The effect of substrate on prey capture does not match natural substrate use in a wolf spider

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Because habitats present different costs and benefits in contexts ranging from foraging to mating to predator avoidance, decisions about habitat use likely involve significant trade-offs across behavioural contexts. We examine this possibility in *Schizocosa floridana*, a cursorial wolf spider whose habitat consists of multiple substrates, including oak and pine litter, and sand. However, *S. floridana* restricts its use of habitat to oak litter. Substrate environments vary significantly in the degree to which they transmit visual and vibratory information. Previous work found that oak litter best transmits the substrate-borne vibrations that are critical to mating communication. However, oak litter may reduce the availability of visual information, which is known to be important for prey capture in other wolf spider species. Here, we test the relationship between substrate and prey capture efficiency in *S. floridana*. We examine substrate use in a foraging context via two laboratory-based experiments to (1) assess differences in prey capture efficiency among the three most common substrates in the field and to (2) determine which sensory modalities are involved in prey capture. We found that prey capture rates were highest on sand despite the fact that sand is the least used substrate by *S. floridana* in the wild. We also found no conclusive evidence that either the visual or the vibratory sensory modalities are critical for prey capture. Our results thus suggest that strict habitat specialization such as that exhibited by *S. floridana* is beneficial in some ecological contexts but costly in others.

Habitats can vary widely in factors ranging from availability of resources (Gillies et al., 2006; Mysterud & Ims, 1998) to predation risk (Mittelbach, 1986; Whittingham & Evans, 2004) to abiotic variables such as temperature (Ahnesjö & Forsman, 2006; Brandt, Kelley, & Elias, 2018). Because of this, many animals choose to use only a subset of available habitats at a given time, with significant corresponding effects on the selective regimes they experience (Morris, 2003; Pulliam & Danielson, 1991; Rosenzweig, 1981). Decisions about habitat use often present important trade-offs. For example, habitat use decisions often involve trade-offs between foraging rate and factors such as predation risk (e.g. Lima, 1985; Werner & Hall, 1988), or less desirable temperatures (e.g. Garner, Clough, Griffiths, Deans, & Ibbotson, 1998; Schmitz, 1991), or territorial defence (e.g. Westneat, 1994). Habitat use is also known to drive selection through its effect on the sensory environment in contexts ranging from animal communication (e.g. Leal & Fleishman, 2003; McNett & Cocroft, 2008; Seehausen et al., 2008) to predator avoidance (Mandelik, Jones, & Dayan, 2003) to competitive interactions (Mitchem, Stanis, Sutton, Turner, & Fuller, 2018). The

interaction of habitat use and the sensory environment is likely important, as selection for habitat use in one behavioural context (e.g. foraging, mating, nesting, etc.) has the potential to shape or constrain the sensory information available in other contexts.

For cursorial arthropods, variation in substrate habitat is likely critically important. Substrates (i.e. the physical structures on which individuals are found) present vastly different terrains and environments and often vary widely over small spatial scales, as do the distributions of the arthropods that inhabit them (e.g. Kruys & Jonsson, 1999; Lowrie, 1948; Rosenthal, Hebets, Kessler, McGinley, & Elias, 2019; Uetz, 1975, 1991). Likewise, substrates also differ significantly in how they transmit sensory information. For example, substrate-borne vibrations are a critical sensory modality for many arthropods (Cocroft & Rodríguez, 2005; Virant-Doberlet & Čokl, 2004), and their transmission varies widely (Elias & Mason, 2014). Likewise, the perceptibility of visual cues is also highly dependent on the structural complexity of the substrate, which can vary from the open spaces of sand or bare rock to the highly complex structures of leaf litter, all of which differ in line-of-sight visual detection distances (e.g. Uetz, Roberts, Clark, Gibson, & Gordon, 2013).

