# Jumping Spiders (*Habronattus clypeatus*) Exhibit Substrate Preferences that Partially Maximize Vibration Transmission Efficiency

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**Abstract** In animal taxa, the behavior of choosing a microhabitat determines the context in which individuals engage in all other behaviors and interactions. Microhabitat choice has particularly important implications for animal communication, because the successful transmission of information between individuals is highly context-dependent. Substrate-borne vibrations, which are commonly produced, detected, and used for communication by arthropods, are especially influenced by substrate choice because substrates vary widely in their vibration transmission properties. In this laboratory-based study, we examine vibration transmission properties of substrates commonly encountered in nature by the jumping spider *Habronattus clypeatus* and also examine whether these spiders exhibit a preference for particular substrates using a choice experiment. We predicted that spiders would prefer substrates that can better transmit vibratory signals. We found that leaf litter minimized the attenuation of vibratory signals, while rocks and sand sharply attenuated the signals. In behavioral trials, more spiders chose leaf litter or rocks as their first substrate over sand. Further, spiders spent more time on, and were more likely to jump to, leaf litter and rocks than sand. These results suggest that substrate preference by *H. clypeatus* partially matches the choice that would maximize signal transmission efficiency, indicating that the ability to communicate with conspecifics may influence these animals' choice of microhabitat.

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## Introduction

An animal's choice of microhabitat determines the context in which all of its interactions—with prey,

predators, competitors, and mates—take place. Thus, particularly for animals that live in heterogeneous environments, microhabitat selection can have fitness consequences through its effect on the nature and outcome of interactions (e.g. Albín et al. 2019; Butman et al. 1988; Kraus and Morse 2005; Martínez-Laiz et al. 2018).

One important way in which microhabitat choice can shape the outcome of an interaction is through its effect on animal communication. The specific relationship between microhabitat choice and communication behavior depends on the modality of communication. Many animals, from insects to mammals, use vibratory signals to detect prey and predators and communicate with one another during sexual and parental interactions (reviewed in Hill 2001). Vibratory signals are mechanical disturbances that propagate through a medium, including airborne and underwater sound, water surface ripples, and substrate vibrations (Cocroft and Rodríguez 2005; Greenfield 2002; Hill 2008).

Substrate-borne vibrations are especially context dependent, particularly for animals that live in heterogeneous environments. The substrate works as the medium in which the vibration is produced and transmitted, and is usually the solid substance on which the animal stands when signaling. The substrates through which animals may communicate using vibrations can vary dramatically by population, species and as an individual moves through its environment. Each substrate has its own attenuation and filtering properties which can constrain vibratory wave propagation and substantially modify and distort the spectral and temporal structure of signals (Čokl et al. 2005; Cocroft et al. 2006; Elias and Mason 2014). This kind of modification and distortion can strongly determine the effectiveness of a given signal produced by an animal, which in turn influences the outcome of behavioral interactions such as foraging, avoiding predators, or courtship (Sandeman et al. 1996; Tautz 1996; McNett and Cocroft 2008; Elias et al. 2010; Rosenthal et al. 2019). Thus, the choice of a substrate on which to send and receive vibrations can be a crucial component of an animal's communication strategy.

*Habronattus* (Salticidae) is a genus of jumping spiders that is found in a wide range of habitats across North America (Maddison and Stratton 1988; Maddison and Hedin 2003; Leduc-Robert and Maddison 2018). *Habronattus* are known to employ elaborate multi-modal courtship signals that include a vibratory component (Elias et al. 2003, 2006). It has previously been argued that the effectiveness of substrate-borne communication in *Habronattus* could be strongly constrained by the substrate (Elias et al. 2004). Evidence that is consistent with this hypothesis has been observed in *H. dossenus*, wherein the proportion of males that mate successfully was three times higher on those substrates with better properties for vibratory signal transmission (Elias et al. 2004, 2005). However, it remains unknown whether *Habronattus* jumping spiders display a preference for particular substrates. Such choice has the potential to be adaptive for the purpose of vibrational communication—spiders may choose substrates through which vibrations are transmitted most efficiently, to facilitate not only intraspecific communication but also, potentially, the detection of predators and prey.

