oak litter was not a general characteristic of wolf spiders at the site, for example, not all wolf spiders were restricted to oak litter substrates. For example, the second most commonly collected species, *R. hentzi*, was most often found on pine litter. *Schizocosa floridana* mating rates were higher on oak and pine litter than on sand, though not different between oak and pine litter. Equal mating rates across oak and pine litter suggest either that their ability to communicate in a mating context alone is not limiting their usage of substrates, or that the vibratory signal's attenuation on pine litter is not sufficient to disrupt effective communication. Finally, *S. floridana*'s unique vibratory component, the abdominal chirp, attenuates more heavily than the other components on all substrates except for oak litter, but the role of this specific component in communication remains an open question. We discuss the implications of these results in detail below.

Strict habitat specialization in *S. floridana*

Schizocosa floridana's specialization on oak litter, in terms of the substrate upon which it is most frequently found, is not reflective of a general pattern of substrate use by all lycosids at the collection site. In fact, none of the other species collected at the site are heavily restricted to a single substrate type (Table 1), and several substrates on which *S. floridana* is almost never found (particularly pine litter) are home to a number of other lycosids. There are a number of reasons why *S. floridana* might restrict its habitat use in this way. First, oak litter may be a high quality habitat for vibratory communication and/or cue detection. Vibratory cues and signals are known to be important for spider foraging, avoiding predators and finding mates (Barth 1985, 1997; Elias et al. 2005; Foelix 2011), and oak litter transmits vibrations well relative to other habitats—a fact that has been reported in other studies in addition to the current study (Hebets et al. 2008, Elias et al. 2010).

In addition to communication and the perception of stimuli important in foraging or predator avoidance, numerous additional interacting ecological, behavioral, and physiological effects influence an animal's use of habitats (e.g., Johnson 1980; Orians and Wittenberger 1991; Mayor et al. 2009; McMahon et al. 2017). Oak litter may be a desirable habitat for many reasons. For example, the complexity of the oak litter substrate may provide more surface area in which to escape from predators (which likely include other lycosids at the site). Similarly, prey availability, density, or composition may differ across substrate types and *S. floridana* substrate use may be influence by these microhabitat characteristics.

Table 1

Number of individuals captured per substrate for the 3 identified species and 8 morphospecies of Lycosids collected during timed collections

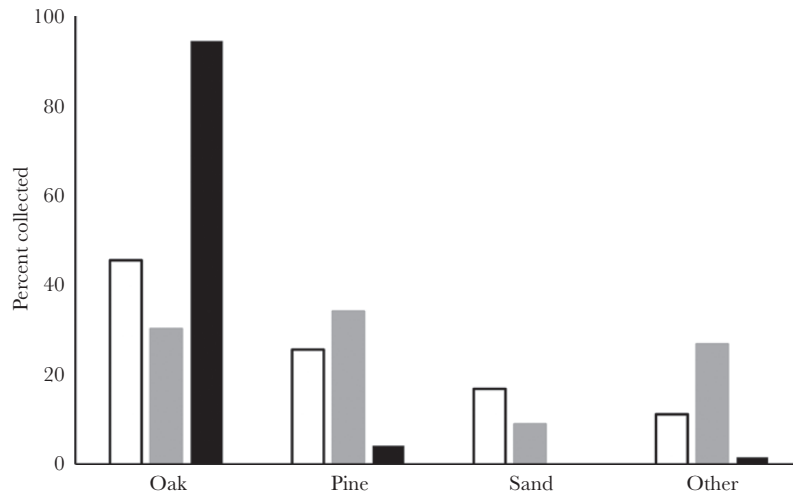| Species	Grass	Shrub	Moss	Oak	Pine	Rock	Sand	Trees	Sticks	Total
S. floridana			2	248	13				2	265
R. hentzi	10	2	1	29	48	5	1	4	7	107
H. carolinensis	1				1		1	1		4
MS1	5		1	7	3		6	2		24
MS2	3			5			4			12
MS3				2	2				1	5
MS4				2	1			1		4
MS5				1	1		1			3
MS6				2						2
MS7				1	1					2
MS8	1									1

Figure 2

A comparison of (a) the expected distribution of *S. floridana*, assuming equal representation on all substrates (white bars), (b) the substrate distribution of non-*S. floridana* lycosids (gray bars) and (c) the substrate distribution of *S. floridana* (black bars). The "other" category includes a number of substrates that cumulatively account for less than 10% of the sampled area (grass, bare rock, tree trunks, fallen logs, brush).

