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ABSTRACT

Metabus gravidus (Araneidae: Araneae) is a parasocial orb-weaving spider. It lives in the forest understory of Costa Rica along small streams. Web silk and spinning is very expensive and the web needs to be placed strategically to obtain maximum benefits. This study investigated the relationship between *M. gravidus* web size and the location and position of the web over the stream as well as the openness of the web. Specifically, the study asked if larger *M. gravidus* webs had a preferential placement, as closer to the water or oriented in a certain direction, to maximize prey capture and minimize web loss. It was assumed that larger spiders would spin larger webs and obtain the best placement among the colony. Data were collected from 141 webs and 14 colonies from 7 a.m. to 10 a.m. for four days beginning the week of July 16, 2005. Studies showed that larger webs were found in more open areas. A mean vertical distance between colonies was also found, demonstrating that web placement is based on the surrounding environment. There was no significant difference between web size and vertical distance from stream or web size and orientation. Future studies should take into account the prey and predators of *M. gravidus*.

RESUMEN

Metabus gravidus (Araneidae: Araneae) es una araña parasocial tejedora. Vive en el sotobosque de Costa Rica, a la orilla de quebradas pequeñas. La seda del tejido y el hilado son muy costosos y la telaraña tiene que estar en una posición estratégica para obtener los beneficios máximos. Este estudio investigó la relación entre el tamaño de la telaraña de *M. gravidus*, así como la localización y la posición de la telaraña, y la apertura del espacio cerca de la telaraña. El estudio determinó si las telarañas de *M. gravidus* más grandes tenían una localización preferencial, tal como más cerca del agua u orientada en una direción especifica, para aumentar el número de presas y reducir al mínimo el daño a la telaraña. Se asumió que las arañas más grandes y hilarían las telarañas más grandes y obtendrían las mejores posiciones en la colonia. Se colectaron los datos de 141 telarañas y 14 colonias desde las 7 hasta las 10 de la mañana por cuatro dias comenzando en la semana del 16 de julio de 2005. Los resultados mostraron que las telarañas más grandes se encontraban en espacios más abiertos. También se encontró una distancia vertical promedio entre las colonias, demonstrado que la localización de las telarañas está basado en el ambiente local. No hubo diferencias significativas entre el tamaño de la araña y la distancia vertical a la quebrada o entre el tamaño de la araña y la orientación de la telaraña. Los estudios en el futuro necesitarán considerar las presas y los depredadores de *M. gravidus*.

INTRODUCTION

Metabus gravidus is a colonial araneid that inhabits the forest understory near small streams in Costa Rica (Tietjen 1986). Colonies may contain up to 70 spiders, each territorial to its own orb web. Juvenile webs have been found to be located close to one another and oriented vertically over the bank of the stream. Adult webs are more spread out with respect to the other webs and placed horizontally. Juvenile webs also tend to be found upstream from those of the adults in the colony (Tietjen 1986). The factors that explain the web placement of adults from that of juveniles have not been documented in detail. This pattern, nevertheless, suggests that web orientation can benefit from both horizontal and vertical webs.

M. gravidus is one of 20 spider species that are known to live in colonies, out of 34,000 species worldwide (Foelix 1996). Its colonial web placement increases the chance that prey will fly into a web or the spiders will escape prey. Each web in the colony is connected by a common scaffolding that allows each spider to flee the interconnected webs if threatened by a predator (Tietjen 1986). Colonial web building allows the spiders to make use of habitats that are unusable by solitary species of spiders (Uetz and Heiber 1997). *M. gravidus* is a parasocial species since each spider spins, defends, and maintains its web (Foelix 1996).

The highest energy costs associated with web weaving spiders are web silk and web spinning (Craig 1989). Prey capture by orb webs depends on web size and the ability of the web to intercept prey. Web loss without prey capture could be very energy expensive for the spider (Craig 1989). The strategic location of the web is very important. The spider not only needs to catch prey, but it also needs to prevent web loss. Strategic location of the web could include the orientation, distance from the stream, and openness of the web.

