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SHORT COMMUNICATION

Niche partitioning and intraspecific shared webs in two species of *Modisimus* Simon, 1893 (Pholcidae: Araneae)

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Abstract. The pholcid spiders *Modisimus bribri* Huber, 1998 and *M. guatuso* Huber, 1998 construct three-dimensional webs, including sheet dome and irregular shapes, occasionally shared by males and females. We studied species spatial disaggregation and confirmed web-sharing and prey capture dominance in shared webs. We observed 22 *M. bribri* and 25 *M. guatuso* webs and recorded their height above the ground, dome dimensions, and web-sharing. In shared webs, we recorded which individual captured prey. *Modisimus bribri* builds webs at greater heights (~6.5 times), with larger dimensions (~2 times) than *M. guatuso*. In both species, neither the occupant sex nor the number of individuals on the web had a significant effect on web dimensions. We confirmed differential web location between species and did not find evidence of chivalrous dominance in prey-capture in shared webs. This study contributes to the general knowledge of three-dimensional web-building spiders, posing new questions for future research.

Keywords: *Modisimus bribri*, *Modisimus guatuso*, prey capture, web dimensions.

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Spider web characteristics are taxonomically and evolutionarily relevant, as these traits tend to be conserved in each species and show great variation between them (Eberhard 1990, 2020; Coddington 2005; Blackledge et al. 2009, 2011; Herberstein & Tso 2011). Spider webs have multiple functions, serving as food traps, refuges, sexual arenas, and sites of maternal care, among others (Vollrath 1985; Zschokke 1997; Harwood et al. 2001; Blackledge & Gillespie 2002; Blackledge et al. 2011; Blamires et al. 2017). Despite their importance, research efforts have concentrated on bi-dimensional webs, while the three-dimensional web-building spiders have been less studied (Blackledge et al. 2003; Harmer et al. 2011; Su et al. 2018).

Modisimus (Pholcidae; Simon, 1893) are three-dimensional web-building spiders that build their webs in the undergrowth of vegetation, against rocks, underneath fallen logs, and between tree roots of tropical rainforests (Eberhard 1992; Huber 1997). Their webs, which have an irregular shape and support threads in different directions, include a sheet dome that is denser in the center, where the spider is commonly found (Eberhard 1992; Huber 1997; Fig. 1A). *Modisimus bribri* Huber, 1998 and *Modisimus guatuso* Huber, 1998, are two of the most common sympatric and synchronic pholcid species found in La Selva Biological Station in Costa Rica (Huber 1997, 1998). To this date, it is unknown whether there is variation in the height of the web location and structure in such a way that allows differentiation between species. This study aimed to determine if there is a difference in web location and architecture between the species *M. bribri* and *M. guatuso*.

According to the observations made by Huber (1997), we expect that the webs of *M. bribri* will be found higher above the ground than the webs of *M. guatuso*. Likewise, *M. bribri*, which occupies more open spaces (Huber 1997), is expected to have larger webs than *M. guatuso*, since several spiders have shown flexibility in web construction and characteristics according to the microhabitat (Barrantes & Eberhard, 2012). The occurrence of these differences in the webs could contribute to pre-copulatory mechanisms of reproductive isolation and reduction of competition for food. Additionally, males and females within the genus have been observed sharing webs. Previous studies suggest that males are dominant in prey capture, chivalrously donating prey to females, possibly as a mating effort to ensure their reproductive success (Eberhard & Briceño 1983, 1985). We therefore proposed to measure, under natural conditions, the occurrence of web-sharing and prey-capturing dominance in shared webs of both species. To ensure copulation, males are expected to make a greater number of captures than females in shared webs (Eberhard & Briceño 1983, 1985).

The study was carried out between 26 and 28 January 2019, at La Selva Biological Station, Sarapiquí, Costa Rica (10°25′ N, 84°00′ W), which is predominantly tropical rainforest (McDade & Hartshorn 1994). At this site, both species co-occur in time and space and are very abundant. The observations and measurements were performed between 8:30 and 12:00 pm, and 1:00 to 5:00 pm, respectively. Upon locating a web, we identified the resident species with a magnifying glass via the abdomen color (green for *M. bribri* and brown for *M. guatuso*; Huber 1998) and recorded whether the web was shared by two individuals or not. To determine web dimensions, we dusted the webs with cornstarch (Eberhard 1976) and recorded height of the web above the ground, dome height, length of the sheet, width, and contour (Fig. 1A). To test prey capture dominance on shared webs, we dropped a worker termite (*Nasutitermes* sp.) on sticky threads approximately equidistant from the two spiders on the web. The selection of this prey species was based on previous tests carried out

