

Differential response to vibration stimulus in *Metabus gravidus* (Araneidae) communities

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ABSTRACT

This study is an investigation on the effect of distance between neighboring spiders on the reaction to an artificially generated vibration stimulus. The study was conducted using a tuning fork at 320 Hz in order to generate a vibration intended to stimulate the spider web. *Metabus gravidus* individuals that were closer to the source of vibration (mean 9.5 ± 2.75 cm) tended to react by fleeing, and those farther from the source (mean 16.5 ± 4.8 cm) typically reacted by approaching. The spider closest to the source of vibration reacted by fleeing and approaching, while the neighboring spider exhibited no response more often than expected by chance ($X^2 = 28.4$). Thus individuals who maintain a greater distance to near neighbors benefit by minimizing interfering vibrations from neighboring webs.

RESUMEN

Este estudio es una investigación sobre el efecto de la distancia entre arañas vecinas y la reacción ante una vibración artificial estimulada. El estudio fue hecho usando un diapasón a 320 Hz para generar una vibración en la tela de araña. Individuos de *Metabus gravidus* que se encontraban cerca de la fuente de vibración (promedio 9.5 ± 2.75 cm) tienden a escapar, y los que se encuentran lejos de la fuente (promedio 16.5 ± 4.8 cm) típicamente tienden a acercarse. Las arañas cercanas a la fuente de vibración reaccionan alejándose y acercándose, mientras que las arañas vecinas no exhiben ninguna respuesta mayor a la esperada ($X^2 = 28.4$). Así individuos que mantienen una gran distancia con los vecinos se ven beneficiados por una menor interferencia con las vibraciones en las telas vecinas.

INTRODUCTION

The strategy of communal living was developed in order to make life easier, and many organisms on earth have come to exploit the benefits of social living. Sociality can provide a variety of benefits including increased reproductive success, increased defense against predation, and more efficient feeding. (Buskirk 1975a)

Communal living in spiders is rather rare; of the 34,000 species of arachnids there are only 20 species known to live in colonies. Among these 20 species there is a lot of variability in the community style. Some orb weavers only live in a colony during the juvenile stage of life, under maternal care. Other species share a single common sheet web that is built and maintained communally (Uetz 1986). In the case of *Metabus gravidus*, the spiders share a common structural scaffolding of non-viscid silk strung over streams. Individuals build and maintain their own orbs (Buskirk 1975a). By sharing structural support, the spiders are able to exploit a unique niche that would be otherwise inaccessible to solitary spiders (Buskirk 1975a).

Some members of the *M. gravidus* community benefit more from the cooperation of others. Past studies indicate trends between spider size/age and their location within

the colony. This information was supplemented by an investigation of insect traffic within different microhabitats of a stream. It was shown that there is more insect traffic closer to the water surface over the center of the stream, as opposed to areas that are farther from the water surface and closer to the stream bank (Buskirk 1975a; Potosek 2000). Not coincidentally, older/larger spiders were shown to dominate the locations of high insect traffic (Buskirk 1975a).

Metabus gravidus individuals are quite active in defending orb orientation. Dominance of web location is asserted through aggressive interactions usually initiated by larger spiders. The spiders use vibratory signals to assert aggression, such as bouncing in place in the hub of the web, plucking radii, and charging other spiders that have come too close. The majority of aggressive interactions occurs during the web building process; when a spider builds a web too close another. Usually vibratory displays are sufficient in communicating aggression, but it can get to the point of destroying parts of a neighboring web or physical confrontation (Buskirk 1975b). The energy spent in aggressive encounters can be an important cost to communal living. They not only have energy costs, but also distract the spider from being able to attack potential prey items (Uetz 1986).

It is understandable that a spider is so territorial over its web; not only does it rely on its web as a source of food, but it is essentially an extension of its sensory structure (Foelix 1996). Vibrations are crucial in the communication behavior of Arachnids, and are used in aggressive interactions, courtship behaviors and prey location (Uetz 1986). Orb-weavers tend to orient themselves in the hub of their webs, allowing the spiders to read and respond to vibrations from all directions. When an object (prey, debris, or perhaps an intruder) enters the web, the impact creates oscillations that are sent down the radii to the center of the web. After detecting the vibration, the spider uses a technique of plucking the silk, sending oscillations to the source of vibration in order to read the oscillations that rebound from the ensnared object. This behavior allows the spider to characterize the nature of the ensnared object before committing to a more energetically costly response, such as attacking or fleeing (Foelix 1996).