In this study, we examine substrate preference in *Habronattus clypeatus*, a species of jumping spider that is found in heterogeneous environments in the Sonoran desert and that produces both visual and vibratory signals during courtship (Elias et al. 2006; Brandt et al. 2018). Jumping spiders have high visual acuity and employ striking visual signals (Caves et al. 2018; Morehouse 2020), but detecting vibrations and the vibratory components of their multimodal display are also crucial components of foraging and mating (Sivalinghem et al. 2010; Girard et al. 2015; Zeng et al. 2019). Our specific goals were to (1) define vibration transmission properties of three substrates from the *H. clypeatus* habitat—leaf litter (leaves and sticks), rocks, and sand; (2) determine *H. clypeatus*' preferences among these three substrates in a laboratory-based choice test. We predicted that, when given a choice among these three substrates, *H. clypeatus* would prefer the substrate through which its vibratory signals were transmitted most effectively and efficiently. Moreover, we compared the substrate preferences of males and females, reasoning that differences between males and females in substrate preference may shed light on the ecological context of foraging, predator avoidance, and mate choice in this species.

## Methods

### Substrate Collection and Processing

The substrates used in this experiment—leaf litter (i.e. leaves and sticks), sand, and rocks (Fig. 1)—were collected by DOE in November 2018, from *Habronattus clypeatus* habitat in the Santa Rita Mountains, east of Green Valley, AZ, on unceded lands of the Tohono O'odham and Hohokam peoples. Four separate sites (200 m – 600 m apart) were chosen as collection locations. We sieved sand to exclude small rocks and plant litter and then mixed the sieved sand from four locations in equal ratios. Leaf litter and rocks from the four sites were similarly mixed for use in trials.

### Vibration Transmission

We examined vibration transmission across the three substrates, following the methods employed by Choi et al. (2019). A plastic box (50 cm × 25 cm × 10 cm) was filled with a layer of sand and then tested directly or tested after placing either a layer of leaf litter or rocks onto the sand. To test vibration transmission, we played a sine sweep (0 ~ 5,000 Hz) with a 10 mm Samsung Linear Resonant Actuator positioned on the surface of the substrate. The sine sweep had been calibrated using a digital equalization filter to correct for natural resonances in the actuator itself (Cocroft et al. 2014). Vibratory courtship in jumping spiders starts when the male is relatively close to a female, at about 10–15 mm (Elias et al. 2003); thus, we recorded propagated vibrations with a laser vibrometer (Polytec PSV-400) at relevant fixed distances (1 mm, 5 mm, 10 mm, 15 mm, 20 mm, and 35 mm) from the actuator source. For sand, we placed the actuator lightly on the surface; for rocks and leaf litter, we fixed the actuator to the rocks or leaf or stick with hot glue, and took measurements on the same piece of rocks or leaf or stick where the actuator was positioned. Leaves and sticks are two main components of leaf litter, and we considered them as distinct substrates when analyzing vibration transmission data, but they collectively represent the properties of leaf litter.

We measured the root mean square (RMS) amplitude of the playback at distances of 1 mm, 5 mm, 10 mm, 15 mm, 20 mm, and 35 mm from the actuator source, with five replicates in each substrate (for leaf litter, five replicates each on leaves and sticks). We stirred the substrate and re-positioned the actuator for each replicate. We calculated amplitude as dB relative to the amplitude of the playback at the source for each replicate.

### Spider Collection and Housing

Immature *H. clypeatus* (Banks 1985; Griswold 1987) were collected by EEB in March and April 2018, from the locations described above, and were raised to maturity in the laboratory. Voucher specimens will be deposited at the Essig Museum of Entomology at UC Berkeley. Spiders were housed individually in plastic containers (AMAC) in the laboratory at UC Berkeley at ~ 25 °C and under a 12:12 light