In this study, we use a series of experiments to assess the potential effects of substrate habitat on *Schizocosa floridana*, a wolf

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spider native to central Florida whose habitat boasts a diverse array of substrate habitats from oak and pine litter to rocks and fallen logs, to tall grass, to bare sand. While all of these habitats are used by various wolf spider species, *S. floridana* exclusively occupies oak litter (Rosenthal et al., 2019). This is known to be beneficial in a mating context. Oak litter is the best available transmitter of substrate-borne vibrations (Choi et al., 2019), and male *S. floridana* attract mates with a substrate-borne vibratory song (Rosenthal & Hebets, 2012; Rundus, Sullivan-Beckers, Wilgers, & Hebets, 2011). As a consequence, mating rates are highest when spiders are courting on oak litter (Rosenthal et al., 2019). Although it has important effects on mating communication, this pattern of oak litter specialization is present during both mature and immature life stages (Rosenthal et al., 2019), although only mature individuals are known to communicate with each other using substrate-borne vibrations.

In *S. floridana* habitats, visual and vibratory sensory efficacy likely trade off across substrates. Oak litter habitats are more structurally complex than sandy habitats, thus presenting shorter lines of sight. Conversely, oak litter transmits vibrations well over longer distances, whereas sand does not. Both vibratory and visual cues are known to be important for prey capture in other wolf spider species (Lizotte & Rovner, 1988; Persons & Uetz, 1996; Rovner, 1980). Here, we assess the effects of *S. floridana*'s habitat specialization, which is known to be beneficial in the context of mating, on performance in another behavioural context, prey capture. Given *S. floridana*'s strict restriction to litter habitats, we hypothesize that across contexts (mating and foraging), leaf litter would be the most favourable among available habitats. Additionally, due to the efficacy and reliability of substrate-borne vibration cues in leaf litter, we hypothesize that the vibratory sense would be used by *S. floridana* for prey capture. We test the first hypothesis by experimentally assessing foraging success on a variety of available substrates, and the second by assessing the relative importance of the visual and vibratory sensory modalities for prey capture success.

METHODS

Collection and Housing

We collected subadult *S. floridana* in January from unceded lands of the Seminole and Timucua in Alachua County, Florida, U.S.A. We also collected 3-gallon (11.4-litre) bags of substrate for each the three most common substrate types at the collection site (oak litter, pine litter, sand; see Rosenthal et al., 2019). We then transported the spiders and substrate samples to Berkeley, California, U.S.A., where the spiders were housed individually in $6 \times 6 \times 8$ cm plastic cages (Amac Plastic Products, Petaluma, CA, U.S.A.) visually isolated from each other with a brown paper wrapping. Spiders were maintained on a 12:12 h light:dark cycle in a rearing room maintained at a constant $24\,°C$. Spiders were fed three body-size-matched crickets (*Gryllodes sigillatus*, Ghann's Crickets – Augusta, GA, U.S.A.) per week and provided water ad libitum. Spiders were housed for approximately 1 month before the beginning of trials, during which time they moulted to sexual maturity.

Experiment 1: Foraging Success on Natural Substrates

To assess the effect of substrate type on *S. floridana* foraging success, we conducted timed foraging trials in arenas floored with the substrates from the collection site. These trials used the same set-up used in Rosenthal et al. (2019) to assess mating success on these substrates. Briefly, trials were run in 30 cm diameter arenas with 50 cm high acetate walls, wrapped in brown paper to visually isolate them. Each arena was filled with sand to a depth of ~2 cm. We conducted foraging trials in three treatments: one arena with oak litter on sand, one arena with pine litter on sand and one arena with sand only. Pine and oak litter were added to a depth of ~6 cm. Between each set of trials, we removed the litter in each arena and replaced it into an adjacent arena in order to ensure that the trial results were not the result of arena-specific effects. Spiders were fed a full meal of three crickets to standardize hunger and were then deprived of food for 1 week prior to being run in foraging trials.

To begin each trial, we placed a cricket into the middle of the arena. After 1 min, one spider was introduced into the arena and allowed to forage or explore for 5 min. At the end of 5 min, we removed the spider from the arena and assessed predation success. For successful captures, the recovered spiders were always observed eating the cricket. Handling the spider or searching through the litter for the spider did not cause it to drop or abandon the prey. For unsuccessful captures, we located the cricket in the arena and removed it prior to the start of the next trial. Spiders were run in one trial on one substrate only. We ran a total of 117 trials (41 oak trials, 38 pine trials, 38 sand trials).

