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# Responses to prey size in *Metabus gravidus* (Araneae: Araneidae) provide evidence for optimal foraging

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## ABSTRACT

Foraging strategy is a critical factor in the fitness of many organisms. The optimal foraging theory states that animals optimize their fitness by selecting food that will provide the most amount of nutrition for the least amount of time and energy spent obtaining food. By minimizing energy spent on foraging, organisms can focus on other activities that benefit them, such as watching for predators, looking for mates, or caring for offspring. Because spiders have a very unique method of predation, they are a useful model organism for the study of optimal foraging. *Metabus gravidus* (Araneae: Araneidae) is a species of tropical orb-weaving spider common in Monteverde, Costa Rica. They forage by selecting and attacking prey that enter their orb-webs (Buskirk 1975). I investigated optimal foraging in these spiders by throwing moths of different sizes into spider webs and observing the spider responses. I found that spiders were more likely to attack smaller, more manageable moths, while larger moths typically elicited negative responses. These results suggest that *M. gravidus* prefer smaller sized prey, because they receive more nutrition for much less effort than pursuit of large prey would necessitate.

## RESUMEN

Las estrategias de forrajeo son un factor crítico en el éxito reproductivo de muchos organismos. La teoría de forrajeo óptimo establece que los animales optimizan su éxito seleccionando presas que le provean la mayor cantidad de nutrientes por la menor cantidad de tiempo y energía utilizada en obtener este recurso. Minimizando la energía utilizada al forrajear, los organismos pueden enfocarse a otras actividades que los beneficien, como observar por depredadores, buscar pareja o cuidar de la descendencia. Debido a que las arañas tienen un sistema de forrajeo único, éstas son usualmente un organismo modelo para el estudio del forrajeo óptimo. *Metabus gravidus* (Araneae: Araneidae) es una especie de araña tropical que construye tela, común en Monteverde, Costa Rica. Estás forrajean seleccionando y atacando presas que caen en sus telas (Buskirk 1975). Investigue el forraje óptimo de estas arañas tirando polillas de diferentes tamaños en sus telas y observando la respuesta de las arañas. Encontré que las arañas son más susceptibles a atacar presas pequeñas, más manejables, mientras que las presas grandes normalmente suscitaron respuestas negativas. Estos resultados sugieren que *M. gravidus* prefiere presas pequeñas, debido a que reciben más nutrientes por un menor esfuerzo que la búsqueda de presas largas puede necesitar.

## INTRODUCTION

For many organisms, foraging behavior is a cost-benefit analysis, and the theory of optimal foraging posits that animals attempt to maximize the amount of food they find per unit of time spent foraging. As a result of optimal foraging strategies, animals can locate the largest amount of food with the least amount of effort (MacArthur and Pianka 1966). In turn, animals can spend less time searching for and handling food, and more time watching for predators, searching for mates, or caring for offspring. Under optimal foraging strategies, the ideal food choice is food

that has the highest ratio of nutritional benefit to handling time. If animals are optimal foragers, then their diet will be primarily composed of low-cost organisms (Pyke 1984).

Among predatory web-weaving spiders, prey selection is a critical behavioral trait. Many spider species search and pursue prey based on certain physical and behavioral characteristics in order to conserve their energy costs. A study on several families of sheet-web-like spiders (Theridiidae, Linyphiidae, and Erigonidae) found that prey exhibiting weak flying capability, larger body surface area, larger size, and higher abundance were more likely to be selected by predators (Nentwig 1980). These factors were important for maximizing food output for spiders, with little energy input in prey pursuit. Studies on the opportunistic tarantula *Brachypelma smithi* (Theraphosidae) reveal optimal foraging behavior. Though these spiders are generalistic predators, they significantly preferred soft-bodied prey such as crickets over hard-bodied scarab beetles. Soft-bodied prey are easier to consume and digest, therefore increasing the feeding efficiency of the spider (Kosiba 2009). In addition to body softness, prey size appears to be a prominent prey selection trait for many spider species. The orb-weaver *Argiope amoena* has a preferred prey size range of 10-15 mm, whereas prey smaller than 5 mm larger than 15 mm were rarely eaten. Very small prey were often able to pass through the mesh of the web, while very large prey could successfully avoid predation by breaking the web or defeating the spider. Insects larger than the leg length of *A. amoena* cannot be wrapped by the spider, so they are not depredated. Therefore prey size is an important factor for prey selection (Murakami 1983).