**Fig. 1** (**a**) Female and (**b**) male *Habronattus clypeatus*. (**c**) Top view of an arena used to assess habitat choice behavior of individual *Habronattus clypeatus*. The spider was introduced to the arena through the syringe at the center. (Photo credit: (**a**) and (**b**): Marshall Hedin, used with permission (**c**) Yuheng Sun)
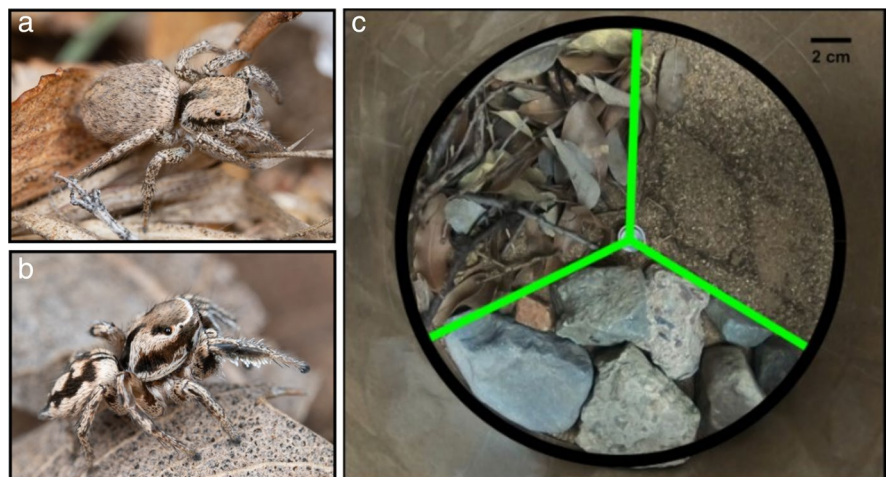
circle with UV-enriched full-spectrum lighting. Spiders were fed with *Drosophila melanogaster* and first instar *Gryllodes sigillatus* twice a week. To provide environmental enrichment, pieces of fiberglass window screen were added to the cages (Carducci and Jakob 2000).

Behavioral Trials

Experiments were performed in December 2018 and January 2019. We placed sand up to a depth of 1.5 cm into a round plastic plate (22 cm in diameter). A hole was cut into the center of the arena to allow for the introduction of the spider during the behavioral trials (see below). We divided the sand into three sectors of equal area, and covered two of the sectors with leaf litter and rocks respectively, leaving bare sand in the remaining sector. The placement of the three substrates was random. A plastic cylinder (21.5 cm in diameter × 14 cm high) was placed around the arena with a brown opaque paper ring pasted outside of the cylinder to prevent visual distractions (Fig. 1). The arena was placed into an incubator (MIR-154-PA, Panasonic Healthcare, Tokyo, Japan) and maintained at 37.5 °C (*H. clypeatus*' preferred temperature; Brandt et al. 2020) for 60 min. A thermocouple and data logger (TC-08, pico technology) with picolog software were used to confirm air and substrate temperature.

We used a modified, inverted syringe to introduce the spider into the center of the arena. The tip of the syringe was cut and replaced with a lid. Spiders were placed in the top 0.5 ml of the inverted syringe, which was then plugged into the center of the arena (Fig. 1). The spider was warmed at 37.5 °C for 30 min, after which we removed the lid to release it. If the spider

did not emerge from the syringe in 10 min, we slowly pushed the plunger to raise the spider onto the substrate surface. Trials were only included if the spider left the syringe within 10 min of being raised to the substrate surface, and lasted for 15 min after it moved away from the syringe (Fig. 2). Spiders that did not leave the syringe were interpreted as spiders that did not have motivation for exploration, and thus could not include them in our analysis. A total of 68 trials (26 females, 42 males) were conducted (a total of 127 trials were attempted; 59 spiders did not leave the syringe in the allotted time). Spiders that remained within the syringe (incomplete trials) did not differ in sex ratio or average mass from the spiders that did leave the syringe and enter the arena (completed trials; Supplementary Table 1).

All movements of the spider were recorded by a GoPro camera above the arena. Surfaces (plastic wall, rocks) were cleaned with 70% ethanol between trials; leaf litter and sand from three separate arenas were pooled and stirred between trials to disperse and thus minimize chemical cues (Elias et al. 2004).