Statistical analysis

All statistical analyses were performed in R v.3.5.1 (R Core Team, 2018). Because there were fewer than five successful captures in two of our substrate treatments, we used a Fisher's exact test to assess whether prey capture success differed significantly across substrates. Significant results were followed up with post hoc pairwise Fisher's exact tests.

Experiment 2: Visual and Vibratory Contributors to Prey Capture

To assess the contributions of the visual and vibratory sensory modalities to prey capture, we carried out predation trials with treatments to eliminate either visual cues, vibratory cues, both, or neither. We ran four trials simultaneously inside of a 60×64 cm wooden frame covered in blackout cloth. The base of the frame was floored with four granite tiles covered in matte white paint. For each set of trials, we placed a circle of filter paper (Whatman no. 1 filter paper; 18.5 cm diameter; Schleicher and Schuell, Keene, NH, U.S.A.) onto two of the four tiles. We then placed an open-bottomed acetate cylinder (15 cm diameter) on each tile. Cylinders were visually isolated from one another by paper separators that sat on top of the tiles but did not contact the edges of the cylinders. Filter paper transmits substrate-borne vibrations well whereas granite does not (see Elias & Mason, 2014; Hebets, Vink, Sullivan-Beckers, & Rosenthal, 2013). Thus, each set of four trials contained two vibration present arenas and two vibration absent arenas. Spiders used in this experiment were also deprived of food for 1 week before trials, and each spider was run through one treatment only.

Furthermore, each set of trials was run in one of two light conditions. We used a remote-controlled LED light bulb with a 60 W equivalence (TechgoMade), which could be set to display red light or full-spectrum white light. Wolf spider eyes are not sensitive to red light (Devoe, Small, & Zvargulis, 1969; Ortega-Escobar, 2002), so this treatment was effectively dark, but allowed for video-recording. To start four trials simultaneously, we placed a cricket in each cylinder under an overturned 2.5-dram plastic vial (Thornton Plastics, Salt Lake City, UT, U.S.A.) connected to a string. We then placed one spider in each cylinder and allowed them to acclimate for 2 min. The strings of all four plastic vials were connected to a line that fed up to the outside of the frame. Pulling this line raised all four vials simultaneously, releasing the crickets into the trial arenas.

Table 1
Sample sizes for analyses of capture success, latency to orient to prey and latency to capture prey

	Dark/Paper	Dark/Granite	Light/Paper	Light/Granite
Success	40	42	46	47
Orient	9	14	17	14
Capture	17	18	22	27

Trials began with the release of the crickets and continued for 5 min. We recorded trials with a GoPro Hero 5 camera positioned above the arenas. At the end of the trials, we scored prey capture success. We then disposed of the filter paper floors and cleaned the granite surface with 75% ethanol before beginning the next set of trials. In total, we ran 175 trials (40 Dark/Paper; 42 Dark/Granite; 46 Light/Paper; 47 Light/Granite). A number of spiders escaped from their arenas before trials began, accounting for differences in sample size among the treatments. From the videorecorded trials, we also scored latency to capture prey as the duration from the beginning of the trial to the moment of capture. We also scored the latency to the first orientation of the spider towards the prey. All video scoring was done in BORIS (Friard & Gamba, 2016). Video quality issues prevented analysis in seven trials (2 Dark/Paper; 4 Dark/Granite; 1 Light/Granite).

Statistical analysis

To test the effect of sensory modality on prey capture, we ran a logistic regression with capture success as the dependent variable, and light environment, substrate type, and the interaction of substrate and light environment as independent variables. To further examine potential effects of the sensory environment on prey capture efficiency, we ran linear models with latency to orient towards prey and latency to capture as dependent variables, and light and substrate environments and their interaction as independent variables. Because not all spiders oriented towards prey or successfully caught prey, the sample sizes for these analyses were smaller than the number of trials run and varied from analysis to analysis. A complete list of sample sizes for each of these analyses is given in Table 1. Additionally, latency to orient and to capture were not normally distributed and were therefore square-root transformed before use in these two analyses.