Spider responses to putative prey have been documented by a few studies. Orb-weaving spiders (Araneidae) construct circular silk webs in order to capture prey (Eberhard 1986). They locate and attack prey on webs by sensing the vibrations that are produced when insects struggle. After the prey is located, there are three main attack behaviors exhibited by orb-weavers. If the prey is very small, then the spider can simply pull the insect out of the web. For larger prey, the spider will bite the prey and inject venom to subdue it. Finally, if the prey is particularly aggressive, the spider may choose to wrap the prey in silk (Olive 1980; Stowe 1986). However, less is known about spider behavior regarding the primary decision of whether or not to attack potential prey. Orb-weavers do not attack or consume every organism that enters their webs. They will reject items that are too large or antagonistic to attack, due to optimal foraging strategies (Stowe 1986). Responses to these prey items are less well understood. Orb-weavers have been observed to cut undesirable animals out of their webs (Stowe 1986). Other Araneidae have been observed to recognize and avoid undesirable animals by their vibrations (Stowe 1986). The responses to specific prey items are extremely interesting because they reflect the use of optimal foraging strategies. Understanding these behaviors is crucial to supporting the theory of optimal foraging.

In this study, I investigate the responses of *Metabus gravidus*, a species of tropical araneid spider, when exposed to a gradient of different sized moths. By doing this, I plan to demonstrate that spiders choose which prey to attack or avoid based on prey size. I explore the role of prey size in spider attack behavior. I predict that 1) spiders attack smaller prey items more frequently than larger prey items and 2) spiders attack smaller prey items faster than they attack larger prey items. From this, I will determine whether or not optimal foraging is an important feeding strategy for *M. gravidus*.

## METHODS

### Study Site

The study site was a portion of the Quebrada Maquina, a stream that runs near the Estación Biológica in Monteverde, Puntarenas, Costa Rica. Sampling occurred in two areas: closer to the headwaters of the stream, downstream from a small waterfall; and several hundred meters downstream, close to the Hotel Belmar. The stream is lined with large rocks and logs, which provide ample substrates for *M. gravidus* colony formation. The upstream site at 1550 m while the downstream site was 1450 m in elevation. In the upstream site, canopy cover was fairly thick, while the downstream site was slightly more abundant in light gaps. Data collection occurred during the beginning of the rainy season, so humidity and cloud cover were relatively high and rains were frequent.

### Study Organisms

*M. gravidus* is a species of tropical orb-weaver spider endemic to Central America. They typically live in colonies of 5 to 70 individuals but forage independently, not sharing prey captured from webs with other colony members (Buskirk 1975; Shear 1986). *Metabus gravidus* construct their colonies over running water, using logs, branches, boulders, and trees as a substrate. Larger spiders build horizontal webs closer to the water, while smaller spiders and juveniles build webs farther from the water, often at an angle anywhere from zero to 90 degrees. Though breeding occurs year-round, spider population densities are greatest in March, April and May (Buskirk 1975).



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FIGURE 1. Representative members of large and small size classes of *M. gravidus*. (A) is a member of the large spider size class, with a body length of 9.0 mm. (B) is a member of the small spider class, with a body length of 5.0 mm. Spider size classes were shown to be significantly different from each other.

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## Spider Responses to Prey Sizes

Data collection occurred between 0800 h and 1400 h during 23 April to 29 April 2010. Spider colonies were located and flagged on the study stretch of the Quebrada Maquina. Test spiders were chosen based on several criteria. Only spiders with intact orbs were used. In addition, spiders residing in smaller colonies (less than five individuals) were selected more often to prevent error in spider identification. Spiders that were already attacking an insect were not used in this study, because they cannot attack more than one prey at a time. Exposure to previous prey may also bias their behavior towards novel prey, especially if they do not feed every day (Stowe 1986).