Prior studies have shown no trends in web sizes among colonies, depth of stream, and site location (Hickey 2003); however more subtle characteristics of the individual webs in a colony have not been documented. This study investigated the relationship between the web size of *M. gravidus* and the location and position of the web over the stream, as well as the openness of the web. This study asked if larger *M. gravidus* webs had a preferential placement, closer to the water or oriented in a certain direction, to maximize prey and minimize web loss. Large *M. gravidus* webs have been observed to be close to the water, more horizontally oriented, and in more open spaces. It is assumed that larger spiders will spin larger webs and obtain the best placement among the colony. It is hypothesized that the best placement would allow the spider to place its web on the substrates that allow it to orient its web horizontally, closer to the water, and in open areas.

MATERIALS AND METHODS

The study was conducted along streams in the Monteverde and San Luis areas in Puntarenas, Costa Rica (Fig. 1). Quebrada Máquina, near the Estación Biológica de Monteverde, and streams in Finca la Bella in San Luis Arriba were sampled.

Data were collected from 7 a.m. to 10 a.m. on July 16, 21, 23, and 24, 2005. Measurements taken include diameter of web, orientation of web, vertical distance of the web from the stream, and openness of web. The diameter of the web was measured finding the longest diameter (to the nearest centimeter) through the center of the innermost ring. The orientation of the web was determined using a protractor (to the nearest degree) to measure the angle of the web with respect to the stream. A level circle was drawn around the circumference of a jar with water in the jar filled to the line. This was used as a level to make sure the protractor was flat. The vertical distance of the web to the stream was measured to the nearest centimeter. The closest point on the web to the stream was used to measure the vertical distance. A rating system from 1-3 was used to measure the openness of the web. A web that had both faces of the web open and was not covered by a log or rock was assigned a three. Webs under a log or rock or with one side of the web face obstructed were assigned a one. All other webs were assigned a two.

Data were collected from 141 *M. gravidus* webs and 14 colonies. A colony was determined to be all the webs within a one meter radius of the inner most web. All webs in a colony that appeared to be intact were measured.

The ANOVA test was used to compare the openness of each web with the diameter of each web. The Fisher's test was then used to compare two of the openness categories. Simple regression was used to determine the correlation, if any, between the diameter of the web and orientation of the web. The vertical distance of the stream with respect to the diameter of the web was also compared using a simple regression test. compared using a Kruskal-Wallis test. A nonparametric test was used, because there were not enough samples in each colony to use a parametric test.

RESULTS

There was a significant difference between the diameter of the web and the openness of the web ($F = 4.257$, $p = 0.0165$, Fig. 2). The webs with an openness of one and three were found to be significantly different ($p = 0.0043$). The orientation of the web with respect to the diameter has a significant P value, however, the low r-squared value indicates that the relationship is not significantly correlated ($r^2 = 0.031$, $p = 0.0357$, Fig. 3). There was no significant correlation between diameter of the web and vertical distance from the stream ($r^2 = 0.001$, $p = 0.6702$, Fig. 4). There was also a significantly different mean vertical distance of the webs from the stream between colonies ($p < 0.0001$).

DISCUSSION

There appears to be advantages and disadvantages for the *M. gravidus* to place its web in open areas away from the stream bank or nearby substrates. An advantage to being in the open is that more of the surface area of the web is exposed for prey capture. On the other hand, there is a greater chance that the web will be seen, allowing the prey to avoid the web or a predator to find it. The threads of an orb web, although only 1-3 micrometers, reflect light and can became very visible (Uetz and Heiber 1997). Due to the number of webs in such a confined space, remaining out of sight is next to impossible. The major predators of *Agelena consociata*, a colonial, orb-weaving spider of similar size, are lizards and larger spiders. These predators take advantage of the high prey densities found in spider colonies (Tietjen 1986). Although the primary predators of the *M. gravidus* are unknown, it is thought that the proximity over the stream could act as a safeguard from these predators. Being placed over the stream would deter lizards from reaching the spiders that are in more open areas. *M. gravidus* placed closer to a substrate or to the bank would be more vulnerable to attack from lizards. If a larger spider attacks the colony, the *M. gravidus* closer to a substrate or bank would be more vulnerable to attack. The *M. gravidus* in the middle would be able to feel the vibrations of the oncoming predator and flee from its web on the community scaffolding webs. Webs found in more open areas are more likely to catch prey and maximize the chance of escape from larger spiders and lizards.