We used Behavioral Observation Research Interactive Software (BORIS; Friard and Gamba 2016) to collect event data from videos. We noted the first substrate chosen by each spider when it moved away from the syringe, measured the time spent by each spider on each substrate, and counted how many times each spider jumped to each substrate, including jumps between substrates and jumps that started and ended on the same substrate. Some of the spiders (n = 19) jumped out of the arena onto the surrounding wall during the trial, but many of these individuals returned to the arena thereafter. Thus, while all individuals (n = 68) were included when assessing the first substrate used, only those spiders that spent a
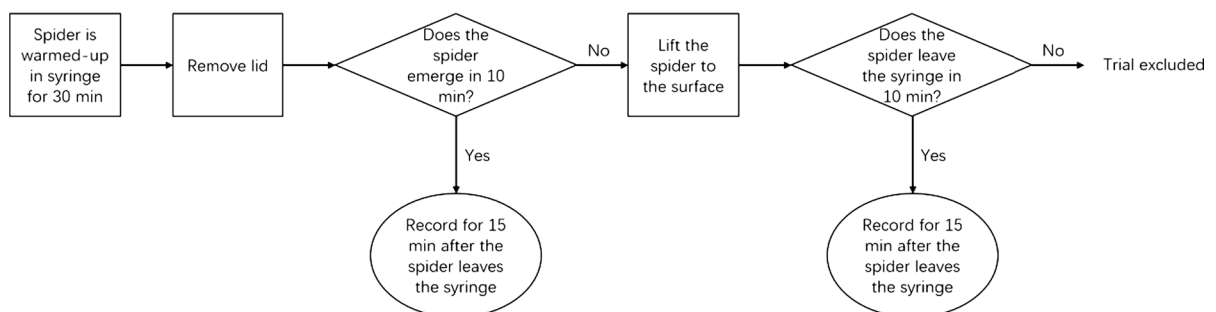


**Fig. 2** Flow chart describing the methods the behavioral trials assessing the habitat choice behavior of *Habronattus clypeatus*

total of ten minutes or more within the arena ($n = 56$) were included when calculating time spent on each substrate and the number of jumps.

## Data Analysis

Statistical analyses were performed in R v. 3.6.3 (R Core Team 2020). All data and code can be found at https://github.com/ambikamath/habronattussubstrate use. To assess differences in vibration attenuation across the various substrates, we used a linear mixed effects model (*nlme*; Pinheiro et al. 2018) with signal RMS as the dependent variable, substrate type, distance from the source, and their interaction as independent variables, and replicate as a random factor.

We used a Chi-squared test to determine whether the first substrate chosen by the spiders was significantly different than random, first for all individuals ($n = 68$) and then separately for males ($n = 42$) and females ($n = 26$). We also ran a Fisher's exact test to test for differences between the sexes in first substrate chosen. We used a Friedman rank sum test to determine on which substrate the spiders spent a majority of their time ($n = 56$), for all individuals and then separately for males ($n = 33$) and females ($n = 23$). Note that we did not compare time spent on each substrate because those values are non-independent of each other. However, we did ask, using a Kruskal–Wallis rank sum test, whether the time spent on the substrate that was first chosen differed by substrate. In other words, was the time spent on leaf litter by individuals who first chose leaf litter different from the time spent on sand by individuals who first chose sand or the time spent on rocks by individuals who first chose rocks? This allowed us to assess whether individuals' substrate preferences indicated by first choice are further corroborated by which substrate they choose to spend their time on. Finally, we used a generalized linear mixed effects model with a Poisson error distribution (*lme4*; Bates et al. 2015) with substrate as a fixed effect and individual as a random effect to test for differences among substrates in how often spiders jumped towards them ($n = 56$).

## Results

### Vibration Transmission

Signal RMS amplitude was significantly predicted by distance from the vibration source ($F_{1,96} = 165.45$, $p < 0.0001$), substrate type ($F_{1,96} = 23.46$, $p < 0.0001$), and their interaction ($F_{3,96} = 78.62$, $p < 0.0001$). In most of the substrates, amplitudes decreased as vibrations propagated farther away, but levels of attenuation were significantly different in the four substrate components (Fig. 3). Vibrations attenuated most rapidly in sand, followed by rock. Attenuation in sticks was very slight at distances less than 35 mm. In leaves, amplitude increased with distance from the source likely due to natural resonance of leaves.

