Wolf Spiders Maximize Speed through Substrate Preferences during Escapes

Christian A. Rodriguez

ABSTRACT

Movement throughout one's habitat is often directly linked to survival. There are a variety of factors that can affect an animal's movement. One key habitat characteristic that not only varies between habitats, but also within habitats is substrate. The wolf spider, *Hogna carolinensis*, was collected from the sandhill prairie habitat that has two distinct substrate types, sand and vegetation. We investigated how variation in in substrate affects the speed and subsequently the substrate preference of escaping *H. carolinensis*. The spiders were run on separate tracks that had each substrate and timed over a two meter distance. Next, we allowed spiders to choose between sand and vegetation substrates during an escape behavior. We discovered that the sand substrate significantly reduced the overall max speed when compared to the other substrates. Likewise, when given a choice between substrates, the spiders showed an overall preference to run on a substrate that maximizes their speed, vegetation. In the wild, spiders need to be able to attain their maximum speed when escaping from predators or trying to catch prey. This performance-preference match illustrates how organisms can make decisions that optimize their performance in meaning behavioral tasks.

Keywords: Hogna carolinensis, performance-preference match

INTRODUCTION

One of the most basic behaviors of many animals is movement, or the act of changing location or position. In many circumstances, when (e.g. timing, duration), how (e.g. speed), and where (e.g. substrate preference) animals move through their environment has a dramatic impact on their survival. For example, when an animal is trying to catch its prey, movement is important because if it does not eat it will not survive. Movement is also important for animals that are avoiding predation, movement is vital for them because it can help them survive. How various factors in an animal's environment interact toaffect the when, how, and where, will largely determine overall movement patterns.

Some factors that affect the when, where and how of movement, are temperature, and substrate. An example of the effect of temperature can be seen in a study done by Johanna M. Kraus, which showed that the Pardosa Lapidicina, a type of wolf spider, migrates to a different habitat depending on the season because of the substrate. In colder weather the spiders migrated to forest litter instead of staying on the cobble beach. Part of the reason for the migration could be because the leaf litter has less temperature variation than the cobble beach. The "leaf litter could provide refuge from extreme temperatures during the winter" (Kraus, 2005). One key factor is variation in the substrate. Substrate variation can have an effect an organism's speed. Loose substrates can influence the grip, so the animal will have a harder time moving. Substrates can have different dimensionalities, they can be very unstable and can also be unleveled, which can have an influence on speed. Substrate has been shown to

affect speed in research done by Malcolm Burrow on the ghost crab (*Ocypode ceratophthalma*), which showed that the average speed of *O. ceratophthalma* was reduced from a max speed on wood of 2.3 m/s to 1.8 m/s when running on sandy substrate (Burrows & Hoyle 1972, Hafemann & Hubbard 1969). A study done by Jonathan B. Losos on *Anolis lizards* determined the effect of perch diameter on escape behavior in 5 species of lizards. His experiment showed that "As diameter decreased, lizards in all but one species tended to escape by jumping more frequently because jumping ability is less affected by diameter than is sprinting ability (Losos, 1996).

When a spider lives in a heterogeneous environment where substrates could directly affect speed, it is important for spiders to be able to maximize their performance to increase overall fitness. The wolf spider, Hogna carolinensis, is found in the sandhill prairie habitat. This environment has two distinct substrates, sand and vegetation. In this study, we investigated the influence of substrate variation the movement of H. carolinensis by looking at whether these substrates affected their speed, and then consequently exhibited a preference for the substrate they performed best on. If one substrate allows for greater overall speed, we would predict that these wolf spiders would express a preference for running on this substrate during escape behaviors.

MATERIALS AND METHODS

Subjects

The spiders (Hogna carolinensis) were collected at

night at the Sand Hills State Park in Hutchinson Kansas on July 11, 2013 and July 16, 2013. All of the spiders were collected at night using the eye shine method. Since the study was a repeated measures design, the spiders were not separated by sex, or into different categories. All spiders were brought back to the lab and housed individually in visually isolated plastic cages (AMAC 83mm X 83 mm X 109 mm), in a room held at 70° F and a 14h:10h day:night light cycle. Each spider was fed three crickets per week, and water was supplied via a cotton wick at the bottom of the cage. 18 spiders were run through three separate treatments to analyze for the effects of substrate variation on speed.