Once a spider was located, its ventral body length (length from top of cephalothorax to end of opisthosoma) was measured using calipers. Spiders were classified in two categories: small and large (Fig. 1). These categories were based on the available distribution of spiders. Spiders with a body length of 0-6 mm were classified as small, and spiders with a body length of 6.01-11 were classified as large. Various species of moths (Lepidoptera) were used as the sample prey item. Moths were chosen as the sample prey item due to their abundance and large relative surface area, increasing the likelihood of getting caught in the web. They are soft-bodied and non aggressive, making them a palatable choice for spiders (Kosiba 2009; Stowe 1986). Moths were collected in and around the forest near the Estación Biológica. They were collected using a UV-light insect trap set up inside the forest, as well as from windows and rooms in the Estación Biológica by hand. I numbered each moth and measured it using calipers. Moths were classified in three categories: small, medium, and large. Moths 6-10 mm long were classified as small, 10.01-14 mm long classified as medium, and 14.01-22.1 mm long classified as large. These classifications were a result of the even division of the distribution of moth body lengths.

A moth was then thrown into the spider web from a distance of about 10 cm. Moth size, spider size, and time to intensity level were recorded. Each spider size category received at least five prey items of each size category of moth. Each trial used a different spider. Moths were thrown to a location about 3 cm away from the spider—never directly at the spider—to prevent a predator-avoidance response from the spider. Only living moths were used to ensure that 1) the spider would recognize prey struggling in the web and 2) any rejection of prey would not be due to prey death. After throwing the moth into the web, I observed the spider for five minutes. This is because some responses are not immediate and are dependent on the spider recognizing the presence of the moth due to its movements in the web. In addition, some spiders have an immediate retreat response but will later attempt to attack the moth. For all encounters, I recorded the last observed response after five minutes.

## Intensity Levels

The spider responses to prey presence in the web were catalogued in an ethogram, with intensity levels corresponding to various behaviors (Table 1). The six behaviors recorded include 1) cut out of web; 2) retreat; 3) no response; 4) approach; 5) approach and attack; and 6) approach, attack and subdue. “Cut out of web” responses (which correspond to intensity level -2) occurred when spiders cut holes in the web to free a moth. Retreat responses (-1) occurred when spiders moved greater than one legspan away from a moth. No response (0) was recorded when

spiders did not change position during the five minute observation period. Approach responses (+1) occurred when spiders moved closer to potential prey, at a distance of less than one legspan. Approach and attack (+2) occurred when spiders began to attack the prey. Finally, approach, attack, and subdue (+3) occurred when spiders were able to fold the wings of the prey and prevent them from moving.

TABLE 1. Intensity level codes and the behaviors that correspond to them. Positive intensity levels indicated an attack response, and negative intensity levels indicated a rejection of prey.

<b>Behavior</b>	<b>Intensity Level Code</b>
<b>Cut out of web</b>	-2
<b>Retreat</b>	-1
<b>No response</b>	0
<b>Approach</b>	+1
<b>Approach and attack</b>	+2
<b>Approach, attack, and subdue</b>	+3

### **Data Analysis**

To ensure evenness of sample demographics, a t-test comparing spider class and spider size, as well as an ANOVA comparing prey class and prey size, were performed. A linear regression analysis was used to determine the relationship between prey size and intensity levels. In addition, a linear regression comparing the percentage of spider body length of the moth and intensity level was performed. To determine whether or not handling time was affected by prey size, I performed a linear regression comparing the two variables. Finally, to examine if spider size is a more important factor for prey size selection, I performed two linear regressions: one comparing intensity level with spider size, and the other comparing time to intensity level with spider size.

### **Additional Observations**

The spiders often had more than one response to the moth. Many of the spiders had an initial retreat response, followed by an attack response. In addition, spiders did not attack dead or dying moths. On the rare occasion that a spider would approach a dead moth, it would immediately reject it. Very large moths (greater than 25 mm) were not able to be used in this experiment because they were heavy enough to break the web. Conversely, very small moths (smaller than 5 mm) also were not able to be used because they were often too small to be caught in the mesh of the web. Finally, web takeovers (the usurpation of a web and/or its prey contents by another spider in the colony) occurred somewhat frequently. Takeovers confounded the results; when they occurred, the trials were excluded.