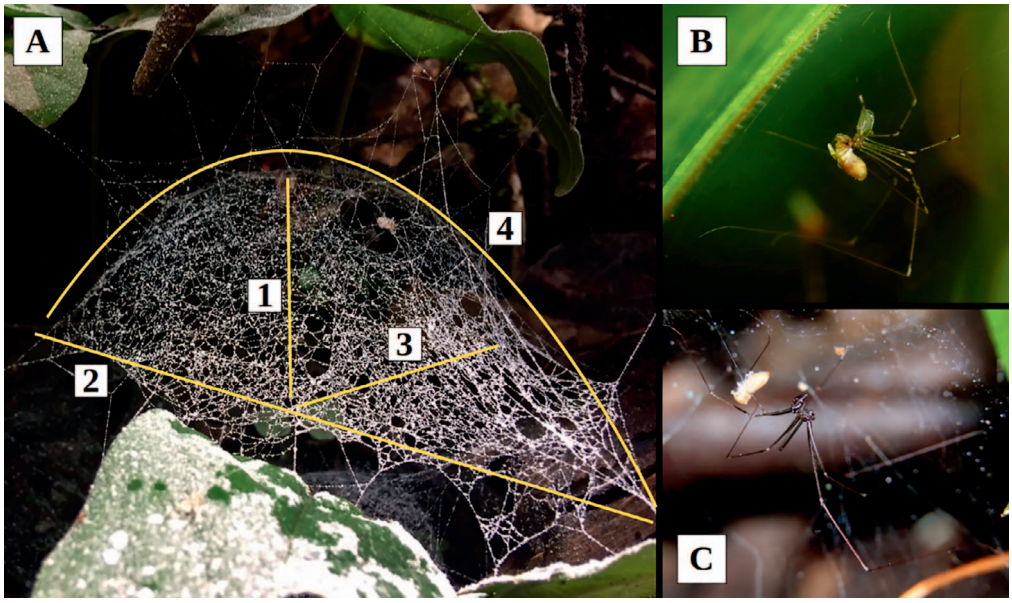

Figure 1.—(A) Web dimensions in *Modisimus* spp. The number 1 represents dome height, 2 is dome length, 3 is dome width, and 4 is dome contour (photo of an *M. guatuso* web after being dusted with cornstarch); (B) *M. bribri* individual, and (C) *M. guatuso* individual, both capturing one of the termites provided. Photos by M. Casacuberta.

by the authors. The termites used were of similar size and were always dropped from the same height (Fig. 1B, C). We waited for five minutes for prey capture. Webs that contained prey prior to observations were not considered in the study. Before data collection, each observer was trained to reduce bias in the study. After observations were made, we captured both individuals in each web and transported them to the laboratory to confirm species identification and determine their developmental stage and sex under the dissecting microscope. Individuals were then released in their same capture site. Data analyses and graphics were performed with R (R Core Team 2018).

We observed a total of 47 webs (22 *M. bribri* and 25 *M. guatuso*), of which 16 were shared by one male and one female ($n = 10$ in *M. bribri* and $n = 6$ in *M. guatuso*). It is worth mentioning that additionally we found a web shared by a *M. bribri* male and a juvenile whose sex could not be identified, as well as a web shared by two *M. guatuso* females. In the case of individual *M. bribri* webs, 8 were occupied by males, and 3 by females, and in *M. guatuso* 7 were occupied by males, 7 by females, and 4 by undetermined juveniles. The species were found on different substrates. Webs built by *M. bribri* were always located on the vegetation under the leaves while *M. guatuso* webs were observed on fallen trunks, litter, between tree roots, and, on one occasion, on a plant.

The average height above ground of adult webs was $\sim$ 6.5 times higher in *M. bribri* than in *M. guatuso* (Wilcoxon test, W = 534, $P < 0.001$; Fig. 2A). Furthermore, the webs of *M. bribri* were larger than the webs of *M. guatuso*. The average height of the dome was $\sim$ 2.1 times greater (W = 448, $P < 0.001$; Fig. 2B), average length of the dome was $\sim$ 1.9 times greater (W = 465.5, $P < 0.001$; Fig. 2C), average width of the dome was $\sim$ 2.1 times greater (W = 514.5, $P < 0.001$; Fig. 2D), and the contour of the dome $\sim$ 1.9 times greater (W = 460, $P < 0.001$; Fig. 2E). We compared web measurements for three groups of webs: those occupied by females alone, those occupied by males alone, and those shared by a male and female. We found no significant differences among the three web types in either species, according to results of Kruskal-Wallis Chi-squared tests: height above the ground (*M. bribri*: $X^2_{(2)} = 0.5$, $P = 0.8$; *M. guatuso*: $X^2_{(2)} = 0.3$, $P = 0.8$), dome height (*M. bribri*: $X^2_{(2)} = 0.5$, $P = 0.8$; *M. guatuso*: $X^2_{(2)} = 2.3$, $P = 0.31$), dome length (*M. bribri*: $X^2_{(2)} = 0.8$, $P = 0.7$; *M. guatuso*: $X^2_{(2)} = 0.8$, $P = 0.7$), dome width (*M. bribri*: $X^2_{(2)} = 1.4$, $P = 0.5$; *M. guatuso*: $X^2_{(2)} = 2.9$, $P = 0.2$), or dome contour (*M. bribri*: $X^2_{(2)} = 2.1$, $P = 0.3$; *M. guatuso*: $X^2_{(2)} = 0.4$, $P = 0.8$).