It was hypothesized that larger webs, thus larger spiders, would have a better chance to attach their webs to the substrates that would orient their webs in the most beneficial way over the stream. Benefits would include maximizing prey capture and minimizing the effects of abiotic factors such as rain and wind. Webs are damaged by abiotic factors; web breakdown is determined by web site (Craig, 1989). Prior studies done by Tietjen have shown that *M. gravidus* adults orient their webs horizontally over the water (1986). In this study, however, no direct correlation was distinguished between orientation and web size. Until more is known about the prey of *M. gravidus*, it will be impossible to tell which orientation would be most beneficial. A horizontal web would be more beneficial for an insect that is leaving the water of the stream, where a vertical web may be more beneficial for an insect that is flying along the stream. Abiotic factors also need to be taken into account. A vertical web would be more likely to be damaged by wind, while a horizontal web would be more likely to be damaged by falling detritus or rain. Although there is no correlation between size and orientation, there still may be an optimal orientation between a horizontal and a vertical web. The mean orientation of this study was 42.6º and the median orientation was 41º.

It was hypothesized that larger webs would have a better placement along the stream. In this case, the larger webs would be placed closer to the water, so the water would force the spider's prey towards the web. The two most likely types of prey are insects that are coming from the water or insects that hover along the stream. In both of these examples, water could possibly force the spider's prey towards the webs. This trend was refuted, however, for there was no significant correlation between the diameter of the web and the vertical distance from the stream. Large spiders don't preferentially choose near water sites more than small spiders. More needs to be known about the prey of the *M. gravidus* before the optimal distance from the water can be determined.

There was also a significant difference in the mean vertical distance of the webs from each colony. This test shows that there is a preferential height for a colony at each site. Each microhabitat offers a different benefit at different heights above the stream. The determination of the height above the stream could be based on substrates present near the stream. The colony must be chosen based on characteristics of the surrounding area. It would make sense that *M. gravidus* adapt for their location. The fact that colonies remain populated year-round (Uetz 1986), suggests that once a site is selected it remains the site of the colony for a long time. Moving the site of the colony would be an energetically expensive task. The colonies that choose the best sites will prevail and endure, while those that don't will likely migrate or perish. Some colonies may be at a site that would suit them better to be located higher above the stream, while others may be suited better closer to the stream.

The effects of abiotic factors on the webs need to be observed to see what orientation is subject to less damage from wind and rain. Little is known about the predators of *M. gravidus*; it is possible that the stream deters them. This would seem likely for terrestrial predators, but wouldn't hold true if their primary predators were birds or large flying insects. Little is also known about the prey of *M. gravidus*. Their prey is most likely small insects that live around streams or perhaps insects that are emerging from the stream. It was observed that many colonies appeared to be one to two meters downstream of a rapid. It is possible that the colony location is not only near a stream, but perhaps more precisely near a rapid.

Lager webs, thus larger *M. gravidus*, place their webs in more open sites to both maximize the use of both web faces for prey capture and reduce the risk of predation from terrestrial animals. There is no significant correlation between the orientation of the web and size of the web. Larger spiders don't place their webs closer to the stream. It appears that there is no obvious beneficial distance from the stream that maximizes fitness. The mean vertical distance of the webs significantly differs between colonies. The most beneficial location at each site depends on the surrounding substrates.