## RESULTS

Overall mean spider size was  $6.76 \pm 2.4$  mm. Mean spider size was  $4.63 \pm 0.74$  mm ( $N = 17$ ) for small spiders, and  $9.03 \pm 1.06$  mm ( $N = 16$ ) for large spiders. Overall mean prey size was  $11.90 \pm 4.09$  mm. Mean prey size was  $7.61 \pm 1.04$  mm ( $N = 12$ ) for small prey,  $11.94 \pm 0.99$  mm ( $N = 10$ ) for medium prey, and  $16.55 \pm 2.36$  mm ( $N = 11$ ) for large prey. Out of 33 spiders tested, the most frequent response to prey was to retreat, with 14 retreat responses (Fig. 2). In eight trials, the spiders attacked, approached, and subdued the prey. In four trials, the spiders cut the prey out of the web. In three trials, the spiders approached the prey. In one trial, the spider approached and attacked the prey. No response was observed in three trials.

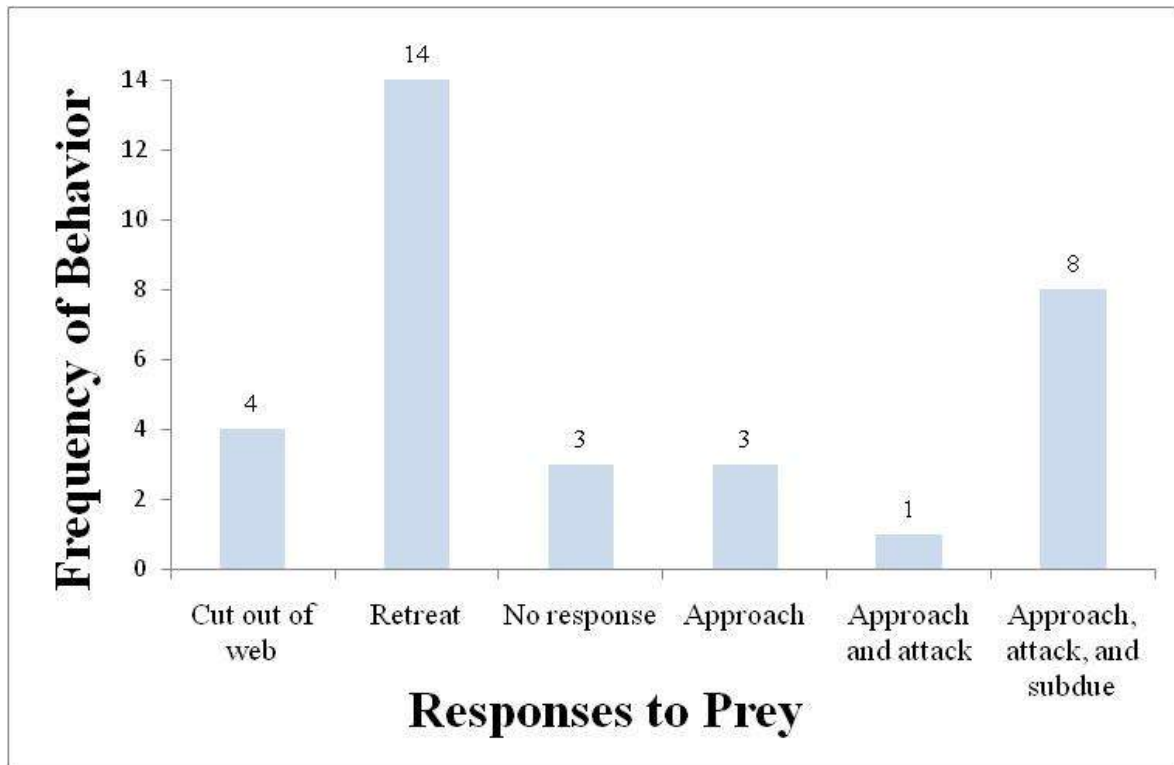


FIGURE 2. Frequency of different *M. gravidus* responses to moth presence in web,  $N = 33$ . Moths were thrown into a spider web and timed until the spider performed one of six responses. The most frequent intensity level response was retreat ( $N = 14$ ). Data was collected along the banks of the Quebrada Maquina, Monteverde, Costa Rica.