The communal spider web can serve a variety of benefits. In colonies of orb-weavers, the aggregation of webs can serve as a gauntlet to insects. If an insect enters one web and bounces free, there is a high likelihood that it will fly into another web within the colony (Uetz 1986). The aggregation of orbs also extends the sensory perception of the spider beyond its own orb, so that it is able to sense vibrations of neighboring webs. This can act as an important early warning system when a predator is in the colony (Tietjen 1986). Vibrations from the neighbor's web can also be costly; responding to vibrations of a neighbor's web could be wasted energy, especially considering that there is minimal prey theft among *M. gravidus* (Buskirk 1975b). The aggression of the older/larger spiders makes the distance between orbs relative to the age of the spider, in that the older/larger spiders exhibit a greater distance to the nearest neighbor than do the younger spiders in the colony (Tietjen 1986). The most-fit spiders maximize the distance from their neighbors which could mean that there is some benefit. I propose that the greater distance to neighbor allows older/larger spiders to focus on their own web, in that they will respond to less vibration generated in neighboring webs and thus waste less energy. Thus I hypothesize that spiders with a greater distance to the nearest neighbor will respond to vibrations generated in a neighbor's web less often.

MATERIALS AND METHODS

Site Location

The study was conducted along Rio Alondra in San Luis, Costa Rica. I found several colonies upstream of where Rio Alondra crosses the road that leads to Catarata San Luis, in between the University of Georgia Ecolodge and the entrance to Catarata San Luis.

Experimental Methods

Ten days of data collection occurred between April 2 and April 15 2008, between 1:00pm and 6:00p.m. To begin data collection, two neighboring spiders were selected from a colony. I clouded the webs with baking flour in order to better see the intricacies of the webs. At times this agitated the spiders, so no data were collected until the spiders had returned to the hub for at least one minute. I measured the shortest distance by web between the two spiders. A tuning fork tuned to 320 Hz (E) was used to generate a vibration that would simulate a prey item. This value is in the middle portion of frequencies that are transmitted through the web of a spider, as well as into the web of another spider (Masters et al1986). I feel it is also important to state that *M. gravidus* individuals do not show selection of prey based on previous experience (Buskirk 1975). Even though the tuning fork may generate an unfamiliar oscillation, I was able to assume that the spiders would react to it. A vibration was generated and applied directly on a non-viscid support line on the periphery of one of the two orbs, and the distance from the source of vibration to the spider closest to it was recorded. The vibration was always applied on a side of the orb opposite to the nearest neighbor, so that the vibration would have to travel through the first web before reaching the web of the neighbor (for experimental clarity, the spider closest to the source of vibration was referred to as "Spider 1" and the spider farthest from the source of vibration was referred to as "neighbor") The tuning fork was left on the silk for five seconds. The reactions of spiders were characterized into the following categories: approach, fleeing, plucking, or no reaction. An approach is defined as any movement away from the hub toward the source of vibration. Fleeing is defined as any movement from the hub away from the source of vibration. Plucking is defined by the jerking of the web radii by the spider while remaining in the hub. No reaction is defined by the lack of any noticeable response to the vibration.

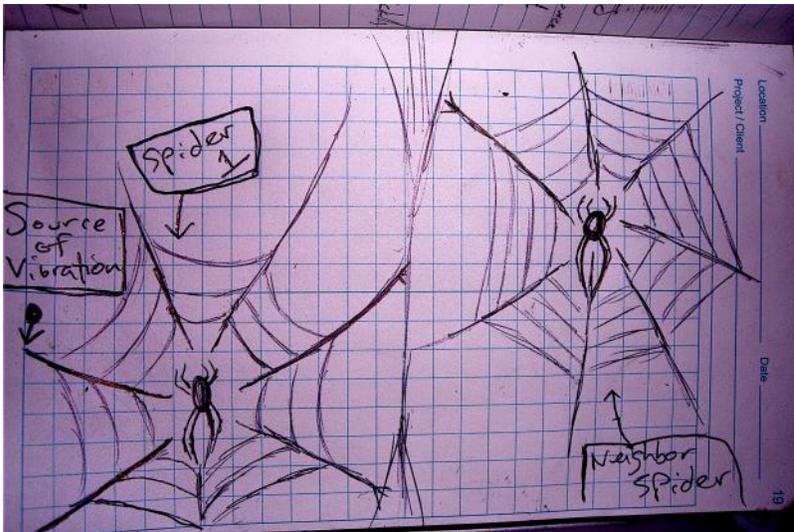


FIGURE 1. Image depicting the application of vibration. Spider 1 was always the spider closest to the vibration.