RESULTS

Experiment 1: Foraging Success on Natural Substrates

Substrate type significantly affected foraging success (Fisher's exact test: $P < 0.0001$; Fig. 1). Prey capture rates were significantly higher on sand (34.2%) than on the two other substrates (oak: 4.8%, $P = 0.001$; pine: 2.6%, $P < 0.0001$). Capture rates on oak and pine did not differ significantly from each other ($P = 0.999$).

Experiment 2: Visual and Vibratory Contributors to Prey Capture

Neither substrate type ($z = -0.111, P = 0.912$), light environment ($-0.272, P = 0.786$), nor their interaction ($z = -0.641, P = 0.521$) predicted prey capture success (Fig. 2a). There was no effect of substrate type ($t = -0.592, P = 0.557$), light environment ($t = 0.616, P = 0.541$), or their interaction ($t = 0.153, P = 0.879$) on the latency to first orienting (Fig. 2b). And for those spiders that did catch prey, there was no effect of substrate type ($t = 0.187, P = 0.852$), light environment ($t = 0.130, P = 0.897$), or their interaction ($t = -0.003, P = 0.998$) on their latency to capture (Fig. 2c).
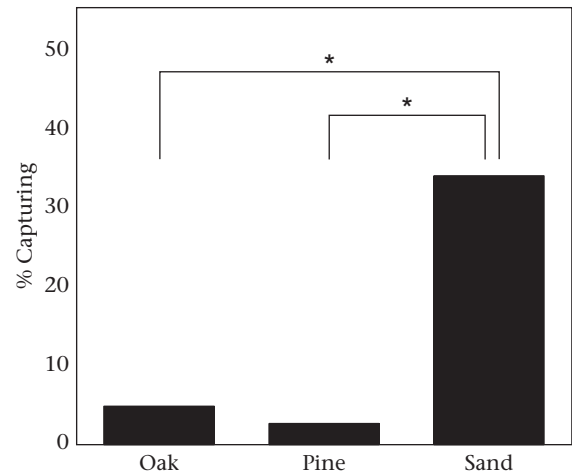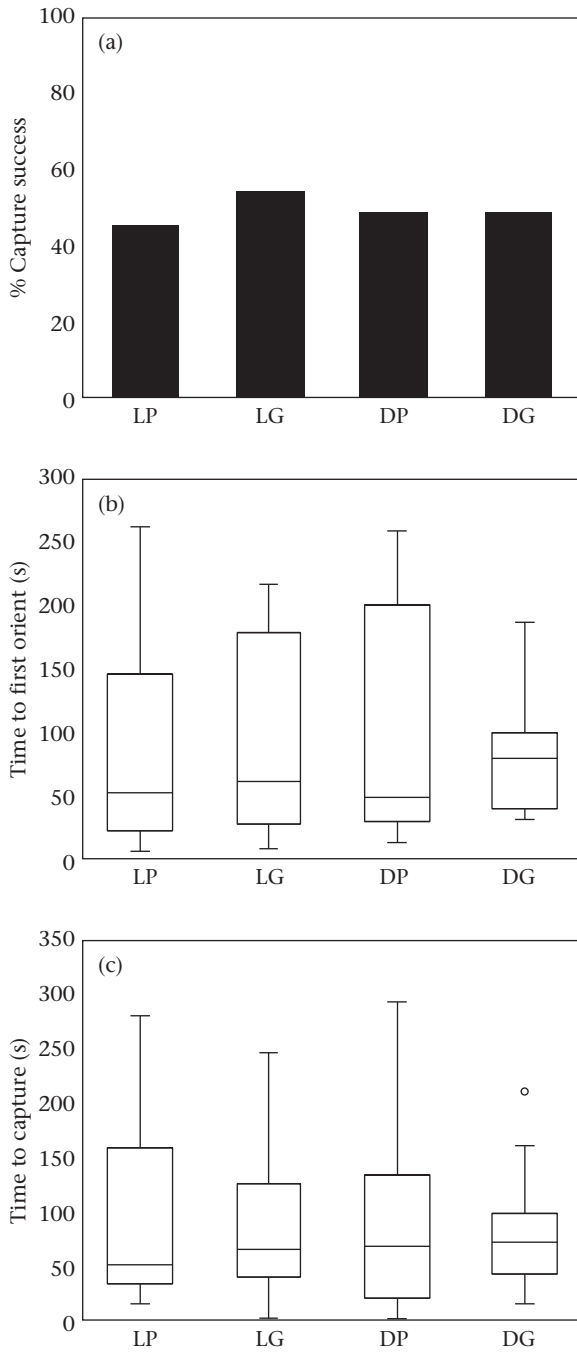

