

Population and individual trophic niche of two sympatric cobweb spiders, *Nihonhimea tesselata* and *Tidarren haemorrhoidale* (Araneae: Theridiidae)

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Abstract. Diet composition of spiders may depend on several factors, such as the relative abundance of potential prey, microhabitat selection, structure and physical properties of webs, adaptations to attract specific prey, among others. Variation in diet composition is probably highly influenced by individual's spatial distribution and web design. In this study, we evaluated the population trophic niche breadths of two sympatric cobweb spiders, *Nihonhimea tesselata* (Keyserling, 1884) and *Tidarren haemorrhoidale* (Bertkau, 1880) (Theridiidae). These species build distinct webs in an area of *Eucalyptus* monoculture in southeastern Brazil. We collected their prey and also recorded parameters of webs like a height from the ground, distance from tree trunks, and distribution across the *Eucalyptus* stand. The diet of the two species was highly distinct. However, diet similarity was not correlated with the distance between webs. There was also no spatial segregation between species within the forest stand. However, *N. tesselata* used more distal portion of *Eucalyptus* branches than *T. haemorrhoidale*, which usually attached several threads to the tree trunk. In addition, diet restriction of *T. haemorrhoidale* may also be determined by the use of gumfooted threads attached to tree trunks (predominantly capturing ants), while aerial webs constructed by *N. tesselata* are more efficient at intercepting several groups of flying insects. Together, these differences in microhabitat and web design allowed effective resource partitioning among these two dominant predators in the studied plantation forest.

Keywords: Diet, web design, microhabitat selection, spatial distribution, prey capture.

Most spider species are euryphagous predators, consuming a wide variety of prey types and sizes (Nentwig 1987; Pekár et al. 2012). Even for those species, however, trophic niches may be constrained by a number of factors, such as morphological traits (Nentwig & Wissel 1986), physical properties of web threads and distribution of their viscid components (Blackledge et al. 2005; Sensenig et al. 2010; Harmer et al. 2011; Diaz et al. 2018), social structure (Nentwig 1985; Guevara et al. 2011), microhabitat selection (Herberstein 1998), and prey capturing behaviors (Li & Jackson 1996; Barrantes & Weng 2006; Souza et al. 2007). In addition, individual trophic niches within euryphagous species may be relatively narrow when compared with the population niche owing to specific nutrient requirements (Higgins & Goodnight 2010; Toft 2013), variation in microhabitat selection (Henaut et al. 2006), and individual body size (Murakami 1983). Selection of specific microhabitats placed 150 cm above ground, for example, determined the interception of large insects by individuals of *Leucauge venusta* Walckenaer, 1842 (Tetragnathidae) in a coffee plantation in southern Mexico. Individuals with webs placed 1 m above the ground captured smaller insects, but at a higher frequency (Henaut et al. 2006).

Another important variable determining types and sizes of insects intercepted is web design (Sandoval 1994; Watanabe 2001). Most studies on the influence of web design in prey interception and retention are restricted to orb-webs (Herberstein & Heiling 1998; Blackledge 2011; Blackledge et al. 2011). The bidimensional structure of these webs is particularly suitable for the evaluation of effects of each web component on capture efficiency. Mesh width, for example, may influence retention times of intercepted insects and it is possible that

individual spiders can target specific taxa of prey by opting for wide or narrow spacing between adhesive spirals (Sandoval 1994; Blackledge & Zevenbergen 2006; Blackledge & Eliason 2007). In addition, some orb-weaver species present specific features in web construction, such as ensuring vertical asymmetry and elongation (Eberhard 1975), constructing a shelter (Moura et al. 2016) or a free sector (Xavier et al. 2017), adding specific chemical compounds (Eberhard 1980; Yeargan 1988), and possibly amplifying power by storing elastic energy in silk (Han et al. 2019), which may determine a higher frequency of interception of particular prey types.