**Fig. 3** Vibratory signal attenuation in different substrates. Sine sweeps (0–5,000 Hz) were transmitted through an actuator and measured with a laser vibrometer at distances from 1—35 mm from the source ($n = 5$ per substrate; error bars $=$ SE). Vibrations attenuated most rapidly in sand, and showed little attenuation in leaf litter components (leaves and sticks) at distances less than 35 mm
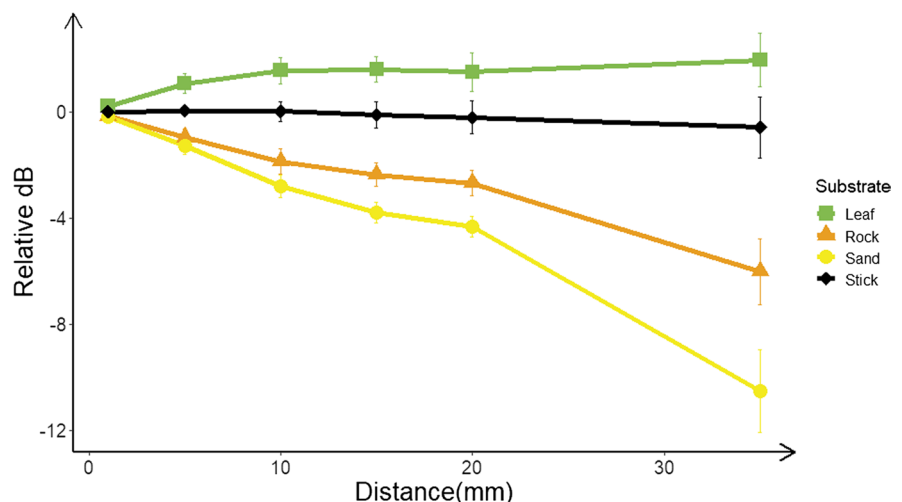
Substrate Choice

When exploring the arena, the first substrate chosen by spiders differed from random (Fig. 4; Supplementary Table 2). Spiders were more likely to choose leaf litter or rocks than sand (37% and 46%, compared to 18%); however, they did not differ in how often they chose leaf litter or rocks. We found a trend towards a difference between males and females in the first substrate chosen ($p=0.057$); males' first choice of substrate did not differ from random, whereas females chose leaf litter or rocks more often than sand (Fig. 4; Supplementary Table 2).

Spiders were more likely to spend a majority of their time on leaves and rocks compared with sand, but did not differ in how often they spent a majority of their time on leaves or on rocks (Fig. 5; Supplementary Table 3). The same patterns held for both males and females, when analyzed separately (Fig. 5; Supplementary Table 3).

Spiders who chose leaf litter or rocks as their first substrate tended to spend most of their time on the substrate they first chose (94% and 73% on average, respectively), but spiders who chose sand as their first substrate spent only an average of 23% of their time on sand ($\chi^2=14.6$, df$=2$, $p=0.0007$; Fig. 6).



