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Differences in web structure of *Tetragnatha tenuissima* (Araneae: Tetragnathidae) due to environmental conditions

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Abstract

Spiders can modify their web construction behaviour according to environmental conditions. Here, we examined how the web structure of *Tetragnatha tenuissima* differentiates depending on habitat type (swamp or river edge) at La Selva Biological Station, Costa Rica. We characterized the web architecture based on length, number of radii, and the spiral spacing relative to web length. There were no significant differences on the length or number of radii between the webs present in the swamp and river habitats. In terms of the spiral spacing relative to web length, there was a significant difference between habitats, with less distance in river-side webs than in the ones on swamps. This could be explained by the potential differential resource availability on each environment. Therefore, habitat type appears as an explanatory variable for differences on the web structure of *T. tenuissima*. Due to the small number of identifiable individuals of other *Tetragnatha* species, the effect of congeneric species co-occurrence on web structure remains as a factor to be tested in future research.

Keywords: Costa Rica • habitat adaptation • niche partitioning • orb-weaving spiders • web differentiation • web structure

Introduction

One of the most characteristic foraging strategies used by spiders is web building. This behaviour implies energy investment in site selection and web construction (Blamires 2020). Recent studies have focused on how biotic and abiotic factors affect web architecture in orb-weaving spiders (Gillespie 1987; Glover 2003; Blackledge & Zevenbergen 2006; Blamires, Thompson & Hochuli 2007; Blamires *et al.* 2011; Blamires 2020). Among those factors are included inter and intraspecific competition (Glover 2003; Kennedy *et al*. 2019), prey availability (abundance, size, and diversity) (Gillespie 1987; Glover 2003; Blackledge & Zevenbergen 2006; Blamires, Thompson & Hochuli 2007; Blamires *et al*. 2011; Blamires 2020), wind conditions (Wu *et al*. 2013), air temperature and openness of the habitat (Blamires, Thompson & Hochuli 2007), and the size of the water body (i.e. river or lake) in which some spiders build their webs (Gregorič *et al*. 2011).

The web modifications could be related with the use of different types of silk (Blamires 2020) or in architectural features (Blackledge & Gillespie 2004; Gillespie 2004; Gregorič *et al*. 2011; Kennedy *et al*. 2019). Among the web components that spiders tend to modify are the number of radii, web length, and spiral spacing (Blackledge & Gillespie 2004; Gillespie 2004; Gregorič *et al*. 2011; Kennedy *et al*. 2019). Sticky spirals are used for prey capture while the radii are non-sticky areas of the web which provide structural support. Orb weavers also use radial strings to attach their webs to the surrounding structures (Zschokke 1999; Blackledge & Gillespie 2004). These strings contribute to counteract the kinetic energy of prey's flight when it is captured (Sensenig *et al*. 2012). The mesh created by all these web components is related to the efficiency of the web in prey capture (Blackledge & Zevenbergen 2006). Therefore,

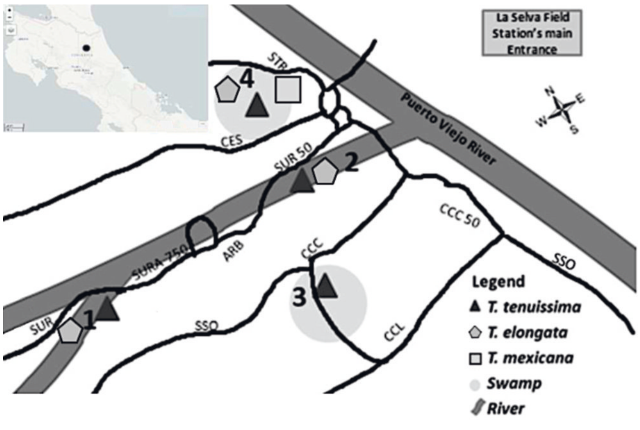

Fig. 1: Schematic map of sampling sties and species occurrences in La Selva Biological Station: Taconazo river (1), El Sura river (2), El Saltito swamp (3), and the Experimental swamp (4). Trails indicated only for reference. Inset: relative location of La Selva Biological Station (dot) in Costa Rica. Map from R Studio packages sf v. 0.9-8 (Pebesma 2018), mapview v. 2.9.0 (Appelhans *et al*. 2020), leaftet v. 2.0.4.1 (Cheng, Karambelkar & Xie 2020), and magrittr v. 2.0.1 (Bache & Wickham 2020).

it is expected that these web features will vary according to different habitat conditions.