Figure 1. Prey capture success across the three natural substrates (oak litter, pine litter, sand). *$P < 0.05$.

DISCUSSION

Schizocosa floridana foraging success was highest on sand, the substrate on which it is least likely to be found in the wild and least likely to be successful in a mating context (Rosenthal et al., 2019). This does not appear to be the result of substrate-based differences in the availability of sensory information, as we found no evidence that the loss of either the visual or the vibratory modality affected prey capture success. This is an interesting finding given the prominent role of the vibratory sense in mating communication (and foraging in other species of *Schizocosa;* Persons & Uetz, 1996, 1999). Critically, *S. floridana*'s substrate specialization does not appear to have led to selection for increased predation efficacy on oak litter. Possibly their hunting strategy (i.e. sit and wait) and their generalist foraging lifestyle do not favour the evolution of traits to take advantage of the increased efficacy of vibratory transmission. Alternatively, they may be using some other sensory modality (e.g. nearfield sound) to locate nearby prey. Taken together, our results thus suggest that specializing on oak litter provides significant benefits in a mating context but may be costly in a foraging context.

Why is foraging success highest on sand? We suggest that variation in prey capture success across the three substrates was driven primarily by differences in habitat structure. Increased habitat structural complexity is known to reduce predation success, potentially due to increased availability of prey refuges. However, wolf spiders are sit-and-wait predators (e.g. Samu, Szirányi, & Kiss, 2003; Wagner & Wise, 1997), and as such, predation may be driven more by probability of prey encounters than by the ability to actively find prey. Prey are more likely to encounter stationary spiders on the simplest substrate, sand, which has the smallest total explorable surface area. They may also be more likely to continue exploring an open habitat as opposed to coming to rest in a refuge that is available in the more complex leaf litter. Generally, we might thus expect that prey capture rates would be highest in experiments performed in open arenas. Supporting this notion, prey capture rates in experiment 2, which used entirely open arenas, were higher than prey capture rates on oak (Fisher's exact test: $P < 0.0001$) or pine (Fisher's exact test: $P < 0.0001$) in experiment 1, but not significantly different from prey capture rates on sand (Fisher's exact test: $P = 0.108$), an equally open arena. Thus, our results do not support the conclusion that differences in the availability of visual or vibratory information drive differences in prey capture across the substrates, rather, it appears to be the structure of the substrate itself.

Figure 2. (a) Rates of prey capture success, (b) box plots of time to first orienting towards prey and (c) box plots of time to prey capture across the four sensory treatments: Light/Paper (LP); Light/Granite (LG); Dark/Paper (DP); Dark/Granite (DG). Box plots show 25% and 75% quartiles (boxes), medians (lines in boxes), outermost values within the range of 1.5 times the respective quartiles (whiskers) and outliers (circles).