Considering that even intricacies of the bidimensional orb-web design may influence prey interception, it is likely that the strong variation in web design in other spider groups may lead to variations in the diet even between sympatric species sharing similar microhabitats. Webs of theridiid species, for example, are very diversified. They include non-viscid three-dimensional structures with gumfooted lines attached to the substrate, tangles constructed above thick bowl-shaped sheets, complex structures covered by viscid droplets, and thick sheets connected with anchor threads used as knockdown traps, among others (Benjamin & Zschokke 2003; Eberhard et al. 2008). The effectiveness of each of web design in the interception of specific types and sizes of prey is probably very distinct. Finally, variation in diet may be observed among individuals belonging to different populations of these species due to spinning plasticity (Zevenberger et al. 2008), variation in individual aggressiveness, and microhabitat selection (Costa-Pereira & Pruitt 2019).

In this study, we investigated microhabitat selection and diet patterns of two sympatric species of cobweb spiders, *Nihonhimea tesselata* (Keyserling, 1884) and *Tidarren haemorrhoidale*

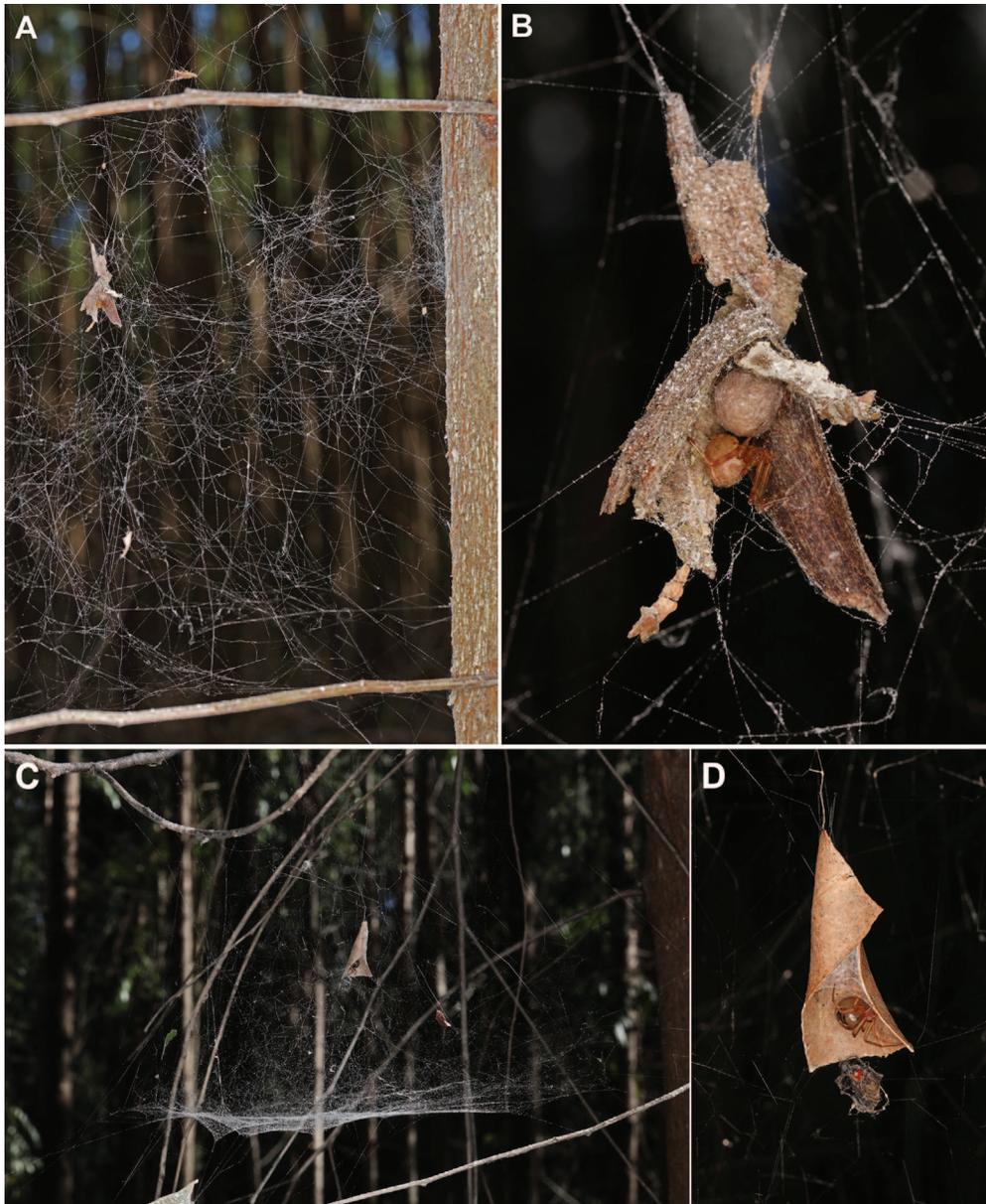


Figure 1.—Webs of the two species studied. (A) and (B) *Tidarren haemorrhoidale*; (C) and (D) *Nihonhimea tessellata*.

