Spider size, web location, and prey capture in the colonial orb-weaver Metabus gravidus

Jamie E. Potosek

Spider Size, Web Location, and Prey Capture in the Colonial Orb-Weaver *Metabus gravidus*

Jamie E. Potosek

Department of Neurobiology and Behavior, Cornell University

ABSTRACT

Metabus gravidus spiders live in colonies of five to 70 individuals and construct their webs over moving water. Buskirk (1975) found larger spiders can take over the webs of smaller spiders and suggested that certain sites within the colony may have greater prey capture rates. Therefore, I hypothesized that larger spiders should occupy these positions in the colony. Colonies of *M. gravidus* were studied at the Quebrada Máquina stream in Monteverde, Costa Rica. I measured spider size, web size, height from water, distance from bank, and prey capture rates for 198 total webs. Twenty-four artificial webs were created to determine prey capture and web position without the presence of spiders.

Spider size and web area correlate positively ($r^2 = 0.458$, $p < 0.0001$). Larger spiders are found at locations closer to the water surface ($r^2 = 0.212$, $p < 0.0001$) and catch more prey than smaller spiders ($r^2 =0.286$, $p< 0.0001$). Larger spiders also show both a higher overall visitation rate by insects to their webs ($r^2 = 0.231$, $p = 0.0032$) and a higher proportion of hits that are successful ($r^2 = 0.112$, $p = 0.0002$). This data support the earlier idea that web placement within the colony and differential prey capture should place larger spiders in these areas. (Buskirk 1975a, Shannon 1996). However, there is no significance between spider size and distance of web from stream bank ($r^2 = 0.017$, $p = 0.0672$). Artificial webs showed no significant difference between upstream /downstream ($p = 0.8614$) and high/low positions over the water ($p= 0.4218$) within each colony, but they did show a significantly greater number of prey captures in the inner quadrants of the webs as compared to the outer quadrants ($p < 0.0001$). These findings support the notion that web position alone does not decide the success of prey capture. It is evident that spider size has tremendous influence on success of prey capture as well.

RESUMEN

Las arañas de la especie *M. gravidus* viven en colonias de cinco a 70 individuos y construyen sus telas arriba del agua moviendo. Buskirk (1975) encontro que las arañas mas grandes pueden tomar posesión de las telas de arañas mas pequeñas. Sugiero que es posible que algunos sitios adentro de colonias tengan proporciones más altas de capturar presa. Por eso, yo asumí una hipótesis que las arañas grandes ocuparían estos sitios. Estudie colonias de *M. gravidus* a la Quebrada Máquina en Monteverde, Costa Rica. Medí el tamaño de araña, el tamaño de tela, la altura sobre el agua, y la distancia de la orilla para 198 telas. Veinticuatro telas artificiales fueron construidas para determinar las capturas de presa y la posición de la tela sin la presencia de arañas.

Tamaño de araña y area de tela tienen una correlación positiva ($r^2 = 0.458$, $p< 0.0001$). Arañas mas grande están encontrado en lugares mas cerca del agua ($r^2 = 0.212$, $p < 0.0001$) y cogen mas presa que las arañas pequeñas ($r^2 = 0.286$, $p < 0.0001$). Las arañas mas grandes exhiben mas visitaciones de insectos a sus telas ($r^2 = 0.231$, $p = 0.0032$) y una proporción mas alta de visitaciones prosperos ($r^2 = 0.112$, $p = 0.0002$). Estos resultados apoyan la idea anterior que la colocación de la tela dentro de la colonia y las capturas de presa deferenciales deben poner las arañas más grandes en estas áreas (Buskirk 1975a, Shannon 1996). Sin embargo, no hay una diferencia significativa entre el tamaño de araña y la distancia de la tela desde la orilla ($r^2 = 0.017$, $p = 0.0672$). Las telas artificiales no mostraron una diferencia significativa entre río arriba/ río abajo ($p = 0.8614$) y alta/baja distancias de la superficie del agua ($p = 0.4218$) dentro de cada colonia, pero mostraron una diferencia significativa entre numeros de capturas de presa en las cuadrantes interiores en comparación de los exteriores ($p < 0.0001$). Estos resultados soportan la noción que solamente la posición de tela no decide el éxito de capturas de presa. Es evidente que tamaño de araña tiene mucha influencia en éxitos de capturas de presa también.