Data Analysis

A Kruskal-Wallis test was used to analyze the relationship between the reaction of Spider 1 and the distance from the source, the distance to nearest neighbor and the reaction of Spider 1, and the distance to near neighbor and the reaction of the neighboring spider. A chi-squared test was used to compare the frequency of each response of the two neighboring spiders.

RESULTS

I was able to find six colonies that were consistently active, ranging from two to 17 active individuals.

In comparing the distance from the source of vibration to the reaction of the nearest spider, it was shown that spiders closer to the source of vibration tended to flee more often (mean 9.5 cm \pm 2.75), those farther away had a greater tendency to approach (mean 16.5 cm \pm 4.8). Plucking (mean 13.5 cm \pm 4.9) (Kruskal-Wallis test, $H = 17.6$, $p < 0.001$; Figure 2).

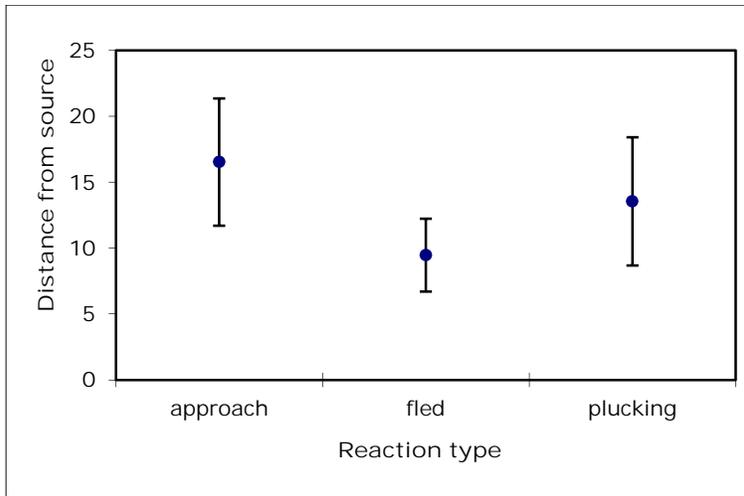


FIGURE 2. Mean distance from the source of vibration, for each reaction behavior type. The spider closest to the source of vibration is analyzed. Spiders closer to the source of vibration were more likely to flee; spiders farther from the source of vibration were more likely to approach. Plucking was exhibited over the middle range of distances ($N = 57$, $H = 17.6$, $p < 0.001$).

As the distance between spiders increased, the neighbor was more likely to show no response (mean 27.52 cm \pm 15.7; Kruskal-Wallis test, $H = 6.96$, $p = 0.07$; Fig. 3).