The sizes of spiders in large and small spider classes were significantly different from each other, meaning that the spider size classes represented a distinct size distribution (t-test;  $t = 13.843$ , d.f. = 31,  $P < 0.0001$ ). The sizes of moths in large, medium, and small prey classes were significantly different from each other, meaning that the moth size classes represented a distinct size distribution (ANOVA;  $F_{2,30} = 89.6725$ ,  $P < 0.0001$ ). Larger prey sizes elicited significantly more negative intensity level behaviors from spiders (linear regression;  $R^2 = 0.3097$ , d.f. = 1,  $F =$

13.9103,  $P = 0.0008$ , Fig. 3). In addition, moths that were a greater percentage of spider body length elicited significantly more negative responses (linear regression;  $R^2 = 0.2378$ , d.f. = 1,  $F = 9.6741$ ,  $P = 0.0040$ , Fig. 4). Prey size and time to intensity levels were not significantly correlated, suggesting that prey size did not have a significant effect on the time necessary to elicit a certain behavior (linear regression;  $R^2 = 0.0207$ , d.f. = 1,  $F = 0.6560$ ,  $P = 0.4242$ ). Intensity levels reached by spiders did not differ with varied spider sizes, which suggests that spider size had no effect on spider behavior (linear regression;  $R^2 = 0.0037$ , d.f. = 1,  $F = 0.1163$ ,  $P = 0.7354$ ). In addition, the time to intensity level did not differ with varied spider sizes, implying that spider size had no effect on the time necessary to reach an intensity level (linear regression;  $R^2 = 0.0392$ , d.f. = 1,  $F = 1.2663$ ,  $P = 0.261$ ).