**Fig. 4** First substrate chosen by female and male *Habronattus clypeatus* after entry into the experimental arena. Letters above bars indicate significant differences between substrates for females (lighter blue lowercase letters), males (darker purple lowercase letters), and both sexes pooled (black uppercase letters). See Supplementary Table 2 for statistical comparisons
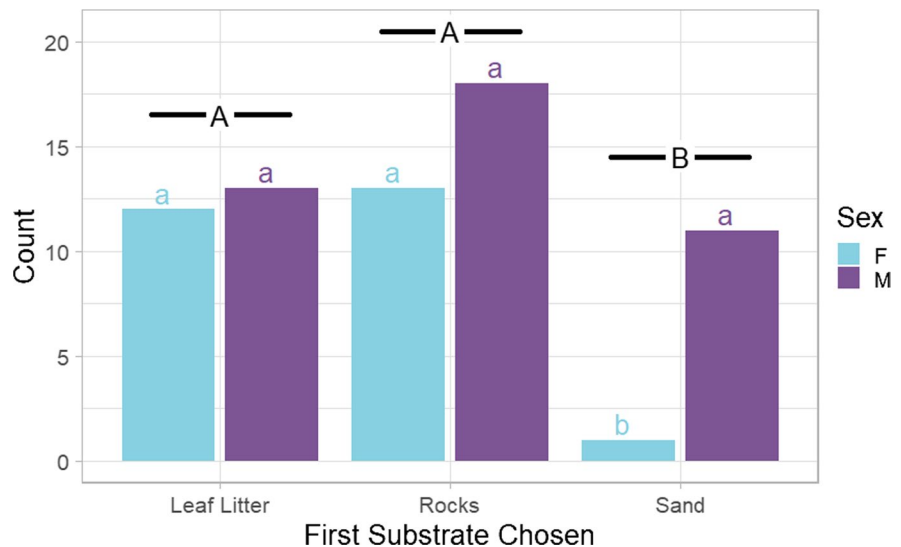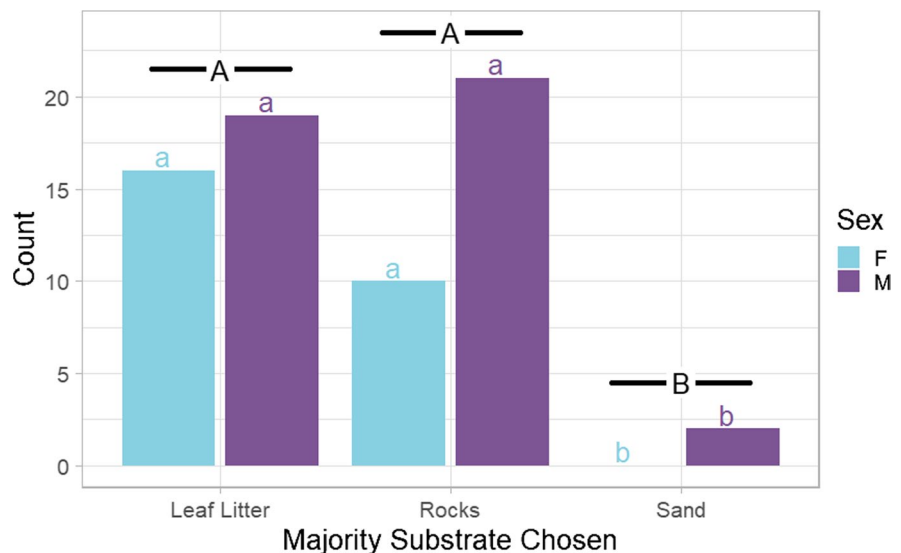


**Fig. 5** Substrates on which female and male spiders spent a majority of their time within each trial. Letters above bars indicate significant differences between substrates for females (lighter blue lowercase letters), males (darker purple lowercase letters), and both sexes pooled (black uppercase letters). See Supplementary Table 3 for statistical comparisons

**Fig. 6** The proportion of total time spent on each substrate by spiders, divided according to first substrate chosen
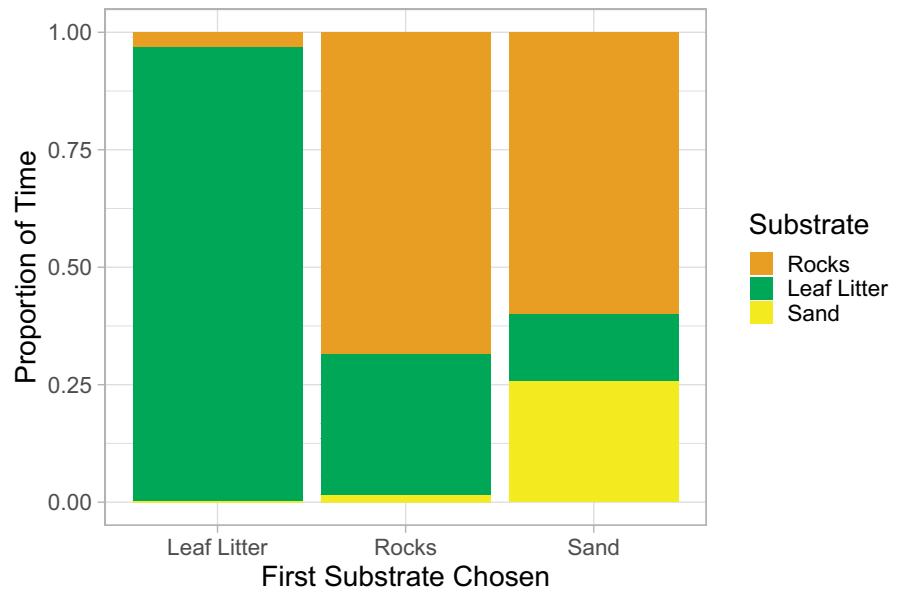