Table 2

Summary of results for linear mixed effects model assessing the interacting effects of distance from the playback source, courtship component type, and substrate type on courtship RMS

Distance	$F_{1,466} = 431.68$	$P < 0.0001$
Component	$F_{2,466} = 54.75$	$P < 0.0001$
Substrate	$F_{2,466} = 1419.29$	$P < 0.0001$
Distance × Component	$F_{2,466} = 0.88$	$P = 0.414$
Distance × Substrate	$F_{2,466} = 19.18$	$P < 0.0001$
Component × Substrate	$F_{4,466} = 4.55$	$P = 0.0013$
Distance × Component × Substrate	$F_{4,466} = 0.12$	$P = 0.974$

Additionally, competitive, or predator–prey, interactions with the other local species of wolf spider may play a role in determining the distribution of species across the substrate types. For example, it is possible that *S. floridana* is restricted to oak litter through competitive exclusion on other substrate types by other co-occurring species (e.g., *Rabidosa*). Simultaneously, it is also possible that *S. floridana* is excluding other species from the optimal oak litter substrate. Future work exploring these potential interactions may be critical to understanding how and why species, such as *S. floridana*, restrict their use of substrate types in the field.

Habitat, signals, and sensory drive

If *S. floridana*'s restricted use of the substrate environment continues into the time of year when they are producing and receiving vibratory mating signals (and further work in preparation suggests that it does), it has the potential to affect the evolution of the mating display. A critical expectation of the sensory drive hypothesis is that selection for detectability will optimize the transmission of signals through a given environment (Endler 1992; Cummings and Endler 2018). Examples of the influence of the signaling environment on display form can be found in species which exhibit visual displays that are high-contrast compared to their specific backgrounds (e.g., *lizards*, Leal and Fleishman 2002), or in taxa that take advantage of an environment-specific light environment (e.g., *cichlids*, Maan et al. 2006). Other examples can be found in species that produce

vibratory signals at frequencies that are optimized for transmission through a given substrate (e.g., *treehoppers*, McNett and Cocroft 2008). In line with this latter study, we also find evidence of a signal–substrate match. Male courtship songs attenuate the least through oak litter, and mating rates are high on oak litter substrates.

However, this may not be evidence of selection solely for a signal–substrate match in *S. floridana* courtship for several reasons. First, *S. floridana* may change its use of substrates after maturation, though this seems unlikely. *Schizocosa floridana's* oak specialization has been anecdotally confirmed at several times of the year, but we nonetheless are currently undertaking further field observations to assess the possibility of a shift in substrate use at maturation. If, however, *S. floridana's* substrate use was different at the time of courtship, this would obviously remove the importance of oak litter transmission properties on signal form.