(Bertkau, 1880), in an area under *Eucalyptus* silviculture in southeastern Brazil. The webs of *N. tessellata* are structured as aerial sheets with a mesh above and a retreat composed of a curled dry leaf attached to threads in the center of the mesh. *Tidarren haemorrhoidale* females also build irregular tangles that support a similar shelter, but there is no sheet in their webs. Instead, several gumfooted threads connect the tangle to the surface of the tree trunk or branches. Both species build their webs attached to *Eucalyptus* trees. We hypothesized that differences in web design, microhabitat or position within the forest stand could explain differences in the diet of these species.

METHODS

Study area.—The study was conducted in a *Eucalyptus* plantation at Fazenda Nova Monte Carmelo (FNMC;

18°45'11"S, 47°51'28"W), Estrela do Sul, MG, Brazil. The areas covered by *Eucalyptus* in the FNMC are interspersed by fragments of Cerrado vegetation, but our research was restricted to regions within the *Eucalyptus* monoculture. All webs were located during the day among rows of *Eucalyptus* trees in an area approximately 42,000 m².

Spider species.—*Tidarren haemorrhoidale* has a wide geographic distribution, occurring from the USA to Argentina (WSC 2019). Their webs are composed of an irregular structure of threads connected to the vegetation at many points and support a shelter, formed by a dry rolled leaf (Fig. 1A, Benjamin & Zschokke 2003; Eberhard et al. 2008). The web presents several gumfooted threads attached to the substrate below the tangle.

The genus *Nihonhimea* was described by Yoshida (2016), and it is currently composed of three species, which were

previously placed under *Parasteatoda* Archer, 1946. *Nihonhi-mea* is closely related to *Tidarren*, according to the phylogeny presented by Eberhard et al. (2008). Populations of *N. tessellata* are restricted to the Neotropics, occurring from Mexico to Paraguay (WSC 2019). Webs spun by *N. tessellata* have been previously described by Benjamin and Zschokke (2003), and included in the *Coleosoma*-type category (see also Jörger & Eberhard 2007). Webs in this category consist of a dense sheet connected with anchor threads to vegetation and lack any sticky elements (gumfooted lines or viscid threads). Threads located above the sheet function as a Knock-down trap (Fig. 1C) (Benjamin & Zschokke 2003). Individuals of both species rarely change web position after adulthood, repairing damage when necessary to maintain web integrity and efficiency. Long lasting webs allowed the conduction of periodic inspections to collect prey.

Diet.—We individually marked all the webs found in the area to conduct periodic inspections searching for prey. During each inspection, we collected all prey items being manipulated or consumed by the spiders by carefully removing their corpses from the webs using tweezers to minimize web damages. We conducted all 20 inspections of webs in the morning, between 8:00 and 11:00, from June to July 2016. The interval between sampling expeditions was 3 days. We identified all prey items to the level of order, in the laboratory. The family Formicidae was isolated from other Hymenopteran families because its foraging behavior is different, which involves active walking on the trunk.

To access overall differences between *N. tessellata* and *T. haemorrhoidale* diets, we conducted a permutational multivariate analysis (PERMANOVA), using prey captured as the response variable. We performed the data analysis in the software R, version 3.5.0. (R Development Core Team 2019), using the ‘vegan’ package (Oksanen et al. 2019).

Spatial position and microhabitat selection.—We recorded the spatial position of all webs of the two species found in an area of 160 m × 260 m (41,600 m²) in the *Eucalyptus* understory. To conduct this procedure, we considered the first tree in the area as having the position X = 0 m and Y = 0 m in a grid. As the trees are equally spaced in the area (3 meters from each other), we could determine each web position by counting the number of trees on both axes from the initial point of the grid to the web location. Based on this, we calculated the distances between all the webs. For each web, we also recorded the height from the ground and the distance from the trunk of the *Eucalyptus* where the web was attached. These measures were considered as a microhabitat component of spiders distribution.