Speed

This experiment consisted of each of the 18 spiders running on a track that was two meters long. The tracks were constructed using a standard (5cm X 10cm X 244cm) piece of wood as the base for the track. Each track used 6 strips of plexiglass two strips (91cm X 15cm) and one strip (61cm X 15cm) on each side of the track to completely cover the sides of the track in order to obtain the straightest run possible. (See Figure 1). Each end of the track had a piece of cardboard to prevent the spider from exiting the track prior to the start of the run, or after the run had finished. Each of 3 tracks had a different substrate: 1) wood, 2) grassy vegetation, enough to make it an uneven substrate, and 3) sand, a 2 inch layer on the track (Figure 1). Each spider was run on each of the three tracks once. A dice was used to randomly determine the order of treatments each individual spider was presented with over the trial period. Before running each trial the individual spider was removed from its cage and put into a vial to be weighed. After being weighed the spider was placed on a part of the track designed for acclimation to the substrate it will be running on. After a minute of acclimation the gate at the start line was removed and a notecard was used to trail the spider to encourage forward movement. The spider ran two meters on the track and the movement was recorded with a camera to later analyze the video. All trials for each substrate were performed in the same exact manner. Each track was cleaned after every run with kimwipes and 70% percent ethanol to eliminate any possible chemical signals or silk left behind by the previous spider. The vial used to weigh the spiders was also cleaned after each weigh in to eliminate anything left by the previous spider that could affect the reading of the weight of the current spider.

Substrate Preference

The arena for this experiment consisted of a two meter long track, with two substrates. The track was built using two standard (5cm X 10cm X 244cm) pieces of wood side by side. Six strips of plexiglass, two strips (91cm X 15cm) and one strip (61cm X 15cm) were used on each side of the track to completely cover the sides. (See figure 1 C). Each end of the track had a piece of cardboard to prevent the spider from leaving the track prior to the start or after the spider was finished. One side of the track had vegetation as the substrate and the other side of the track had sand as the substrate. The trials were split up into two days, day one used ten spiders and day two used the remaining ten spiders. Prior to starting the substrate preference trial each spider was weighed and then placed in the acclimation part of the track where they were exposed to both substrates before starting the trial. After a minute of acclimation the starting gate was be removed and the spider was trailed by notecards to encourage movement. The trial was recorded from above to capture the substrate the spider ran on and the distance it ran on each substrate to later be analyzed for preference. In order for a spider to have a preference for a substrate, it must run two-thirds of the total distance on the same substrate. After each trial, the track was cleaned with kimwipes and seventy percent ethanol to eliminate any chemicals or silk left by the previous spider that can have an effect of the next trial. The vial used to weigh the spiders was also cleaned to eliminate anything left behind by the previous spider that can have an effect on the weight of the next spider.

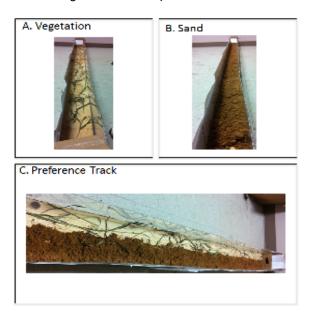


Figure 1: Tracks used in speed trials for (A) Vegetation substrate, and (B) Sand substrate. (C) Shows the experimental track used in the substrate preference trials.

Data Analysis: We checked all of our variables for normality. Due to several variables not being

normally distributed, we used nonparametric tests. To analyze the effects of substrate on total time and max speed in our trial, we performed a Friedman's ANOVA. Following a significant Friedmans test, we used separate Wilcoxon Signed Rank tests to perform all pairwise comparisons. To investigate substrate preference, we analyzed only those spiders that exhibited a preference of one substrate during their trial. Preference was determined by the 66% rule which stated that a spider would have preference if it ran on one substrate 66% or more of the distance. We performed a chi-square test on the frequencies of spiders preferring each substrate type. All results are presented as mean ± standard error. All statistical tests were performed using SPSS (version 21, IBM).

RESULTS

Speed

Overall, the time it took spiders to move across our experimental track was different depending on the substrates they ran on (Friedman test, χ_2^2 = 7.00, *P* = 0.03). Spiders ran the 2 meter distance faster on wood (\bar{x} = 7.19 ± 0.37 sec) compared to both vegetation (\bar{x} = 8.39 ± 0.79 sec; Wilcoxon Signed Rank, Z = 2.59, P = 0.01) and sand ($\bar{x} = 9.11 \pm 0.48$ sec; Wilcoxon Signed Rank, Z = 2.07, P = 0.04). Spiders running on vegetation were generally faster, but this difference was marginally non-significant (Wilcoxon Signed Rank, Z = 1.46, P = 0.15). The differences in total time taken to run the two meter track were not due to variation in the number of stops during the trial, as these were similar across all substrates (Wood: ; Sand: ; Vegetation: ; Friedman test, χ_2^2 = 3.73, *P* = 0.16). The max speed of each spider using their max continuous distance was different depending on the substrates that they ran on (Friedman test, χ_2^2 = 14.78, *P* = 0.001). Spiders running their max speed ran faster on wood (\bar{x} = 38.48 ± 3.37 cm/sec) compared to sand (Wilcoxon Signed Rank, Z = 3.38, P < 0.001), but were not faster than on vegetation (Wilcoxon Signed Rank, Z = 1.07, P = 0.29) (See figure 2). Spiders also were significantly faster on vegetation than they were on sand (Wilcox0on Signed Rank, Z = 3.03, P = 0.002) (See figure 2).