INTRODUCTION

Metabus gravidus is one of a very few orb-weaving spider species that is gregarious, constructing its colonies over streams. The proposed benefits of group living include greater efficiency group defense, increased resource exploitation, communal raising of young, and the ability to learn from the foraging methods of others (Alcock 1984). For *M. gravidus*, coloniality is probably related to resource exploitation and the fact that single webs cannot be placed over streams. Large populations of *M. gravidus* can be found in Monteverde, Costa Rica occupying stream banks, and living in colonies of up to 70 individuals suspended over running water (Buskirk, 1975a). The colony utilizes common support lines to connect individual webs and facilitate movement within the colony. Each individual spider builds and maintains its own individual web, rarely feeding from other webs in the colony.

Prey capture at webs depends on web size, web placement, and the ability of the web to intercept prey, including factors of web angle and stickiness (Kajak 1964 et al. cited in Craig 1989). Prior studies of *M. gravidus* have shown that certain locations within the colonies tend to trap more prey than others. Buskirk (1975a) observed that in such colonies, web positioned closer to the water surface, farther from the bank, and over slower currents caught more prey than at other web locations. In addition, larger spiders are expected to capture the largest amounts of prey because they will be able to dominate the best locations within the colony. There is evidence that larger spiders are able to do so by initiating aggressive behaviors towards smaller spiders within the colony. Spiders exhibit behaviors of bouncing, web-jerks, chasing, displacement of orbs, and fighting which defend individual feeding areas and space out the webs within a colony (Buskirk 1975b). These aggressions often result in displacement of the smaller spider or prey robbery from the orb. Shannon (1996) found that aggressive behavior only resulted in prey or web acquisition when the aggression was initiated by a larger spider. Building from these previous studies, certain locations within the colonies are expected to be more favorable for prey capture than others. These locations should be upstream, farthest from stream bank, and at the lowest heights above the water. It is also assumed that larger spiders will occupy the superior sites and therefore, experience the highest rates of prey capture within the *M. gravidus* colony.

MATERIALS AND METHODS

Site Description

The study was conducted in premontane wet forest in Monteverde, Costa Rica: Puntarenas province; at an elevation of 1470m. *Metabus gravidus* colonies were studied along the Quebrada Máquina stream, which at this altitude, averages four meters in width and one-half to one meter in depth. The stream is located in protected primary forest near the Estación Biológica Monteverde.

Spider and Web Size

Observations were made from 24 October 2000 through 3 November 2000 of spider size in relation to the variables of web area, distance from the bank, height over the water, stream location, and number of prey catches over a set time period to ascertain whether the large spiders in fact are able to place themselves preferentially within the colony and catch more prey. Each web within a colony was measured with tape measure for circumference (later transformed to area in data analysis), distance from stream bank, and distance above the water surface. In addition, the length of each spider was measured with a caliper.

Prey Capture

- **Real Webs**

Five similarly measured colonies were subsequently observed from 1600 to 1800 hours and the numbers of insect hits and misses upon each web in the colony were recorded. Hits were defined as being successful prey captures, misses being when insects flew into the web but were not caught. This time period was chosen because Buskirk (1975) observed diurnal changes in insect numbers over the water, with increasing numbers in the late afternoon, peaking at 1800 hours. An hour was spent observing each upstream and downstream location in each colony.