Since the structure of the web is correlated with the type, availability, and size of the prey (Brown 1981; Yoshida 1981), as well as a medium to avoid competition (Glover 2003), and to survive environmental conditions (Gregorič *et al*. 2011; Wu *et al*. 2013), it can be considered as a proxy for their trophic niche (Blackledge & Gillespie 2003). It has been shown that orb weavers can accomplish niche partitioning by the structure and positioning of their webs (Brown 1981). For example, within the adaptive radiation of Hawaiian *Tetragnatha* spiders, it has been demonstrated that different species co-exist in the same area by using distinct web architectures to prey on different organisms (Blackledge & Gillespie 2004; Gillespie 2004; Kennedy *et al*. 2019).

The orb-weaving spiders from the family Tetragnathidae have a worldwide distribution including the rainforests of Costa Rica (Okuma 1992). Their webs are placed near trees, among plants close to the water, or in the canopy foliage of forests (Yoshida 1981; Nasir 2016). They also sometimes aggregate their webs to provide protection from predation (Blamires, Thompson & Hochuli 2007). Many tetragnathids have species-specific webs, while others build more generic ones. Relative body sizes can also affect web structure. Amongst the genera in this family, *Tetragnatha* are known to build unique webs, with different structures according to the species (Nasir 2016). Out of the seven *Tetragnatha* species reported from Costa Rica (Banks 1909, 1913; Okuma 1992), three of them are present at La Selva Biological Station: *Tetragnatha elongata*, *T. tenuissima*, and *T. mexicana* (Cotoras pers. obs.). They are present in swamp and riverside habitats. *T. tenuissima* appeared to be the most abundant and wide spread of them (Cotoras pers. obs.).

The physical proximity of the suitable habitats for *T. tenuissima* at La Selva Biological Station allowed us to explore what is the effect of the local environment on the web structure. Particularly, we set out to ask: will the web structure of *T. tenuissima* vary amongst different types of habitats, such as swamps and rivers? We predict that *T. tenuissima* webs will have a different architecture depending on the environment because of the expected differential prey availability and local environmental physical constraints (i.e. exposure, water flow, substrate availability, etc.). This research brings new insights into the degree of plasticity in web construction, given the habitat conditions, on a continental *Tetragnatha* species.

Methods

Eight sampling areas (four river margins and four swamps) were selected based on the land use denomination (Clark & Clark 2000; Romero *et al*. 2013) of La Selva Biological Station (10°25′N 84°00′W). In addition to habitat type, the selection criteria for the sampling sites were based on *Tetragnatha* abundance and accessibility. We visited each site three times over a six-week period, between June and July 2017. Surveys happened during the early morning or the following evening if it rained during the morning. We timed specimen collections to a total of 150 minutes per visit. The search time was stopped when a *Tetragnatha* web was found. Each web was dusted with corn starch to enhance visual contrast and photographed with a ruler for scale. The web was then destroyed to avoid organisms getting trapped in a spider-less web. Spiders were preserved in 95% ethanol. Date, time, and area of collection were recorded for each spider and web.

Adult spiders were identified down to species using original descriptions and a dichotomous key (Okuma 1992). Juvenile spiders could only be classified to genus. Specimens that could not be identified at the species level were not included in the study to prevent having as a confounding factor the between species variation. The webs belonging to adult spiders were processed on ImageJ to measure the web length, number of radii and the spiral spacing. The web parts were classified following Zschokke (1999) and Blackledge & Gillespie (2004). Webs were measured vertically, horizontally, and diagonally (from the last spiral of one end to the last spiral on the other end). From these three measurements, a total average length was calculated for each web. Radii were considered as the lines starting at the center and tracing up to the last spiral line and divided the web into triangular sub-sections (Zschokke 1999; Blackledge & Gillespie 2004). To calculate the spiral spacing, we used the distance between two spiral intersections on the radii with most of them, or on the one with fewer tangled spiral lines. A fix number of eleven spiral distances were evaluated in order to include all webs. To correct by the size effect of the web, we used the ratio of the spiral distance to the web length. Similar methods to characterize web structure have been previously used (e.g. Gillespie 1987; Blackledge & Gillespie 2003; Kennedy *et al*. 2019).