Second, mating rates on oak and pine litter in the laboratory were not significantly different, suggesting that reduced signal transmission, in terms of amplitude of signaling, does not always reduce the ability of pairs to mate. This may be due to any number of factors. For example, the separate vibratory components of *S. floridana* courtship may serve as efficacy backups (e.g., Hebets and Papaj 2005), and thus reduced signal transmission in one component may not compromise communication. The thumps and taps of *S. floridana* transmit fairly well through both oak and pine, despite reduced transmission of chirps on pine, and the perception of these 2 components may be sufficient for females to accept a male. Likewise, while pine litter decreases the distance over which vibrations transmit, spiders in close proximity may still be able to communicate effectively. The effect of reduced signal efficacy on pine litter might therefore affect mate searching more heavily than close-up mate choice, a possibility that is impossible to address given our experimental design. Also, other studies on *S. floridana* have found significant shifts in selection on male courtship across experimental treatments that did not differ in overall mating rate (male diet: Rosenthal and Hebets 2012; light environment: Rosenthal et al. 2018). It is therefore possible that while mating rates are similar on oak and pine, the display components under selection may vary across those substrates. For instance, mating success may be
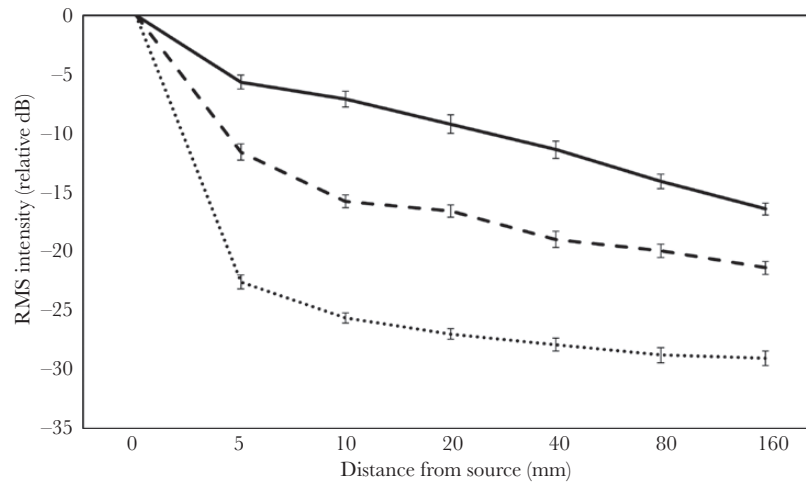
Figure 3
Attenuation of *S. floridana* vibratory courtship across the 3 most common substrates, oak litter (black line), pine litter (dashed line), and sand (dotted line). Error bars represent standard errors.
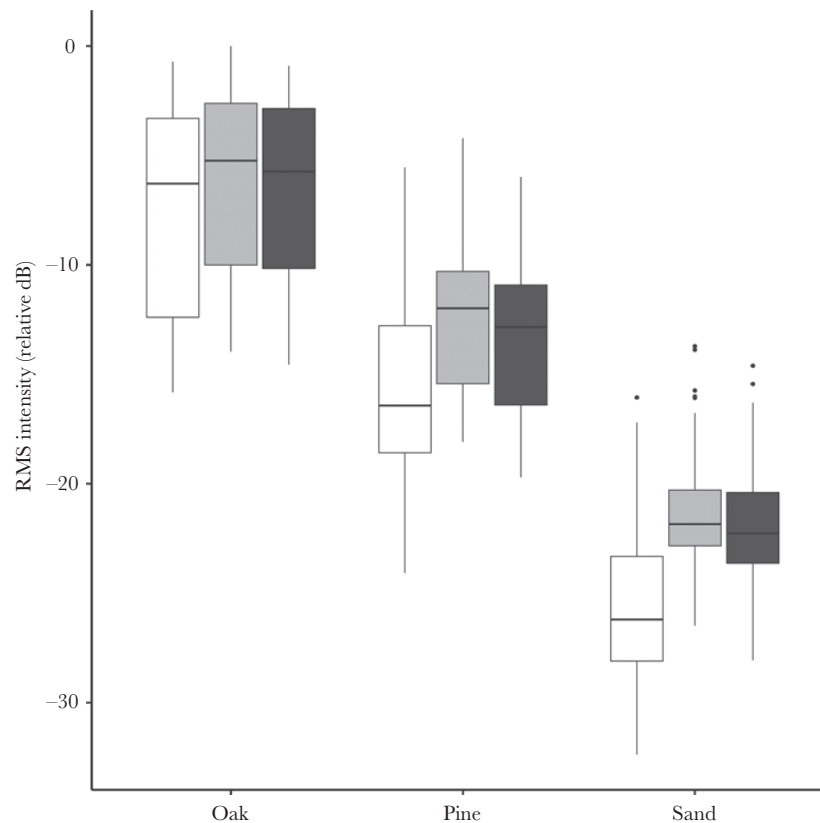

Figure 4
Average RMS intensity (dB) of *S. floridana* chirps (white boxes), taps (gray boxes), and thumps (black boxes) on oak litter, pine litter, and sand.

correlated with some aspect of chirps on oak but not on pine, a substrate on which the chirps transmit poorly. Future work will examine this possibility as well.