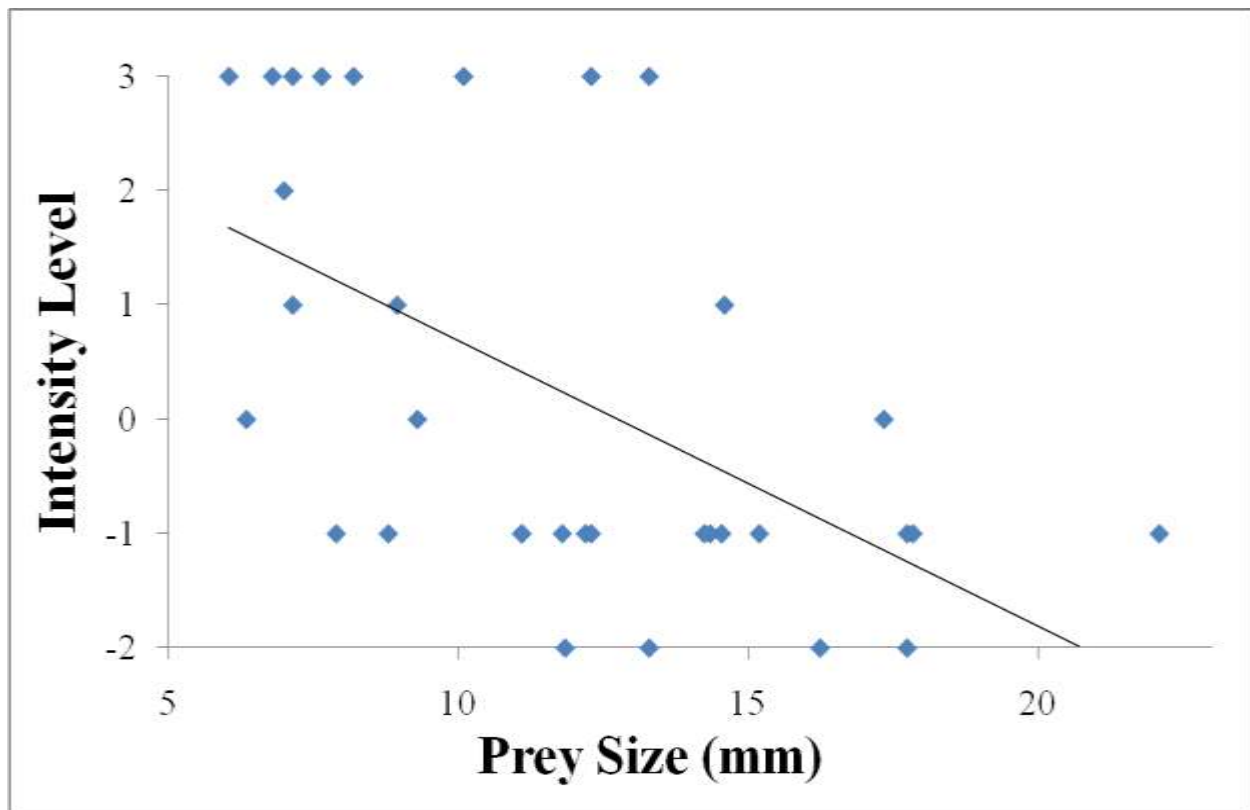


FIGURE 3. Prey size is negatively correlated with intensity level. Larger moth sizes are associated with negative behaviors in *M. gravidus*, such as retreat and removal from web.



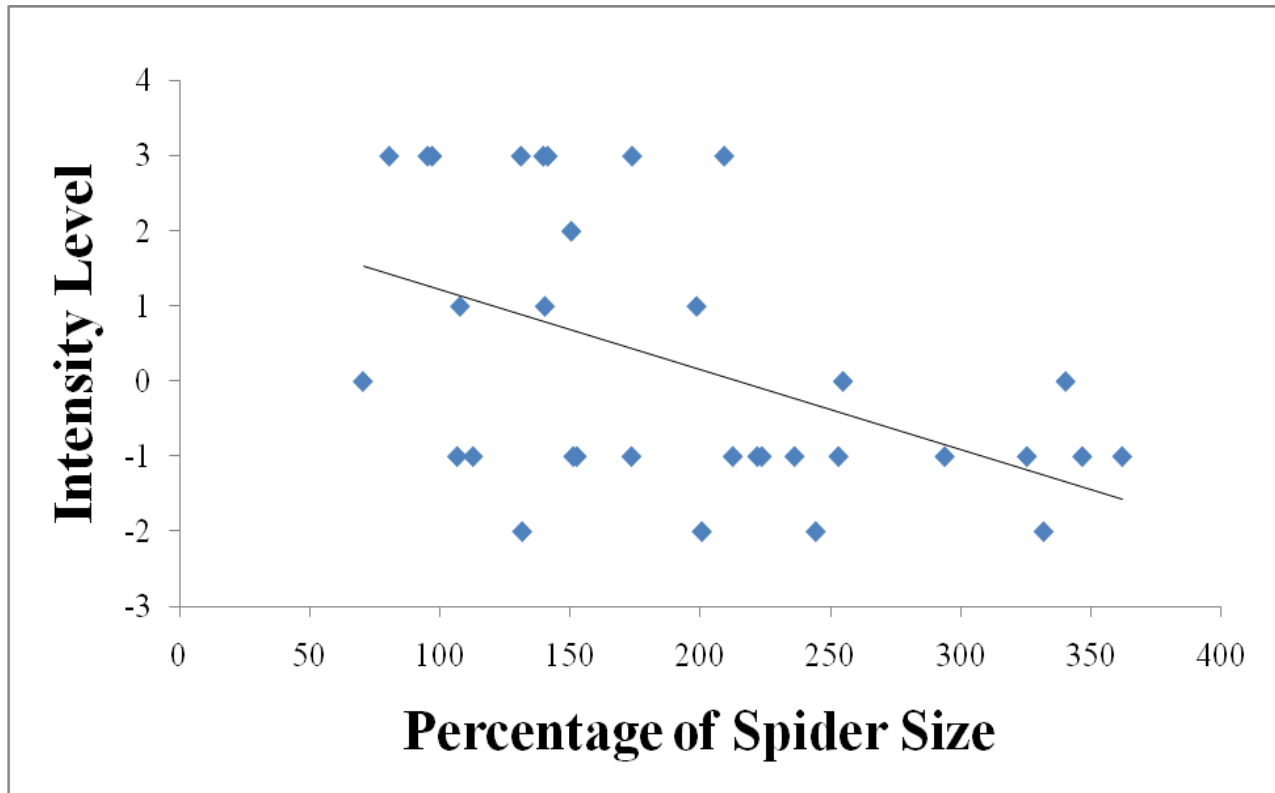


FIGURE 4. Percentage of spider body size in moths is negatively correlated with intensity level. Moths with a larger percentage of spider body length elicit more negative spider responses.