To assess whether web characteristics differed between riverside and swamp habitats, we used box plots, Analysis

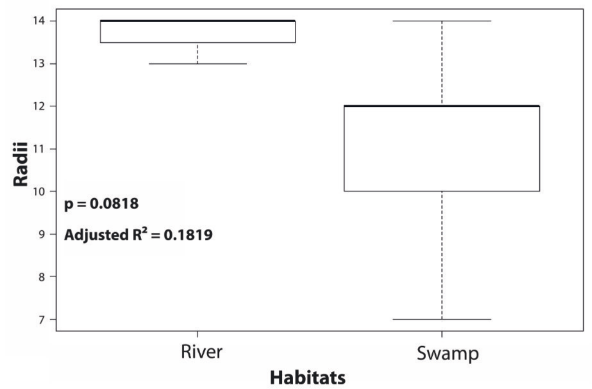

Fig. 2: Number of radii lines by habitat type.

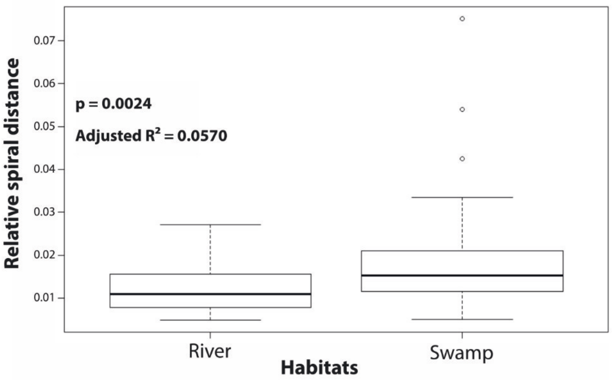

Fig. 3: Relative spiral distance by habitat type.

of Variance (ANOVA), and Linear Mixed Models, as implemented in the R Suite (version 3.4.0) (R Core Team 2018) packages lme4 v1. 1-26 (Bates *et al*. 2015) and dplyr v 0.7.6 (Wickham *et al*. 2018).

Results

Specimen collection

A total of 66 webs were photographed over the duration of the study. Out of these, 13 corresponded to adult *T. tenuissima*. The rest were unidentified juvenile *Tetragnatha* or belonged to the species *T. elongata* or *T. mexicana*. Web data corresponding to *T. tenuissima* was collected in four of the eight sites. Two sites corresponded to rivers (3 individuals) and two to swamps (10 individuals) (Fig. 1). In the rivers, we found *T. tenuissima* co-occurring with *T. elongata* and unidentified juvenile *Tetragnatha*. In Taconazo river there was one *T. tenuissima* out of seven collected specimens; while in Sura river, there were two *T. tenuissima* out of three collected specimens. In the swamps, we found *T. tenuissima* co-occurring with *T. elongata*, *T. mexicana* and unidentified juvenile *Tetragnatha*. In El Saltito swamp by the CCL trail, there were four *T. tenuissima* out of 20 collected specimens; while in the Experimental swamp by the CES trail, six *T. tenuissima* out of 55 collected specimens. *T. tenuissima* was the most common identifiable species of the three recorded on the study site (Fig. 1).

Web length

There were no significant differences in the average lengths between webs present in swamp and river habitats (Adjusted R^2 = 0.01804, p = 0.293).

Number of radii

There were no significant differences amongst the number of radii between webs present in swamp and river habitats (Adjusted R^2 = 0.1819, p = 0.0818; Fig. 2). The data dispersion is higher on the webs present on swamps, while more concentrated on the ones from rivers.

Spiral distances relative to web length

There were significant differences on the spiral distances relative to web length between webs present in swamp and river habitats. Webs from swamps display larger spiral distances relative to web length than the ones present in rivers (Adjusted R^2 = 0.0570, p = 0.0024; Fig. 3).

Discussion

In general, orb-weaving spiders can adapt their behaviour according to environmental factors (Glover 2003; Wu *et al*. 2013). However, the particular effect of local environmental factors (biotic and abiotic) on web-building behaviour is still understudied (Eberhard 1982; Gregorič *et al*. 2011). Here, we set out to test how differences between river and swamp habitats affect the web structure on the Neotropical continental species, *T. tenuissima*. We evaluated web length, number of radii, and spiral distancing relative to web length.