It is surprising that the loss of one or both of these important sensory modalities does not affect prey capture success, given that other species are known to use them in a foraging context. Reliance on particular sensory cues may be species specific, as different species occupy vastly different sensory environments. Additionally, it may still be the case that vibratory or visual information about prey abundance plays a role in broader foraging decisions such as patch residence time (e.g. Persons & Uetz, 1996). Concerning the mechanics of prey capture, however, our results suggest that the spiders are relying most on some other sensory modality

(i.e. nearfield sound, olfactory cues) or on physical contact with prey to effect a capture. Supporting this, nearly half of all spiders that successfully captured prey did so without having oriented to it first. It is possible that our treatments did not completely eliminate visual or vibratory information, or that cricket locomotion does not produce loud enough substrate-borne vibrations. However, both visual and vibratory ablation treatments of this kind have been used effectively in this species before (e.g. Hebets et al., 2013; Rosenthal, Wilkins, Shizuka, & Hebets, 2018), and wolf spiders are extremely sensitive to even low-amplitude substrate-borne sound. It is also possible that behavioural changes across treatments in spiders, crickets, or both might obscure differences in sensory information use. For example, the loss of visual information in the dark might be offset by increased spider movement. Although no obvious differences were evident, and we observed crickets moving in all substrates, testing for such complex interactions lies beyond the scope of this study. However, the interacting dynamics of spider and prey movement deserve future study.

It is interesting that *S. floridana* restricts its habitat use to oak litter even in life stages that do not involve vibratory communication. Other arthropod predators do not seem to be so restricted. The jumping spider *Habronattus dossenus,* also a generalist predator, benefits from a restricted set of substrates for the propagation of its courtship song but does not restrict its substrate use (Elias, Mason, & Hoy, 2004). Likewise, the other wolf spiders at the *S. floridana* collection site are present on multiple substrates including sand (Rosenthal et al., 2019), although oak litter also provides them with an optimal substrate for vibratory signalling (Choi et al., 2019). Why is *S. floridana* forgoing foraging opportunities on substrates that may be more favourable by restricting substrate usage at all life stages? One possibility is that selection for habitat specialization in one context (i.e. mating) has constrained habitat selection non-adaptively, even during other life stages. Alternatively, the sum benefits of oak litter specialization, many of which we may not have yet identified, may simply outweigh the costs to foraging efficiency. Similarly, there may be other costs to foraging in sandy habitats that these experiments did not capture. For instance, *S. floridana* may experience higher predation risk on sand for the same reasons that it experiences higher prey capture success. Or, the open habitat of sand may increase desiccation risk or be in some other way unsuitable. Finally, it is possible that prey capture rates in the field are more strongly influenced by prey abundance than by foraging efficiency. Substrate depth, structure and complexity are all known to affect prey diversity and abundance (Crowder & Cooper, 1982; Marshall & Rypstra, 1999; Schmidt & Rypstra, 2010). If prey abundances are higher on oak litter, then it is possible that sand is the substrate on which the ability to catch a specific prey animal is highest (as we found in the present study), but not the substrate on which the probability of catching prey in general is highest. Future work sampling prey arthropod abundance in the field and assessing heterospecific habitat use and competitive interactions will address all these possibilities.

Conclusions

In this study, we provide evidence that the extreme habitat partitioning behaviour of *S. floridana* is potentially costly in a foraging context. Our findings suggest the possibility that selection for specializing on a specific habitat in one behavioural context is so strong that it constrains habitat use across *S. floridana*'s entire life history. These results highlight the importance of investigating the effects of habitat across multiple behavioural contexts and the role of the sensory environment in predatory behaviour. Overall, our results emphasize the fact that decisions concerning habitat use are

likely multifactorial, balancing multiple distinct costs and benefits across time, space and behavioural contexts.

Acknowledgments

References

Ahnesjö, J., & Forsman, A. (2006). Differential habitat selection by pygmy grasshopper color morphs; interactive effects of temperature and predator avoidance. *Evolutionary Ecology, 20*, 235–257.

Brandt, E. E., Kelley, J. P., & Elias, D. O. (2018). Temperature alters multimodal signaling and mating success in an ectotherm. *Behavioral Ecology and Sociobiology, 72*, 1–14.

Choi, N., Bern, M., Elias, D. O., McGinley, R. H., Rosenthal, M. F., & Hebets, E. A. (2019). A mismatch between signal transmission efficacy and mating success calls into question the function of complex signals. *Animal Behaviour, 158*, 77–88.

Cocroft, R. B., & Rodríguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *Bioscience, 55*, 323–334.