- **Artificial Webs**

From 6 November 2000 to 15 November 2000, imitation webs were constructed at six sites along the same stream, in suitable locations, but where *M. gravidus* colonies were not present. Four webs were created at each experimental colony. Four strips of contact paper simulating webs were constructed at each “colony”, at high and low distances above the stream ranging from .08m to 1.08m in height, two upstream and two downstream (Figure 1). Webs of equal area were assembled from clear contact paper and covered with automotive grease. After several days, the webs were revisited and insect abundances totaled for each web. Web height, distance from bank, and stream location were measured. Distance from bank was recorded in quadrants of each web. Each web was broken up into four quadrants, two closest to the bank, and two farthest from the edge of the stream. Spider size and web size were thus eliminated from the experimental design.

RESULTS

Spider and Web Size

Factors of web location reveal differences in corresponding spider size in the *M. gravidus* colonies. Spider size (Mean + SD = 2.07 + .99cm) and web area (Mean + SD =1407.32 + 1130.03cm²) show a positive correlation with a simple regression in this study (r^2 = 0.458, $p < 0.0001$). As spider size increases, web sizes increase accordingly (Figure 2). Therefore, just spider size was used in subsequent comparisons. A multiple regression was run on web placement variables versus spider size, with height of web from the water surface (Mean + SD = 20.57 + 16.56cm) being the only significant abiotic factor to correlate with spider size (r^2 = 0.212, $P< 0.0001$). Height of web above water was found to correlate negatively with spider size in a simple regression analysis (Figure 3). A further simple regression shows that web distance from the stream bank (Mean + SD = 193.889 + 68.956cm) shares no significant correlation with spider size (r^2 = 0.017, p = 0.0672) for the *M. gravidus* colonies observed (Figure 4).

Prey Capture

- **Real Webs**

Spider size, as well as web location, was found to affect the trends in prey capture in *M. gravidus* colonies. Analyzed with simple regression, the number of prey captures versus spider size show a positive correlation, (r^2 =0.286, $p < 0.0001$), with larger spiders catching more prey than smaller spiders, (ANOVA Test: Figure 5). The number of total visits by potential prey correlates significantly with spider size as well (r^2 = 0.231, $p < 0.0001$). Webs of larger spiders had more visits than those of smaller spiders (ANOVA Test Figure 6). The overall proportion of successful prey captures (defined as the number of hits/total number of visits) correlates significantly with spider size as well (r^2 = 0.112, p = 0.0002). Larger spiders experience a higher success rate of prey captures than smaller spiders (Figure 7).

Prey captures were found to be greater at downstream locations (Mean + SD = 1.02 + .758) than at upstream locations (Mean + SD = .881 + .739), but the difference was not significant when analyzed with an ANOVA post-hoc – test ($p = 0.3676$). A multiple regression analysis showed that the number of prey captures is positively correlated with spider size ($r^2 = 0.398$, $p < 0.0001$) and distance from stream bank ($p = 0.013$) as well is negatively correlated with height above the water ($p = 0.0025$).

- **Artificial Webs**

Web placement alone was not seen to affect prey captures in the artificial "colonies". Each of the four positions within each colony were compared in an ANOVA post-hoc test. Upstream and downstream locations show no significant difference in the amount of prey these webs caught ($p = 0.8614$) nor did high and low heights above the water ($p= 0.4218$). There was overall no significant difference between the four quadrants sampled (Figure 8) in regards to height and stream location. However, a significant difference was found with a paired t-test between the inner and outer quadrants of the artificial webs in terms of prey capture ($p < 0.0001$) with inner quadrants showing higher numbers of prey captured than the outer quadrants.

DISCUSSION

Patterns of web location and prey capture discovered in previous investigations were both upheld and rejected in this study. It has previously been shown that the most desirable web locations within the *M. gravidus* colonies tend to occur farthest away from the bank, upstream, and closest to the surface of the running water (Buskirk 1975). A negative correlation of height from water surface versus spider size was expected, and the analysis was in fact significant. Larger spiders may prefer lower sites for several reasons. Kerzicnik (1993) found that while *M. gravidus* is not directly dependent on the water surface for prey capture, it may aid in camouflaging the web from flying insects and protect the spiders from kleptoparasites which rob prey from webs.