Finally, while exploring the arena, spiders jumped to sand (1.1 ± 3.0 jumps per trial) significantly less often than to leaf litter and rocks (2.8 ± 6.0 and 2.7 ± 5.1 jumps per trial respectively; leaf litter vs. rocks: β = -0.12 ± 0.11, $p = 0.27$; leaf litter vs. sand: β = -0.99 ± 0.14, p < 0.0001; rocks vs. sand: β = -0.87 ± 0.14, p < 0.0001).

## Discussion

In this study, we examined vibration transmission through three substrates found in the natural habitat of the jumping spider *Habronattus clypeatus* and then examined how males and females of these species chose among these substrates in a controlled laboratory environment. We found that levels of vibration attenuation were significantly different between three substrates found in the environment of *H. clypeatus,* namely leaf litter (made up of leaves and sticks, which were analyzed separately for this test), rocks and sand. Leaves were the best substrate for avoiding the attenuation of vibratory signals. In fact, our results found that signal amplitude increased with distance as it propagated across a leaf (Fig. 3), possibly due to resonance. The situation might be similar in nature and evidence suggests that many animals use plant resonance to increase the efficacy of their signals (Čokl

et al. 2005; Polajnar et al. 2012). In sticks, signals showed very slight attenuation at distances less than 35 mm. Because spiders' interactions involving vibratory signals such as courtship take place at distances of 5–8 mm (Elias et al. 2003), our results for leaves and sticks collectively indicated that leaf litter is an ideal substrate for vibratory signal transmission in these animals.

In contrast, vibrations attenuated significantly in rock, likely because rock is relatively inelastic, and even more so in sand, because the structure of sand can be considered as small particles of rocks, and energy is further lost while the signal is transmitted between particles. Overall, our results are consistent with those of Elias et al. (2004), which concluded that leaf litter was the best substrate for the spiders' courtship communication and, consequently, for their mating success. Similar effects are likely to be observed in other vibratory communication contexts, such as detecting predators and prey.

Overall, microhabitat choice behavior of *H. clypeatus* can be characterized as an avoidance of sand. Females were unlikely to first choose to move to sand (Fig. 4), and spiders that did choose sand as their first substrate spent only 23% of their time on sand (Fig. 6). Both males and females were unlikely to spend a majority of their time on sand, and jumped to sand less often than they jumped to leaf litter or rocks. This habitat choice behavior may be a consequence of

the poor vibration transmission capabilities of sand, as described above. However, spiders did not prefer leaf litter over rocks, even though rocks are much less effective than leaf litter in signal transmission.

In our experiments, spiders were free to choose their first substrate, as well as subsequently move to other substrates. The fact that the least preferred substrate based on first choice was also the substrate on which spiders spent the least time suggests that spiders were able to jump to their preferred substrate at the beginning of the trial. We observed spiders spending time looking around about before their first jump to a substrate, which suggests that the spiders' active choice of their first substrate was likely based on visual assessment (Harland and Jackson 2000; Cross et al. 2006; McGinley et al. 2015).