Crowder, L. B., & Cooper, W. E. (1982). Habitat structural complexity and the interaction between bluegills and their prey. *Ecology, 63*, 1802–1813.

Devoe, R. D., Small, R. J. W., & Zvargulis, J. E. (1969). Spectral sensitivities of wolf spider eyes. *Journal of General Physiology, 54*, 1–32.

Elias, D. O., & Mason, A. C. (2014). The role of wave and substrate heterogeneity in vibratory communication: Practical issues in studying the effect of vibratory environments in communication. In R. B. Cocroft, M. Gogala, P. S. M. Hill, & A. Wessel (Eds.), *Studying vibrational communication* (pp. 215–247). Berlin, Germany: Springer.

Elias, D. O., Mason, A. C., & Hoy, R. R. (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.

Friard, O., & Gamba, M. (2016). BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution, 7*, 1325–1330.

Garner, P., Clough, S., Griffiths, S. W., Deans, D., & Ibbotson, A. (1998). Use of shallow marginal habitat by *Phoxinus phoxinus*: A trade-off between temperature and food? *Journal of Fish Biology, 52*, 600–609.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., et al. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology, 75*, 887–898.

Hebets, E. A., Vink, C. J., Sullivan-Beckers, L., & Rosenthal, M. F. (2013). The dominance of seismic signaling and selection for signal complexity in *Schizocosa* multimodal courtship displays. *Behavioral Ecology and Sociobiology, 67*, 1483–1498.

Kruys, N., & Jonsson, B. G. (1999). Fine woody debris is important for species richness on logs in managed boreal spruce forests of northern Sweden. *Canadian Journal of Forest Research, 29*, 1295–1299.

Leal, M., & Fleishman, L. J. (2003). Differences in visual signal design and detectability between allopatric populations of *Anolis* lizards. *American Naturalist, 163*, 26–39.

Lima, S. L. (1985). Maximizing feeding efficiency and minimizing time exposed to predators: A trade-off in the black-capped chickadee. *Oecologia, 66*, 60–67.

Lizotte, R. S., & Rovner, J. S. (1988). Nocturnal capture of fireflies by lycosid spiders: Visual versus vibratory stimuli. *Animal Behaviour, 36*, 1809–1815.

Lowrie, D. L. (1948). The ecological succession of spiders in the Chicago area dunes. *Ecology, 29*, 334–351.

Mandelik, Y., Jones, M., & Dayan, T. (2003). Structurally complex habitat and sensory adaptations mediate the behavioural responses of a desert rodent to an indirect cue for increased predation risk. *Evolutionary Ecology Research, 5*, 501–515.

Marshall, S. D., & Rypstra, A. L. (1999). Patterns in the distribution of two wolf spiders (Araneae: Lycosidae) in two soybean agroecosytems. *Environmental Entomology, 28*, 1052–1059.

McNett, G. D., & Cocroft, R. B. (2008). Host shifts favor vibrational signal divergence in *Enchenopa binotata* treehoppers. *Behavioral Ecology, 19*, 650–656.

Mitchem, L. D., Stanis, S., Sutton, N. M., Turner, Z., & Fuller, R. C. (2018). The pervasive effects of lighting environments on sensory drive in bluefin killifish: An investigation into male/male competition, female choice, and predation. *Current Zoology, 64*, 499–512.

Mittelbach, G. (1986). Predator-mediated habitat use: Some consequences for species interactions. *Environmental Biology of Fishes, 16*, 159–169.

Morris, D. W. (2003). Toward an ecological synthesis: A case for habitat selection. *Oecologia, 136*, 1–13.

Mysterud, A., & Ims, R. A. (1998). Functional responses in habitat use: Availability influences relative use in trade-off situations. *Ecology, 79*, 1435–1441.

Ortega-Escobar, J. (2002). Evidence that the wolf-spider *Lycosa tarantula* (Araneae, Lycosidae) needs visual input for path integration. *Journal of Arachnology, 30*, 481–486.