Third, the majority of vibratory signal loss, or attenuation, occurs when vibrations are transmitted from one structure (e.g., 1 oak leaf, pine needle, or grain of sand) to another. As such, it is likely that oak litter transmits all vibrations well regardless of the species-specific form of the vibratory signal. The relatively broad and long surfaces of oak litter decrease the number of structures that vibrations must propagate through over a given distance. With this information in mind, we might predict that the songs of all wolf spider species found at the site will transmit best through oak, regardless of their spectral characteristics and independent of their patterns of substrate use. Future work will also
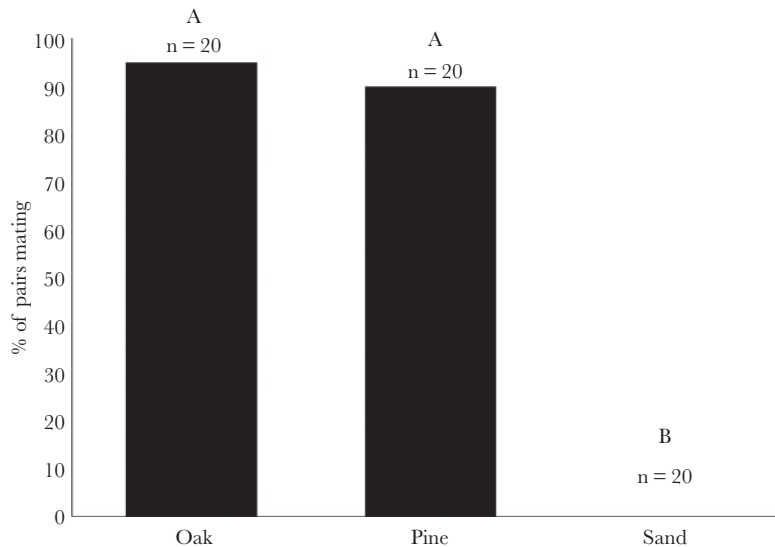
Figure 5
Percentage of successful mating for pairs of *S. floridana* in arenas floored with oak litter, pine litter, or sand.

assess this possibility, but in support of this idea: it is known from other studies that the vibratory songs of several other spider species (e.g., Hebets et al. 2008; Elias et al. 2010), as well as artificially produced broadband stimuli (unpublished data), do transmit most effectively in oak litter.

All of these facts, however, do not negate the potential for the transmission properties of oak litter to influence the evolution of *S. floridana*'s song. Rather than leading to a simple signal–substrate match, we suggest that reduced environmental constraints on signal transmission resulting from substrate specialization may have allowed *S. floridana* to evolve novel song components. *Schizocosa floridana* is unique among *Schizocosa* in that its song contains a narrow bandwidth component, the chirp, which is produced by abdominal movement (Rundus et al. 2011). Frequency sweep data suggest that transmission constraints on oak litter are smaller relative to other substrates (unpublished data), and in this study we find that chirps transmit less effectively than the other components of *S. floridana*'s display through pine and sand environments, but equally well through oak environments. Specializing on oak litter may have indirectly led to the evolution of a novel display component, not through increasing selection for detection, but by relaxing selection for detection that would otherwise prevent the evolution of narrow-band signal components. This is assuming that current patterns of substrate use reflect historical patterns of substrate use, and thus past selection. It is worth mentioning that this may not be the case, in which case the arrow of causation might point the other direction, with previously existing narrowband courtship restricting the ability of *S. floridana* to spread across multiple substrates. Regardless, *S. floridana* songs contain a novel component—the chirp—unlike any other song currently described in the genus, and this novel component transmits most efficiently on oak litter. Future work is now necessary to determine the role of this specific component in courtship communication.

CONCLUSIONS

Our findings further emphasize the fact that habitat structure varies greatly even at small spatial scales, as do species distributions and space use. The highly specialized habitat use of *S. floridana* restricts its distribution to only a narrow subset of signaling substrates, even in an extremely heterogeneous environment. Habitat use dictates the sensory environment that animals inhabit, and the transmission of *S. floridana*'s vibratory song matches well with the substrate environment it is found in. Future work will examine whether this signal–substrate relationship differs for other species at the site which have different substrate use patterns, most notably *R. Hentzi*, which is considerably more generalist in its substrate use. Most intriguingly, the transmission properties of oak litter and *S. floridana*'s substrate use patterns may shed light on the evolution of a unique narrow-band song component, the chirps. We suggest that the variation in the sensory environment may do more than just drive selection for a match between signal form and the transmission properties of the environment. *Schizocosa floridana*'s song transmits best through oak, but this is likely true of the songs of all species, including nonoak specialists. Rather, the degree to which the sensory environment constrains (or does not constrain) signal transmission may be the context determining how, and whether, novel signals evolve. Pure efficacy-based hypotheses on signal transmission may, in fact, be too simplistic. Incorporating other hypotheses (e.g., bandwidth constraints, noise constraints) will help further illuminate sensory drive processes.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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