Spider size did not significantly correlate with distance from stream bank, but prey capture was greater at sites farther away from the edge in both the real and artificial webs. Using traps to capture prey, Buskirk (1975a) observed that the upstream end of a colony caught more insects relative to downstream. The results of this study contrast these earlier findings in that downstream locations tended to catch more prey than upstream locations at the Quebrada Máquina, but the trend was not significant in either the observed or manipulated webs. A possible explanation for these inconsistencies may be that other factors about the colony site have a larger influence on prey capture, such as sunlight intensity and availability of favorable substrates upon which to attach webs. In the artificial web experiment, exceptionally low prey captures were noted for one colony that was in a large gap, thereby subject to an exceptionally large amount of light. Favorable substrates were certainly more abundant at some colonies than others. This could account for larger amounts of prey capture at these places than otherwise expected taking into account web location.

The observation that more prey were caught at a greater distance from the bank is consistent with Buskirk's earlier findings. It is possible that it is beneficial for the spiders to be far away from the bank thus locating themselves in the area through which most potential prey fly. It is also possible that the spiders may simply be organizing themselves away from each other in an avoidance of competition, since spider size did not vary with distance from bank. Buskirk's (1975a) study found a trend such that the river was narrower in sections where spider colonies were found than those lacking colonies. This was only upheld in the rainy season. This suggests that there is perhaps a point at which increased distance from the bank is no longer desirable, and results may differ at streams of different sizes.

Body size plays an integral role in web location and number of collected prey. Shannon (1996) found large spiders to catch significantly more prey on a per hour basis than small and medium sized spiders. The data gathered in this study also show a positive correlation between spider size and the number of prey catches. Positive correlations between spider size and total visits, as well as success rate were seen as well. This pattern is well – documented in many biological systems; larger spiders are able to dominate the locations that are most resource-rich (Buskirk 1975, Shannon 1996). Clearly within these existing colonies, larger spider size is the dominating factor that leads to higher prey capture among *M. gravidus*.

Orb weaving spiders rarely feed on each prey caught within the web, rejecting many of the smaller insects that get caught. Foster (1994) observed *M. gravidus* to feed only upon damselflies, which were caught infrequently in the webs. Therefore, prey capture may not be the primary factor in web placement among *M. gravidus*. In Metepeira incrassate, a species of social spider, individual spiders choose their web site location by making trade – offs between foraging success and predation risk (Rayor and Uetz 1990 cited in Shelton 1992). It is thus possible that spiders may actively sacrifice the best colony locations in order to avoid predation.

While there was a correlation in stream location vs. prey capture for the artificial webs as expected, the data also showed that prey capture did not vary in relation to height above water or stream location. This again supports the idea that spider size may be the dominating factor in prey capture. However, it is also possible that, in the experimental design the artificial webs were more effective in catching prey and thus stickiness was able to prevail over all other variables.

This study supports Buskirk's (1975a) findings that certain web locations in *M. gravidus* colonies are favored over others in terms of prey capture. Larger spiders were found in these choice sites, and were observed to catch more prey than smaller spiders. However, my data also suggests that spider size has a much larger influence on successful prey catches than is apparent in previous studies. In the absence of spiders on the artificial webs, no differences were seen in prey capture for height above water and stream location. In conclusion, it is evident that many different factors, both abiotic and biotic, are influential in the colony distribution of *M. gravidus* spiders in Monteverde, Costa Rica.

Much further work remains to be done with these unique spiders. All day observations would help to account for temporal differences in activity pattern between young and adult spiders. More extensive experimentation would be beneficial to control for each variable separately.