Signaling can be a major reason for why animals may prefer certain types of substrate over others, given that signaling environments impose substantial constraints on the ability of animals to transmit, detect, and process acoustic information (Elias and Mason 2014). The Acoustic Adaptation Hypothesis (AAH) suggests that habitat acoustics impose a selective pressure that drives the evolution of both signal structure and choice of calling sites by signalers (Jain and Balakrishnan 2011; Morton 1975). This hypothesis has been supported in some birds, anurans, and mammals; for example, male gray treefrogs avoid making their advertisement calls close to the ground, where their calls are sharply degraded (Schwartz et al. 2016), and grasshoppers have a tendency to choose positions with better conditions for call propagation in grass (Lang 2000). However, other studies have also found mixed support, with variation across species and local habitats (e.g. Sueur and Aubin 2003; Jain and Balakrishnan 2011; reviewed in Ey and Fischer 2009). Specifically, for vibratory communication, the signaling environment is often extremely heterogeneous at small scales (Kotiaho et al. 2000), and for spiders using vibratory signals to court, their signaling microhabitat is the substrates which they stand on when signaling (Elias et al. 2004). If substrate-borne courtship signaling can directly influence fitness, then we expect spiders to evolve to choose those substrates through which vibration transmission is most effective.

Our results thus show mixed support for the AAH. We observed a difference between sexes of their likelihood of choosing substrates that are effective for vibratory signaling. Females showed significant preference for leaf litter and rocks compared to sand when they chose their first substrate, which is consistent with the AAH. However, males moved to the three substrates randomly (Fig. 4), which is puzzling in light of the AAH, especially since male *H. clypeatus* produce the vibratory courtship signal. However, this behavioral difference can be explained by the mate searching process in *H. clypeatus*. Evidence from the field suggests that male *H. clypeatus* move longer distances than females (Brandt 2019; Taylor et al. 2019; see also Blackburn and Maddison 2015). This dimorphism in movement behavior is found in many other animals as well (e.g. Kotiaho et al. 1998; Stark et al. 2005; Kamath and Losos 2018), which is consistent with males moving in search of females to mate with. Specifically, male *Habronattus* use silk drag lines laid down by females as cues by which to locate females (Blackburn and Maddison 2015; Taylor et al. 2019), and so male microhabitat choice behavior that is agnostic to substrate and is instead based on cues of female presence might maximize mate location by males in the face of context-dependent and idiosyncratic habitat use by females in complex natural conditions (Guevara-Fiore et al. 2010). We predict that in laboratory-based choice tests, mature males will move towards female silk drag lines regardless of substrate type; in natural conditions, we expect that matings will be more likely to occur when males locate and court females on leaf litter compared with rocks or sand.

Moreover, it is likely that the effectiveness of vibratory signal propagation is only one of many factors influencing substrate choice in *H. clypeatus*. For example, exposure and height varies a lot across substrates. *Habronattus clypeatus* individuals in the field are observed at locations above the ground, on slightly raised perches (EEB, DOE *pers. obs.*). These sites could provide spiders a better vantage point from which to observe things below. It is therefore possible that, in the context of our experiment, spiders chose leaf litter and rocks simply because they were higher than bare sand. Other potential reasons for habitat choice

include protection from predators, temperature preferences, and to provide favorable backgrounds for visual communication. For example, leaf litter might provide more shade and shelter for the animal to hide, allowing for both behavioral thermoregulation and predator avoidance. In contrast, a sandy surface without additional cover is a very open and exposed environment. However, we noticed in our behavioral observations that *H. clypeatus* individuals do not hide very often, and instead were almost always visible on the top surfaces of the substrates (it is worth noting here that the individuals included in our analysis likely represent a disproportionately bold subset of *H. clypeatus*, because we could not measure the habitat use behavior of individuals that did not leave the syringe to begin the behavioral trial). In nature, temperature is also likely to differ between substrates and because microhabitat choice can be an important way to behaviorally regulate body temperature, especially for ectothermic animals (Kearney et al. 2009; Brandt 2019), this could influence substrate choice. In this experiment however, all surfaces were the same temperature during trials, thus while thermal properties could still be a potential factor, active choice was not based on the surface temperature of each substrate. Finally, optical properties of the substrates could be important as some may be more effective backgrounds for the visual display (Boughman 2002; Endler 1983; Seehausen et al. 1997). Future studies should investigate the covariation of substrate type with temperature as well as visual environment, for a fuller understanding of how animals navigate complex heterogeneous environments and the fitness consequences of these navigational choices.

**Data and Code Availability Statement** Data and code for statistical analyses are available at https://github.com/ambikamath/habronattussubstrateuse

**Declarations**

**Conflict of Interest Statement** The authors declare that they have no conflicts of interest.

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