## DISCUSSION

As predators, spiders are influential organisms in the cloud forest ecosystem. Understanding the feeding strategies of spiders is an important part of exploring optimal foraging theory. I found that spiders more frequently prefer to attack smaller moths over larger moths. Large moths elicited more negative responses from the spiders, such as retreat and web-cutting. Also, encounters in which the moth body length was a greater percentage of the spider body length were more often negative responses. These data suggest that *M. gravidus* spiders selectively predate on the insects that will provide the most food for the least amount of expended energy. Spider size had no effect on either the intensity level reached or the time to intensity level. This suggests that spiders of all sizes react in the same manner to prey and the relationship between prey size and spider behavior is most likely not confounded by spider size.

There are several explanations for these results. Spider morphology is an important limiting factor in prey selection. Spiders use their legs to apprehend potential prey (Murakami 1983). If a moth is too large, *M. gravidus* cannot physically use their legs to effectively subdue it. If this is the case, then the invading insect could even be a potential threat to the spider

(Murakami 1983). Spider morphology limitations would explain negative responses, as well as a lack of responses. In addition, it is possible that spiders have the ability to detect which insects hit their webs without direct contact with the insect. Insects that are caught in spider webs typically have a standard behavior for web escape. For example, moths typically beat their wings without fully extending them when they encounter a spider web. Because spiders detect the presence of prey through vibrations on the web, patterns of prey movement in the web may signal to spiders which insect is present. The spider can then choose whether or not to attack the prey based on this knowledge (Stowe 1986). Studies investigating prey choice and memory retention in spiders reveal that spiders have the ability to distinguish prey that is more suitable and recognize certain frequencies of vibration (Bays 1962). This mechanism may then be important in prey selection for *M. gravidus*. In addition, immediate retreat responses were a common occurrence during this experiment. These behaviors appeared to be in response to a potential predator threat from the moth. Many spiders will remove insects from their web that are too aggressive or chemically defended (Stowe 1986). The relationship between foraging and predator avoidance would be very interesting to study in these organisms.

The role of colony size on foraging is an interesting topic. Because *M. gravidus* is a colonial species of spider, it may have differing optimal foraging strategies than other species. I observed many web-takeovers and instances of kleptoparasitism from spiders in the same colony as the test spiders. Takeovers and kleptoparasitism may occur and reduce the fitness of a spider (Buskirk 1975). Spiders residing in colonies have a greater proximity to other spiders, and may forage in a pattern that accounts for these effects. It is possible that in these colonial spider species, optimal foraging strategies are enhanced. It would be very interesting to study this phenomenon in spider foraging.

The relationship between prey size and time to intensity level was not found to be significant in this study. In many trials, moth behavior (struggling, agonism with the spider) delayed successful attack responses, because spiders needed to spend more time processing the prey, regardless of prey size. In addition, spiders will not recognize prey that do not create sufficient vibration in the web, which is necessary for prey location (Stowe 1986). For moths that did not actively struggle in the web, there was either no response, or responses may have been provoked by the accidental discovery of prey. In these cases, time to intensity level was confounded. A control for this behavior would be useful in future experiments. Another taxon of model prey, such as Coleoptera, might yield different results due to behavioral differences.

This study provided a useful, experimental measure of optimal foraging in spiders. Many studies on optimal foraging on spiders rely on trapping and observation to determine prey choice, but this study provided experimental data. The experiment also effectively examined spider behaviors regarding insect presence in webs. Negative response behaviors, on which there is little data, were explored in detail in this study. Many aspects of spider foraging behavior remain to be discovered. The mechanism by which *M. gravidus* are able to selectively forage is still an important question—vibrational data have been implicated, but more research is necessary. Colony, competition, and predator-avoidance effects on foraging are also topics that have not been extensively explored. Finally, little information is available on the life history of *M. gravidus*, which is crucial for fully understanding this system. Further research in these areas will improve the study of optimal foraging in *M. gravidus*.

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