ACKNOWLEDGEMENTS

Many thanks must be extended to all of the people who assisted during my project. Thank you to Mauricio Garcia, Andrew Rodstrom, and Tim Kuhman for general, day to day spider advice and supplies (yes, car grease really did work-despite my doubtfulness!), as well as statistics help; to Alan Masters for all of his insight and much needed guidance from the beginning; and to all my fellow students here in the Fall 2000 program for providing endless entertainment and means of procrastination when it was most needed. Gracias a La Estación Biológica Monteverde for use of the stream and forest y mi familia en Cañitas por todo. Finally, to my parents, thanks for making this whole venture possible through your generous funding and support.

LITERATURE CITED

Alcock, Jon. 1984. Animal Behavior: An Evolutionary Approach. Third Edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Buskirk, Ruth E. 1975. Coloniality, Activity Patterns, and Feeding in a Tropical Orb-Weaving Spider. Ecology 56: 1314-1328.

Buskirk, Ruth E. 1975. Aggressive Display and Orb Defence in a Colonial Spidar, *Metabus gravidus*. Animal Behavior 23: 560-567.

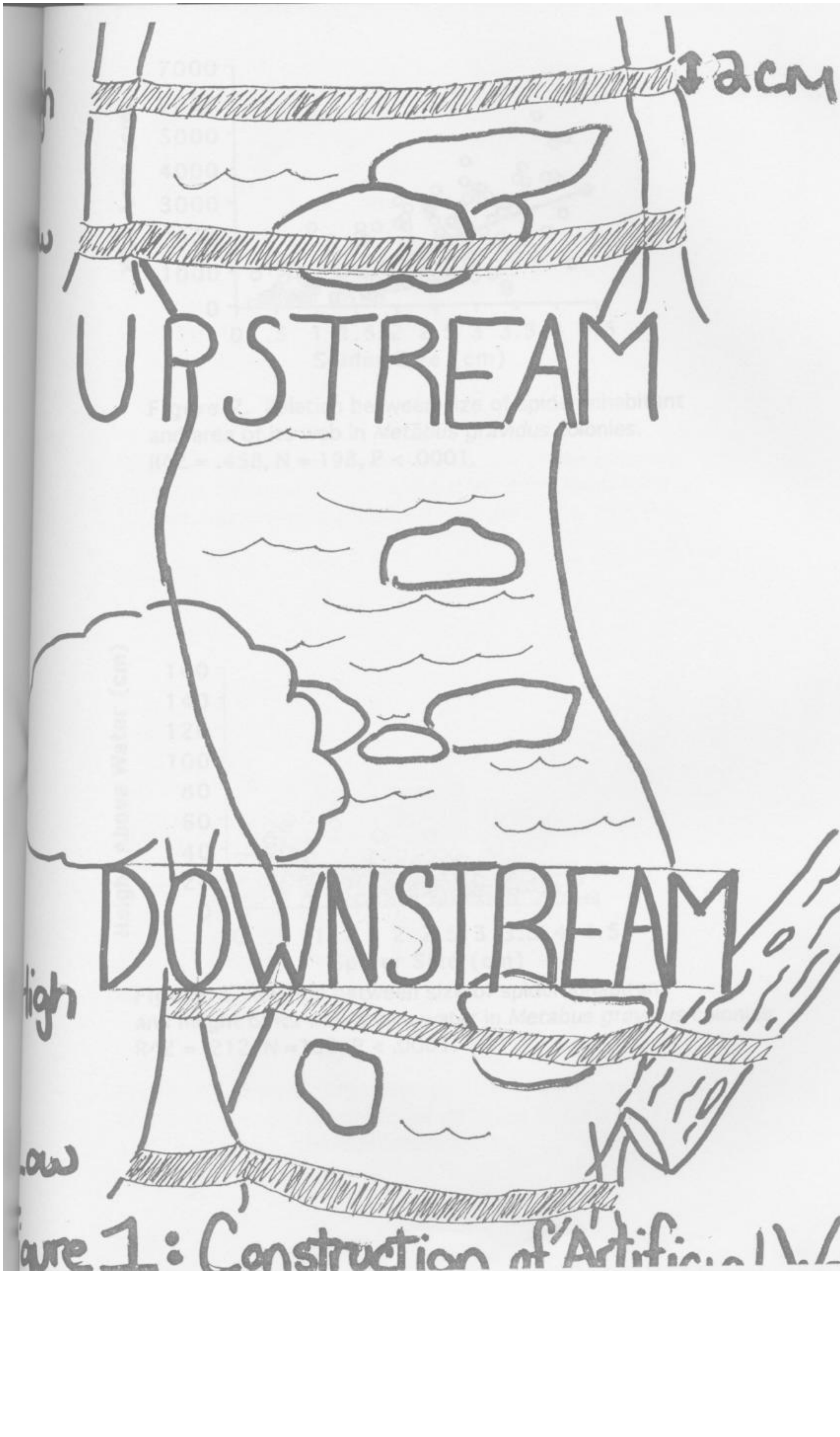
Craig, Catherine. 1989. Alternative Foraging Modes of Orb Web Weaving Spiders. Biotropica 21(3): 257-264.