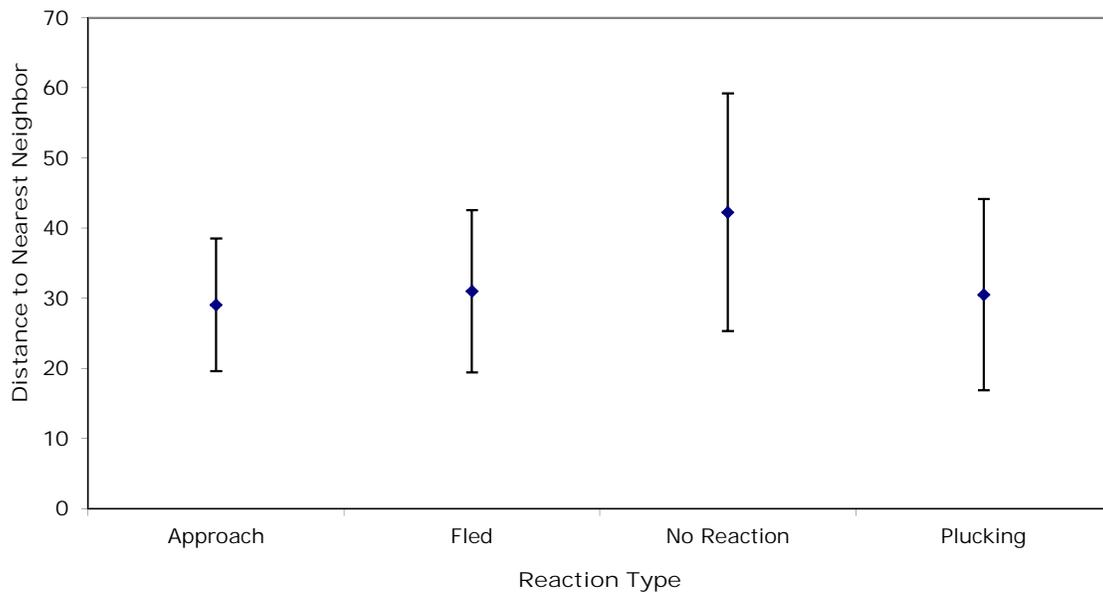


FIGURE 3. Mean near neighbor distance is shown for each of the four reaction behaviors of the neighbor spider. No response was most common at greater distances ($N = 57$, $H = 6.96$, $p = 0.07$).

The spider closest to the source of vibration approached and fled more often than expected, while the spider farther from the source exhibited no response more often than

expected. Plucking reactions for both spiders were close to the expected values (chi-squared test, $X = 28.4$; Fig. 4).

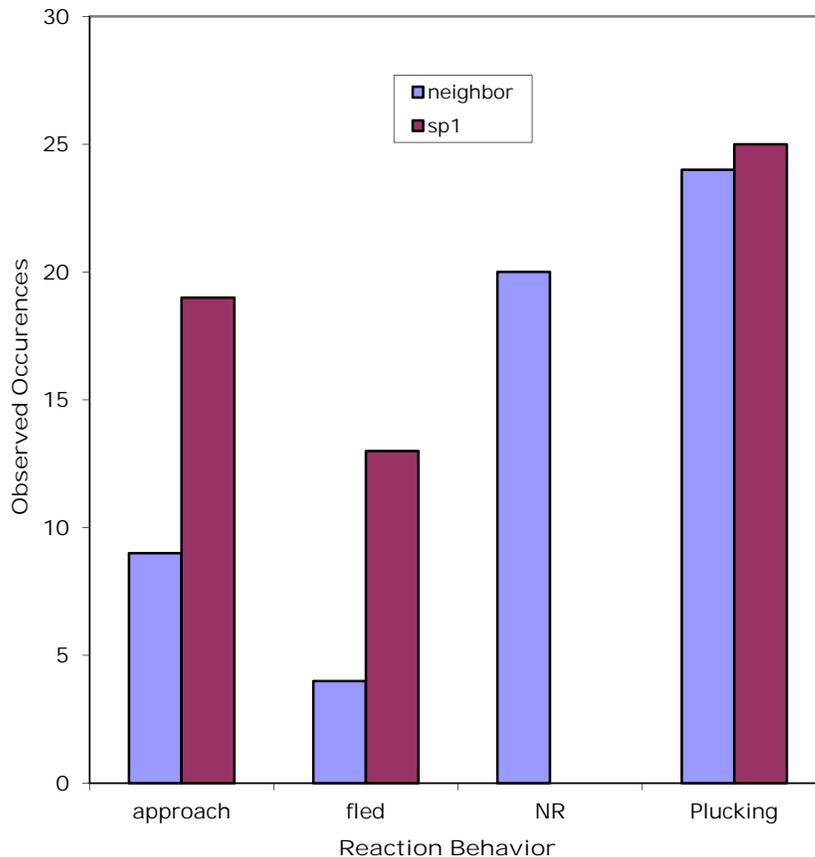


FIGURE 4. The observed number of behaviors for both spider 1 (the spider closest to the source) and the neighboring spider (spider farthest from the source) are compared. Spider 1 approached and fled more times, and never showed no response (chi-squared = 28.4).

Comparing the distance to the nearest neighbor to the reaction of the spider nearest the source of vibration did not show any significant results (Kruskall-Wallis test, $H = 1.2$, $p = 0.54$)

On three occasions, spiders left the colony retreat after the application of a vibration and proceeded to occupy empty web hubs. The distance from the source of the vibration to the retreat was greater than 30 cm on two of the occasions, and was not measured on the third. One time a spider that was on the shared support line responded to a vibration by occupying a web, but no distance data were recorded.