In the 10 pair-shared webs in *M. bribri*, females captured the prey when we offered it on 5 occasions and males on the other 5 (Pearson's Chi-squared Test; $X^2_{(1)} = 0$, $P = 1$); in *M. guatuso*, the prey was captured 4 times by females, 1 time by a male, and 1 time it was not captured at all ($X^2_{(1)} = 1.8$, $P = 0.2$). Therefore, the number of captures did not differ between the sex of the individuals in both species. In the web shared by two females of *M. guatuso*, one of the females caught the prey without fighting with the other.

Our results regarding the differences in the dimensions and locations of webs between *M. bribri* and *M. guatuso* (Fig. 2) contribute to the biology of the *Modisimus* genus, supporting with statistical evidence the observations made by Eberhard (1992) and Huber (1997). These differences could work in tandem with chemical, vibrational and other signals that result in facilitating reproductive isolation and/or niche separation between these species, reducing interspecific competition for territory and potential prey (Herberstein 1997; Foelix 2011; Tahir et al. 2012; Wawer & Hajdamowicz 2018). It might be that *M. bribri* adopts the strategy of searching for greater heights for building larger webs, as well as reducing competition with *M. guatuso*. On the contrary, the differences could be the adaptations to the microhabitat selected by the species, and to their differentiated resource requirement (i.e., web placement structures or prey types), and not only due to interspecific competition (Wise 1993). These two explanations are not exclusive; however, other studies are required for their confirmation.

The high number of pair-shared webs both in *M. bribri* and *M. guatuso* agrees with the observations in other Pholcidae (Eberhard & Briceño 1983; Blanchong et al. 1995). Several pholcid species are polyandric and the last male to copulate is expected to show the highest reproductive success (Schäfer & Uhl 2002; Schäfer et al. 2008). Males of some of these species perform mate guarding after mating and remain for long time periods with the female, preventing the female from mating with other males (Kaster & Jakob 1997; Calbacho-Rosa et al. 2010). In a previous study, males of three *Modisimus* species and one of *Blechroscelis* sp. were observed capturing prey in a shared web more often than females, and later delivering the prey to the female