Persons, M. H., & Uetz, G. W. (1996). The influence of sensory information on patch residence time in wolf spiders (Araneae: Lycosidae). *Animal Behaviour, 51*, 1285–1293.

Persons, M. H., & Uetz, G. W. (1999). Age and sex-based differences in use of prey sensory cues in wolf spiders (Araneae: Lycosidae). *Journal of Insect Behavior, 12*, 723–736.

Pulliam, H. R., & Danielson, B. J. (1991). Sources, sinks, and habitat selection: A landscape perspective on population dynamics. *American Naturalist, 137*, 550–566.

R Core Team. (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www/R-project.org/.

Rosenthal, M. F., & Hebets, E. A. (2012). Resource heterogeneity interacts with courtship rate to influence mating success in the wolf spider *Schizocosa floridana*. *Animal Behaviour, 84*, 1341–1346.

Rosenthal, M. F., Hebets, E. A., Kessler, B., McGinley, R., & Elias, D. O. (2019). The effects of microhabitat specialization on mating communication in a wolf spider. *Behavioral Ecology, 30*(5), 1398–1405.

Rosenthal, M. F., Wilkins, M. R., Shizuka, D., & Hebets, E. A. (2018). Dynamic changes in display architecture and function across environments revealed by a systems approach to animal communication. *Evolution, 72*, 1134–1145.

Rosenzweig, M. L. (1981). A theory of habitat selection. *Ecology, 62*, 327–335.

Rovner, J. S. (1980). Morphological and ethological adaptations for prey capture in wolf spiders (Araneae, Lycosidae). *Journal of Arachnology, 8*, 201–215.

Rundus, A. S., Sullivan-Beckers, L., Wilgers, D. J., & Hebets, E. A. (2011). Females are choosier are dark: Environment-dependent reliance on courtship components and its impact on fitness. *Evolution, 65*, 268–282.

Samu, F., Szirányi, A., & Kiss, B. (2003). Foraging in agricultural fields: Local 'sit-and-move' strategy scales up to risk-averse habitat use in a wolf spider. *Animal Behaviour, 66*, 939–947.

Schmidt, J. M., & Rypstra, A. L. (2010). Opportunistic predator prefers habitat complexity that exposes prey while reducing cannibalism and intraguild encounters. *Oecologia, 164*, 899–910.

Schmitz, O. Z. (1991). Thermal constraints and optimization of winter feeding and habitat choice in white-tailed deer. *Holarctic Ecology, 14*, 104–111.

Seehausen, O., Terai, Y., Magalhaes, I. S., Carleton, K. L., Mrosso, H. D., Miyagi, R., et al. (2008). Speciation through sensory drive in cichlid fish. *Nature, 455*, 620.

Uetz, G. W. (1975). Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. *Environmental Entomology, 4*, 719–724.

Uetz, G. W. (1991). Habitat structure and spider foraging. In S. S. Bell, E. D. McCoy, & H. R. Mushinsky (Eds.), *Habitat structure* (pp. 325–348). Dordrecht, The Netherlands: Springer.

Uetz, G. W., Roberts, J. A., Clark, D. L., Gibson, J. S., & Gordon, S. D. (2013). Multimodal signals increase active space of communication by wolf spiders in a complex litter environment. *Behavioral Ecology and Sociobiology, 67*, 1471–1482.

Virant-Doberlet, M., & Čokl, A. (2004). Vibrational communication in insects. *Neotropical Entomology, 33*, 121–134.

Wagner, J. D., & Wise, D. H. (1997). Influence of prey availability and conspecifics on patch quality for a cannibalistic forager: Laboratory experiments with the wolf spider *Schizocosa*. *Oecologia, 109*, 474–482.

Werner, E. E., & Hall, D. J. (1988). Ontogenetic habitat shifts in bluegill: The foraging rate–predation risk trade-off. *Ecology, 69*, 1352–1366.

Westneat, D. F. (1994). To guard mates or go forage: Conflicting demands affect the paternity of male red-winged blackbirds. *American Naturalist, 144*, 343–354.

Whittingham, M. J., & Evans, K. L. (2004). The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis, 146*, 210–220.