DISCUSSION

The amount of silk a vibration travels through has an effect on the distance the vibration travels, as well as the strength of that vibration. There were some interesting data when the distance between neighbors was related to the reaction of the neighboring spider. The neighboring spider had a higher incidence of no-reaction as the distance to the near

neighbor was increased. This illustrates that the vibration is indeed diluted as it travels through one web and continues through to the next. This agrees with my idea that a spider presumably benefits from maintaining a greater distance to the near neighbor in that it is not as influenced by vibrations generated in a neighbor's web. The significance of this result was supplemented by a chi-squared test comparing the frequency of the four different reaction types between Spider 1 and the neighbor spider. The spider whose web was closest to the source of vibration always exhibited a reaction, whereas "no-reaction" was the most frequent behavior of the neighboring spider, especially as the distance between neighbors was increased (Figure 3). This difference in behavior illustrates the effect of distance on the travel of vibration through the spider colony.

The fact that the neighboring spider does not respond to weaker vibrations does not necessarily mean that the vibration goes unfelt; it could be that it is too subtle to be of interest to the spider. I say this because of the few occasions where spiders came out from the colony retreat, in order to occupy empty webs after the application of a vibration on an occupied web. The estimated distances from the retreat to the source of vibration were greater than 30 cm, yet the spiders were still interested in the vibration. Peak insect activity is the late afternoon, and a corresponding trend of orb-building occurs just prior to it (Buskirk 1975). Perhaps vibrations from prey capture of other webs functions as an alarm clock to spiders in retreat, signaling the rise of insect activity.

A significant trend was shown when comparing the distance of the source of vibration to the reaction of the spider closest to it (Figure 1). Vibrations generated close to the spider resulted in fleeing reactions. This could perhaps be due to the fact that the close distance produced a stronger vibration that might simulate a large/dangerous prey item. The most common reaction was plucking which also occurred over the greatest range of distances, overlapping both the lower range of the distances, which elicited approach and the upper range of distances, which elicited flight. That plucking is the most common reaction, occupying the median range of distances, coincides with the use of this behavior by orb-weavers to read the source of web vibrations (Foelix 1996). Before approaching a prey item it is beneficial to characterize the size and intensity of the prey item to avoid danger and/or wasted energy, especially considering that the tuning fork likely creates unfamiliar frequencies. It is also important to consider that a plucking reaction requires less energy than either flight or approach. The tendency to approach vibrations generated farther away from the hub could imply that the gentler vibration simulates a more attractive prey item, or at least a less intense one. It could also simulate the approach of an intruding conspecific spider, which is generally not tolerated and often results in aggressive encounters as the spider tries to defend its web (Buskirk 1975). Yet another possibility is that the spider approaches a vibration generated farther away out of curiosity: being able to sense a vibration that is not quite intimidating, but not being able to characterize it.

I was unable to find a trend between the distance to the nearest neighbor and the reaction of the spider closest to the source of vibration. This indicates that the spiders do not react to signals based on the presence of a close neighbor. This can be accredited to the minimal levels of prey theft within the colony, something that is much more common in other communal spider species (Buskirk 1975). These spiders live communally, which must mean that the benefits of the community outweigh the costs (Tietjen 1986). Though the amount of prey theft is low in this species, orb take-over is quite common (Buskirk 1975). This increases the benefit of having a greater distance to the nearest neighbor; a

longer support line to the web means that the spider occupying the hub has more time to react to the intruding spider.

There have been many studies done on *M. gravidus* that document the patterns of arrangement of spiders and orbs within the community. This study is an attempt to investigate some of the reasons the colony is consistently arranged the way it is, and it is evident that effect of vibration differs with the amount of silk it travels through. It would be interesting to conduct a study that compared the reactions of *M. gravidus* to other orb-weaving species, both solitary and colonial. It would also be of interest to broaden the scope of the data I have collected, with emphasis on finding larger colonies and testing a wider range of frequencies. This could provide a more encompassing depiction of the preference of frequency as well as an examination of the effect of colony size on behavior.

ACKNOWLEDGEMENTS

Much thanks to Rio Alondra and the University of Georgia Ecolodge that allowed me to study in the forest surrounding it. I would also like to thank Tania for her wealth of constructive criticism, Pablo for his statistical knowledge, Katelyn for her paper probing, and Karen for her contagious excitement.

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