Substrate Preference

The substrate preference trials used a total of twenty spiders. Out of the twenty spiders, 30% of the spiders ran only on one substrate, which was vegetation. The other twelve spiders experienced both substrates during their run. Of the 20 spiders some significantly preferred one substrate over the other, and others did not show a significant preference. Of the spiders that showed a preference, 50% of the spiders preferred the vegetation substrate. 15% of the spiders had a preference for the sand substrate (χ^2 = 3.77, *df*= 1, *P*= 0.05), and 35% did not show any preference.

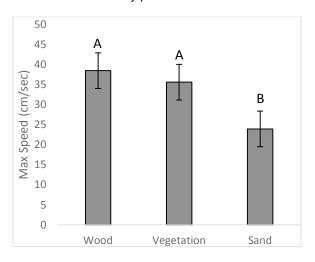
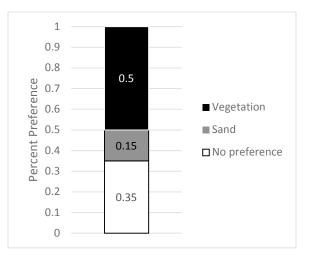
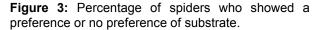


Figure 2: Maximum speed in cm/sec on each of the three substrates.





DISCUSSION

We found that substrate definitely affected the maximum speed of the *H.* carolinensis. From the substrates that were used we found that sand tended to slow the spiders down more than the vegetation. Due to the reduction in maximum speed, we expected to find a preference for the substrate that maximized their speed. We found that spiders significantly preferred the substrate that maximized their speed.

The reduction in speed from sand compared to vegetation could be due to the fact that sand is a very loose substrate. The sand is not a solid substrate, so

when the spider applies pressure to accelerate the sand may move and cause a reduction in force of the spider, which can reduce the speed. Since the vegetation is a substrate that is more sturdy than sand, it can help increase the speed of the spider. When the spider applies force to run the vegetation will not move as much as the sand so the speed will be increased. The experiment done on ghost crabs by Malcolm Burrows shows that ghost crabs were significantly faster on the deck of a ship than on sand.

Animals throughout the world show preferences to substrates that maximize their performance. The preference for substrate can also be to improve their chances for survival. A good example of an animal choosing one substrate to increase chances of survival comes from a study done by Roy A. Stein on the behavioral response of cravifsh to a fish predator. His study showed that "in the presence of a predator, cravfish selected substrates affording most protection" (Stein, 1976). By going to the substrate with most protection the crayfish can avoid being eaten by bigger fish and they will be able to survive. The reason for spiders to prefer one substrate over another could be because one substrate allows them to move faster than the other. If they see a prey, they need to be able to move as fast as possible to ensure that they get the prey. Also if they are trying to escape from a predator, they must be able to escape as fast as possible or else they will be eaten. A good example of this is a study done by Burt P. Kotler on factors that affect gerbil foraging behavior. His study on gerbils showed that "Gerbils foraged less in the open than in the bush habitat" (Kotler, 1991). The gerbils preferred to forage in the habitat that provided them more cover because it gave them a better chance of avoiding predation from owls. The gerbils showed a preference for a substrate that benefited them the most, similar to how spiders preferred to run on vegetation, because it maximized their speed.

One of the shortcomings of my experiment is that the experiment was done in a lab setting and not in the spider's natural habitat. Also the runway does not reflect the true variation amongst the substrate it is only an approximation. It is likely that the sand and vegetation substrates are different in their natural habitat, so the runway was just an approximation and not the exact substrate. It would be interesting to see how this study compares to studies done in a completely natural environment to these spiders. The escape response can also be different in the wild compared to the escape response in the lab. The thing used to spook the spiders is much different from the things that spook them in the wild, so the response can be different.

This kind of research helps us to better understand how organisms are able to survive in environments that are heterogeneous. When given a choice, organisms prefer to move on environments and substrates that will maximize their performance.

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