Foster, Jane. 1994. The Effect of Moisture on *Metabus gravidus* Webs. CIEE: Tropical Biology and Conservation Program. Summer 1994. 191-197.

Kerzicnik, Laurie. The Relationship of the Water Surface and Prey Capture with the Colonical Orb-Weaving Spider, *Metabus gravidus*. CIEE: Tropical Biology and Conservation Program. Summer 1993. 154-165.

Shannon, D.N. 1996. Variations in Colony Activity Among *Metabus gravidus* Spiders of Different Sizes. UCEAP: Monteverde Tropical Biology Program. Fall 1996. 186-196.

Shelton, Angie. 1992. Web Site Tenacity and Behavior of the Social Spiders *Metabus gravidus*. CIEE: Tropical Biology and Conservation Program. Summer 1992. 82-94.



ure 1: Construction of Artificial Web

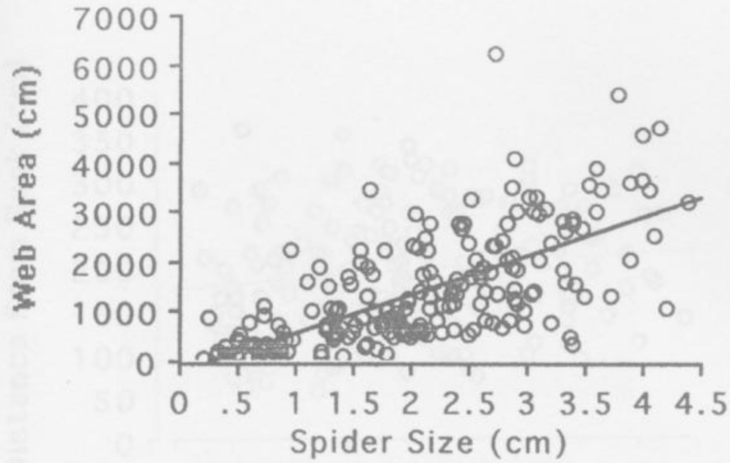


Figure 2. Relation between size of spider inhabitant and area of its web in *Metabus gravidus* colonies. R^2 = .458, N = 198, P < .0001.

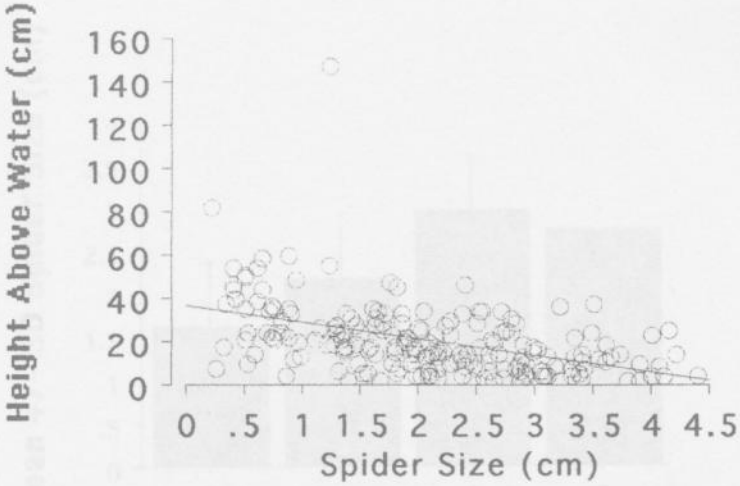


Figure 3. Relation between size of spider inhabitant and height of its web above water in *Metabus gravidus* colonies. R^2 = .212, N =198, P < .0001.