There were no significant differences on the length or number radii between webs present on swamp and river habitats. Some orb weavers are known to create larger webs when there is more competition and to aggregate in areas with higher number of structures for web anchorage (Glover 2003). Nevertheless, we found a higher number of webs in the swamps compared to the rivers, but the size of the webs did not vary significantly. Regarding the number of radii, we found a non-significant tendency (p = 0.0818) for more radii in those webs present on riverbanks. The fact that radii are support structures (Zschokke 1999; Blackledge & Gillespie 2004), could explain why in an area more exposed to the wind, such as rivers, webs would tend to have more of them (Wu *et al*. 2013). Previous evidence suggests that orb weaving spiders invest more on structural support on webs placed in rivers (Gregorič *et al*. 2011), which is congruent with the tendency described for *T. tenuissima*. However, an increased sample size would be required to resolve if this tendency remains non-significant or reaches statistical significance.

In terms of spiral spacing relative to web length, there was a significant difference between habitats with less distance in river-side webs with respect to those in swamps (p = 0.0024). Klecka (2015) provided evidence for differences in potential prey-species composition between swamps and rivers in a similar environment to the one in this study. This differential resource availability could be a factor to explain the web differentiation detected between swamps and rivers (Fig. 3). It has been previously suggested that webs with a denser mesh might be more effective in absorbing the kinetic energy of moving prey (Sensenig *et al*. 2003) and capturing larger organisms (Blackledge & Zevenbergen 2006), then it could be possible that there is an abundance of larger prey in the rivers compared to the swamps.

There are also habitat-specific modifications described for orb weavers on aquatic environments, in those cases the spiders use large amounts of silk to resist potential structural damages produced by the environmental conditions of large rivers (Gregorič *et al*. 2011). These types of modifications were not assessed on this study.

The small number of *T. elongata* and *T. mexicana* identifiable specimens prevented us to explicitly evaluate the effect of species co-occurrence on web structure, which has been assessed for Hawaiian web building *Tetragnatha* (Blackledge & Gillespie 2004; Kennedy *et al*. 2019). In that case, the presence of species from the same genus was the factor that influenced web structure. However, a key difference between the continental *Tetragnatha* at La Selva and the Hawaiian *Tetragnatha* is the fact that the latter are closely related and had differentiated in the context of an adaptive radiation. This is not the case for the widespread continental species from Costa Rica. Therefore, web structure changes due to interspecific competition might not be present on the species from La Selva. Another possibility is that resources are not limited at La Selva and, despite all *Tetragnatha* occupying the same niche, the selective pressure due to competition is low so it does not result in web structure differentiation.

In summary, the observed web differentiation due to environmental conditions is congruent with previous studies which suggest that orb-weaving spiders differentiate their webs according to specific conditions present in different habitat types (Wu *et al*. 2003; Blamires, Thompson & Hochuli 2007; Gregorič *et al*. 2011). Further studies with a larger sample size of *T. tenuissima*, including other *Tetragnatha* species, assessing prey availability, and measuring specific habitat conditions will provide a more complete and detailed understanding to the relative effect of these factors on web architecture.

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References

APPELHANS, T., DETSCH, F., REUDENBACH, C. & WOELLAUER, S. 2020: *mapview: Interactive Viewing of Spatial Data in R. R package version 2.9.0.*, online at https://cran.rproject.org/web/packages/mapview

BANKS, N. 1909: Arachnida from Costa Rica. *Proceedings of the Academy of Natural Sciences of Philadelphia* **61**: 194–234.

BANKS, N. 1913: Notes on some Costa Rican Arachnida. *Proceedings of the Academy of Natural Sciences of Philadelphia* **65**: 676–687.

BATES, D., MAECHLER, M., BOLKER, B. & WALKER, S. 2015: *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-8*, online at https://cran.rproject.org/web/ packages/lme4

BLACKLEDGE, T. A. & ZEVENBERGEN, J. M. 2006: Mesh width influences prey retention in spider orb webs. *Ethology* **112**: 1194–1201.

BLACKLEDGE, T. A., BINFORD, G. J. & GILLESPIE, R. G. 2003: Resource use within a community of Hawaiian spiders (Araneae: Tetragnathidae). *Annales Zoologici Fennici* **40**: 293–303.

BLACKLEDGE, T. A. & GILLESPIE, R. G. 2004: Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. *Proceedings of the National Academy of Sciences of the USA* **101**: 16228–16233.

BLAMIRES, S. J. 2020: Biomechanical costs and benefits of sit-and-wait foraging traps. *Israel Journal of Ecology and Evolution* **66**: 5–14.