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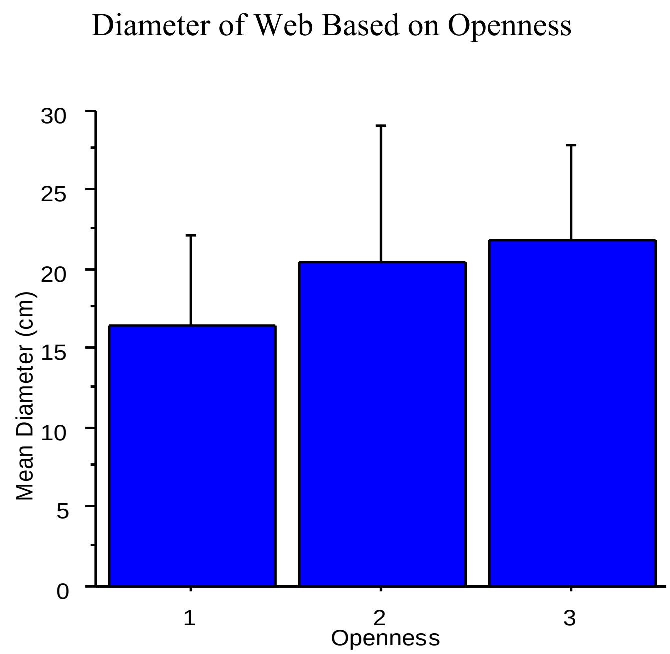

Fig. 2 The average diameter of the *M. gravidus* web increases as the openness of the web increases (ANOVA, $F = 4.257$, $p_{1\text{-}3} = 0.0165$, $p_{1\text{-}2} = 0.0507$, and $p_{2\text{-}3} = 0.3830$).

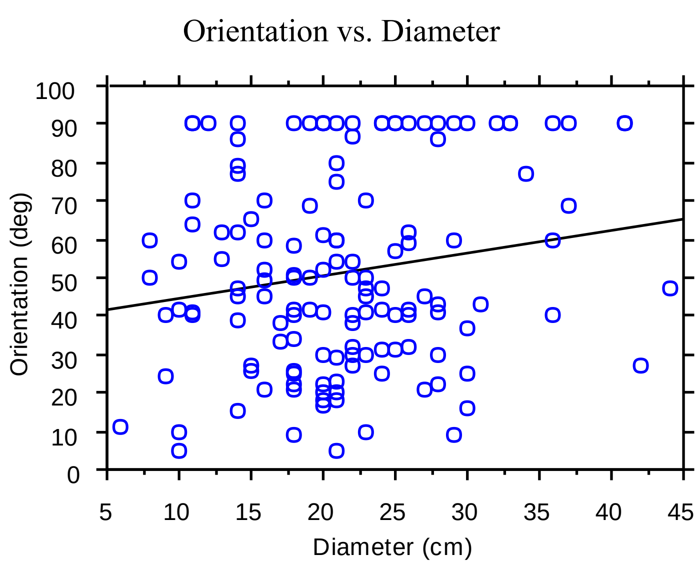

Fig. 3 There is no correlation between the orientation and diameter of the *M. gravidus* webs (Simple Regression, $r^2 = 0.031$, $p = 0.0357$). The equation for the line is $Y = 38.337 + 0.605 * X$.

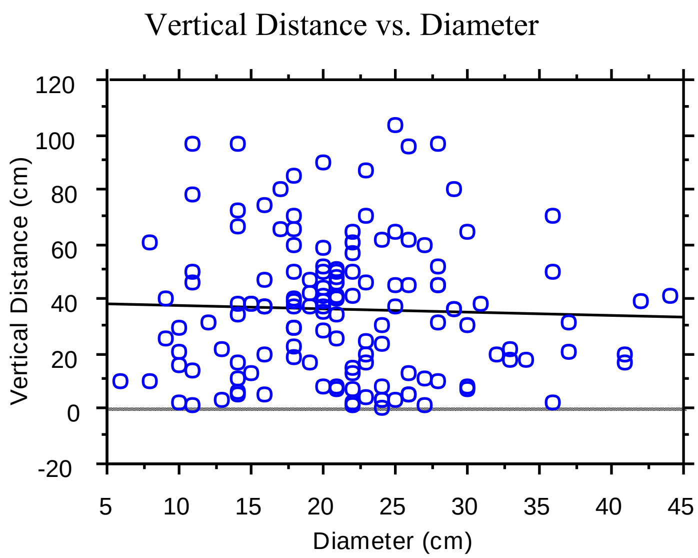

Fig. 4 There is no correlation between the vertical distance and diameter of the *M. gravidus* webs (Simple Regression, $r^2 = 0.001$, $p = 0.6702$). The equation for the line is $Y = 39.07 - 0.121 * X$.