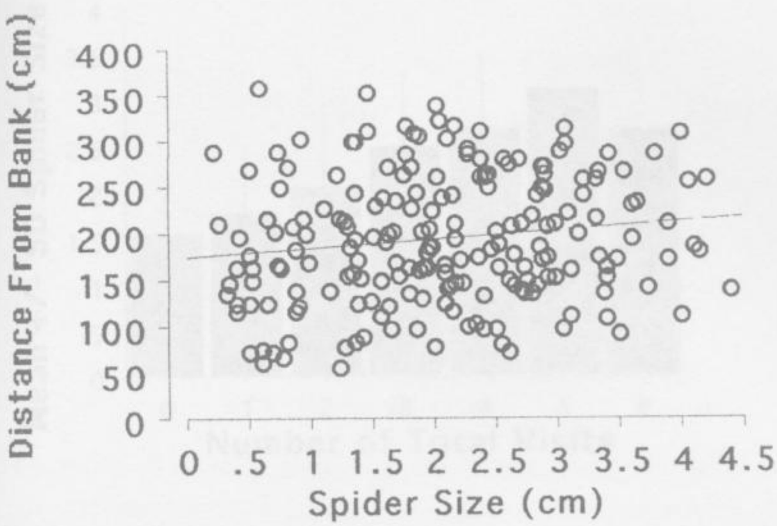


Figure 4. Relation between sizes of individual spiders and the distance of their webs from the stream bank in Metabus gravidus colonies. $R^2 = .017$, N = 198, P = .0672.

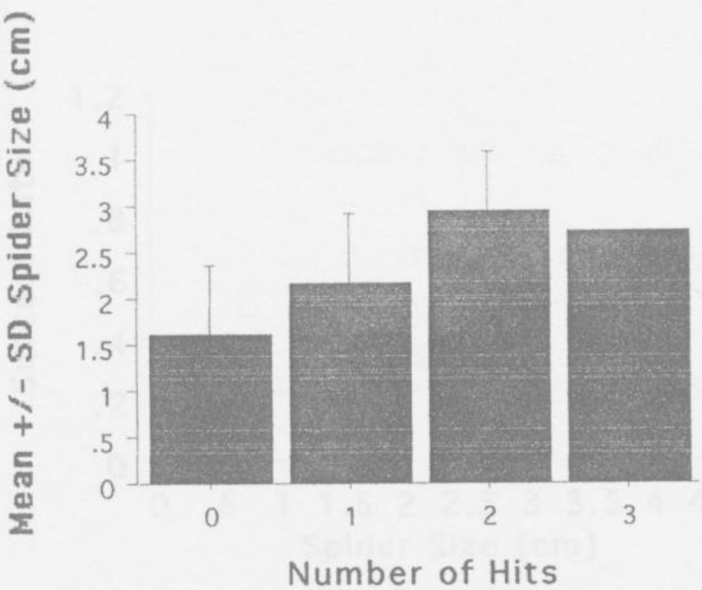


Figure 5. Differences in average (+/- 1 SD) number of prey captures for spiders of differing sizes(N = 119) in *Metabus gravidus* colonies.