BLAMIRES, S. J., CHAO, Y. C., LIAO, C. P. & TSO, I. M. 2011: Multiple prey cues induce foraging flexibility in a trap-building predator. *Animal Behaviour* **81**: 955–961.

BLAMIRES, S. J., THOMPSON, M. B. & HOCHULI, D. F. 2007: Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): do they compromise foraging success for predator avoidance? *Austral Ecology* **32**: 551–563.

BROWN, K. M. (1981: Foraging ecology and niche partitioning in orb-weaving spiders. *Oecologia* **50**: 380–385.

CHENG, J., KARAMBELKAR, B. & XIE, Y. 2021: *leaflet: Create Interactive Web Maps with the JavaScript 'Leaflet' Library. R package version 2.0.4.1.*, online at https://CRAN.R-project.org/ package=leaflet

CLARK, D. B. & CLARK, D. A. 2000: Landscape-scale variation in forest structure and biomass in a tropical rain forest. *Forest Ecology and Management* **137**: 185–198.

EBERHARD, W. G. 1982: Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* **36**: 1067–1095.

GILLESPIE, R. G. 1987: The role of prey availability in aggregative behaviour of the orb weaving spider *Tetragnatha elongata*. *Animal Behaviour* **35**: 675–681.

GREGORIČ, M., AGNARSSON, I., BLACKLEDGE, T. A. & KUNTNER, M. 2011: How did the spider cross the river? Behavioral adaptations for river-bridging webs in *Caerostris darwini* (Araneae: Araneidae). *PLoS One* **6**: e26847.

GILLESPIE, R. 2004: Community assembly through adaptive radiation in Hawaiian spiders. *Science* **303**: 356–359.

GLOVER, N. 2013: The habitat preferences of web building spiders. *The Plymouth Student Scientist* **6**: 363–375.

KENNEDY, S., LIM, J. Y., CLAVEL, J., KREHENWINKEL, H. & GILLESPIE, R. G. 2019: Spider webs, stable isotopes and molecular gut content analysis: Multiple lines of evidence support trophic niche differentiation in a community of Hawaiian spiders. *Functional Ecology* **33**: 1722–1733.

KLECKA, J. 2015: Aquatic insects of a lowland rainforest in Papua New Guinea: assemblage structure in relation to habitat type. *Biologia* **70**: 1621–1630.

NASIR, M. D. M. 2016: *Distribution of spiders in Malaysia with special emphasis of the systematics and ecology of the orb-web spider* (*Araneae: Tetragnathidae*). PhD thesis, University of Malaya.

OKUMA, C. 1992: Notes on the Neotropical and Mexican species of *Tetragnatha* (Araneae: Tetragnathidae) with descriptions of three new species. *Journal of the Faculty of Agriculture Kyushu University* **36**: 219–243.

R CORE TEAM 2013: *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing, online at http://www.R-project.org

ROMERO, A., O'NEILL, B. J., TIMM, R. M., GEROW, K. G. & McCLEARN, D. 2013: Group dynamics, behavior, and current and historical abundance of peccaries in Costa Rica's Caribbean lowlands. *Journal of Mammalogy* **94**: 771–791.

PEBESMA, E. 2018: Simple features for R: standardized support for spatial vector data. *The R Journal* **10**: 439–446.

SENSENIG, A. T., LORENTZ, K. A., KELLY, S. P. & BLACKLEDGE, T. A. 2012: Spider orb webs rely on radial threads to absorb prey kinetic energy. *Journal of The Royal Society Interface* **9**: 1880–1891.

WICKHAM, H., FRANÇOIS, R., HENRY, L. & MÜLLER, K. 2018: *dplyr: A Grammar of Data Manipulation. R package version 0.7.6.*, online at https://cran.r-project.org/web/ packages/dplyr

WU, C. C., BLAMIRES, S. J., WU, C. L. & TSO, I. M. 2013: Wind induces variations in spider web geometry and sticky spiral droplet volume. *Journal of Experimental Biology* **216**: 3342–3349.

YOSHIDA, M. 1981: Preliminary study on the ecology of three horizontal orb weavers *Tetragnatha praedonia*, *T. japonica*, and *T. pinicola* (Araneae: Tetragnathidae). *Acta Arachnologica* **30**: 49–64.

ZSCHOKKE, S. 1999: Nomenclature of the orb-web. *Journal of Arachnology* **27**: 542–546.