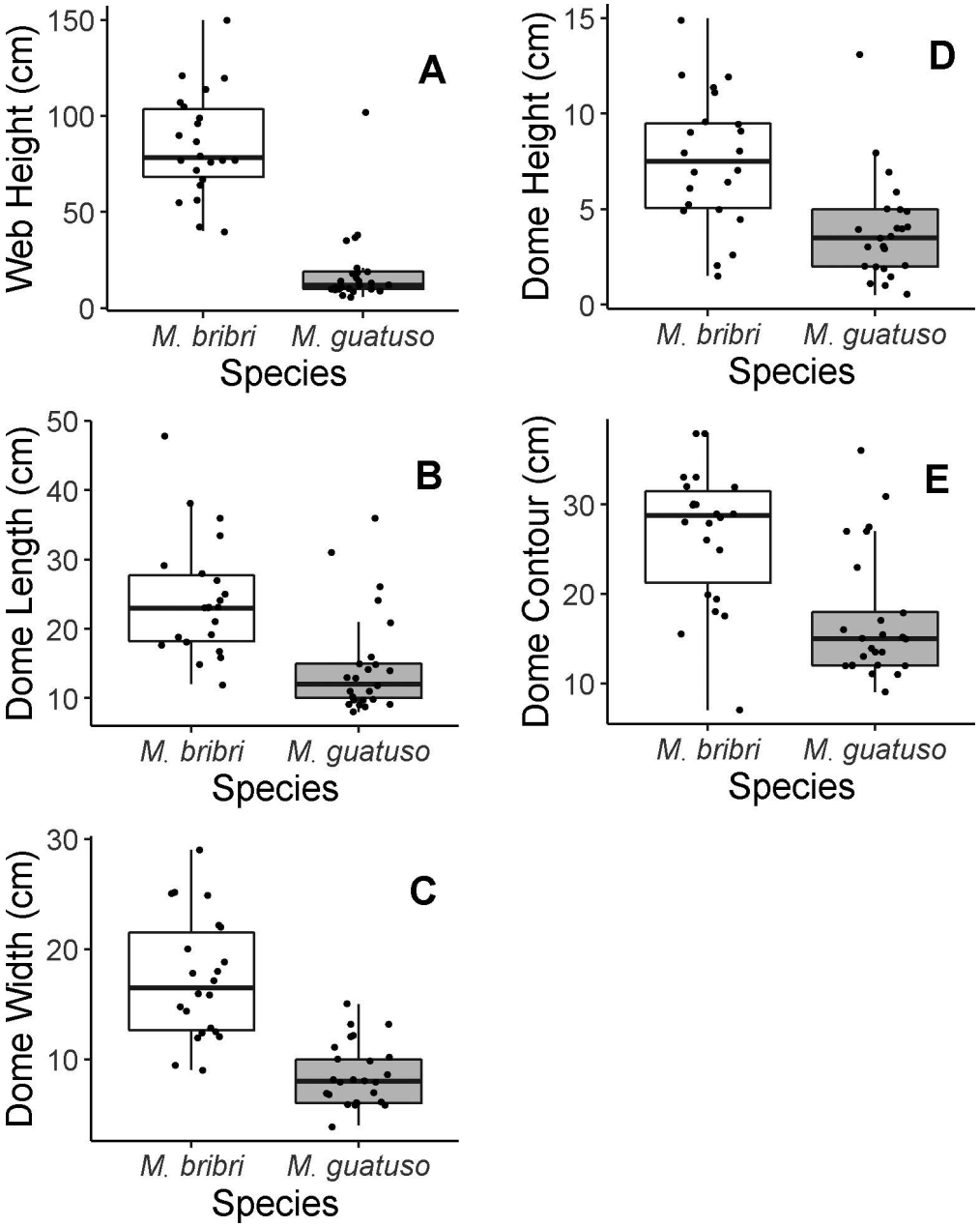

Figure 2.—Box plot of the (A) height above the ground, (B) dome length, (C) dome width, (D) dome height, and (E) dome contour for both species. *M. bribri* ($n = 22$), and *M. guatuso* ($n = 25$). Boxes indicate interquartile ranges; black bars indicate medians; whiskers comprise values not surpassing 1.5 times the interquartile ranges. The scattered points are the data of each spider web measured according to the species.

(Eberhard & Briceño 1983). However, the current study did not find robust evidence for dominance in prey capture in either sex, leaning towards what was observed in other pholcid species by Blanchong et al. (1995). In shared webs belonging to *M. bribri* pairs, we observed a case in which the female captured the prey, but after capture both individuals (female and male) fought for the prey, and both ate it. In another case, the male made the capture, and the female took the prey away and ate it. In another shared web, the male made the capture and the female finished wrapping the prey. Additionally, in a shared web belonging to a *M. guatuso* pair, it was observed that the female captured the prey and avoided the male.

A few webs in both *Modisimus* species were found occupied by solitary males. This could be due to the male evicting the female from the web as was observed by Eberhard & Briceño (1983) in *Modisimus* sp. species. On the other hand, males could have constructed the web as subadults and were detected before leaving the web or constructed the web as adult males, which would be extremely unusual in spiders (Foelix 2011). Finally, we found two adult females of *M. guatuso* in one shared web, which would be the first report of this non-territorial periodic-social behavior in this species, and a subsocial behavior rarely seen outside colonial or gregarious species (Avilés 1997). Unlike the cohabitation observed by male-female pairs, which can be attributed to mate guarding, conflict behavior can also occur after capture, as was recorded in a shared web of the same species where the female made the capture, followed by conflict and both individuals feeding on the prey. The female-female pair observed raises questions about its origins. Possible explanations for this behavior include energy savings by cooperation in web construction,

capture of larger prey, and/or shared egg caretaking (Matlack & Jennings 1977; Avilés 1997; Miller 2006). It is also possible that the nutritional and reproductive status of individuals could affect this behavior. The absence of conflict during the capture of the prey may mean that there is cooperation between both females. For future research, we recommend prolonging the observation time in webs shared by individuals of different and same sexes until the prey is consumed. We also recommend that the weight, size, nutritional and reproductive status of individuals be determined.

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