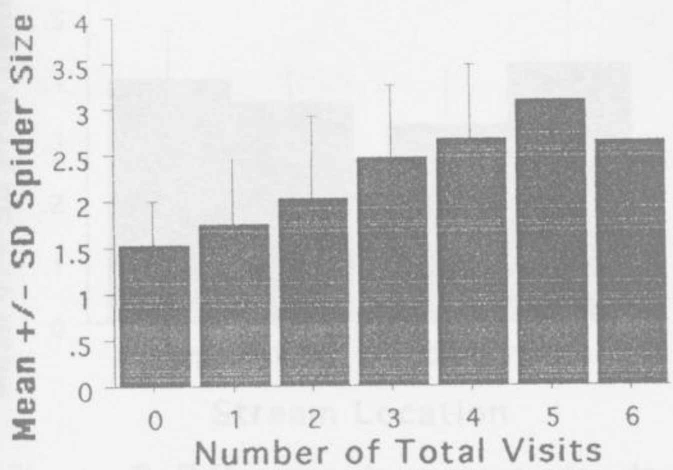


Figure 6. Differences in average number of prey visits for different sized spiders (N = 119) in *Metabus gravidus* colonies.

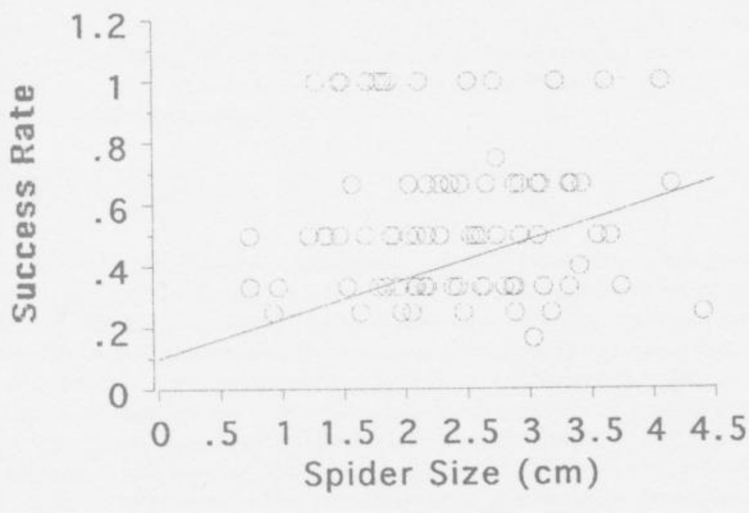


Figure 7. Relation between size of spider inhabitant and proportion of successful prey catches in *Metabus gravidus* colonies. $R^2 = .112$, N = 119, P = .0002.

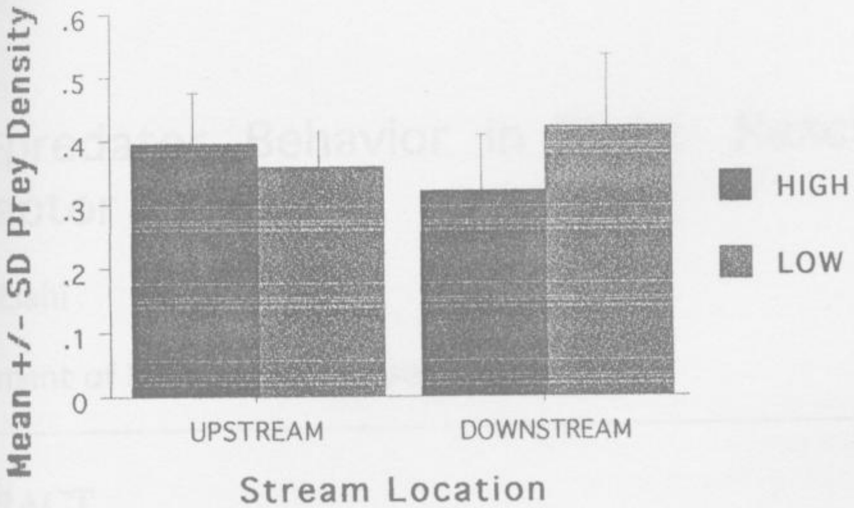


Figure 8. Differences in average prey density caught at different stream locations of artificial webs (N = 24).