To calculate the web volume, we used the polyhedron that most resembled the shape of the webs for each spider species. We measured the height (*h*), the longest (*a*) and the shortest (*b*) diameters of the base of the webs of *N. tessellata*. To calculate the web volume (*V*), we used the equation of a cone with an elliptic base: $V = \pi/3 * h * a/2 * b/2$. For webs of *T. haemorrhoidale*, we used the formula of a truncated cone. We measured the height (*a*), the shortest diameter of the base (*b*), the longest diameter of the base (*c*) and the depth (*d*) to apply the equation: $V = [(b + c) * a/2] * d$. Then, *t*-tests were used to determine if there were any differences between the species in terms of the volume and microhabitat position of webs. In

order to determine if the spatial distribution of *N. tessellata* and *T. haemorrhoidale* webs influences diet composition, a Mantel test was performed, correlating the matrices of the distance between webs and diet dissimilarity. The data of the first matrix constitute the linear distances between all pairs of sampled webs (Euclidean distances) and the second matrix involves the Bray-Curtis dissimilarity of the diet overlap between pairs of webs. Clark-Evans tests of aggregation with a Donnelly’s correction were performed to evaluate the web distribution of spider species in the study area. We excluded webs in which only one prey was collected from spatial analyses. All data analyses were conducted in the software R version 3.5.0 (R Development Core Team 2019), using “vegan” (Oksanen et al. 2019), “ecodist” (Goslee & Urban 2007), and “EcoSimR” packages (Gotelli et al. 2015).

RESULTS

Diet.—We collected a total of 484 prey items captured and consumed by both species. A total of 117 individuals of *N. tessellata* captured 392 insects, belonging to nine orders. Psocoptera was the most abundant (38.7%), followed by Hemiptera (18.1%) and Hymenoptera (only ants) (16.8%). The 39 individuals of *T. haemorrhoidale* captured 92 insects, also included in the nine orders, with Hymenoptera (only ants) being the most abundant (69.5%), followed by Hemiptera (11.9%) and Coleoptera (8.6%) (Fig. 2A,B). The PERMANOVA test indicated that the overall diets of *N. tessellata* and *T. haemorrhoidale* were different ($F_{1,74} = 31.71$, $P = 0.001$).

Spatial position and microhabitat selection.—The spatial distribution of *N. tessellata* webs in the study area showed no significant deviation from randomness (Clark-Evans test: $R = 1.06$, $P = 0.44$), while webs of *T. haemorrhoidale* were uniformly distributed (Clark-Evans test: $R = 1.23$, $P = 0.03$) (Fig. 3). These patterns of spatial distribution were not correlated with diets of individuals of either species (*N. tessellata*: $r = -0.08$, $P = 0.94$; *T. haemorrhoidale*: $r = 0.05$, $P = 0.30$).

All the spiders used thin branches of *Eucalyptus* trees to support their webs. At the microhabitat scale, the position of webs was different considering their distances from the trunk of trees ($t = 9.73$, d.f. = 38, $P < 0.001$; Fig. 4A). Webs of *T. haemorrhoidale* were located, on average, four times closer to the trunk than webs of *N. tessellata* (*N. tessellata*: 50.75 ± 0.83 cm; *T. haemorrhoidale*: 11.65 ± 0.33 cm; mean ± standard error). However, there was no difference in the height of webs from the ground between the spider species (*N. tessellata*: 150.60 ± 1.42 cm; *T. haemorrhoidale*: 148.60 ± 1.99 cm; $t = 0.18$, d.f. = 38, $P = 0.85$) (Fig. 4B). In addition, webs of *T. haemorrhoidale* had a volume two times greater than that of webs of *N. tessellata* (*N. tessellata*: $8,782.55 \pm 152.10$ cm³; *T. haemorrhoidale*: $18,129.15 \pm 505.39$ cm³; $t = -3.96$, d.f. = 38, $P < 0.001$).

DISCUSSION

The trophic niches of the syntopic species *N. tessellata* and *T. haemorrhoidale* were highly distinct even within this very homogenous *Eucalyptus* stand. The difference in their trophic niche may be a consequence of variation in prey interception promoted by differences in microhabitat, variation in subdu-

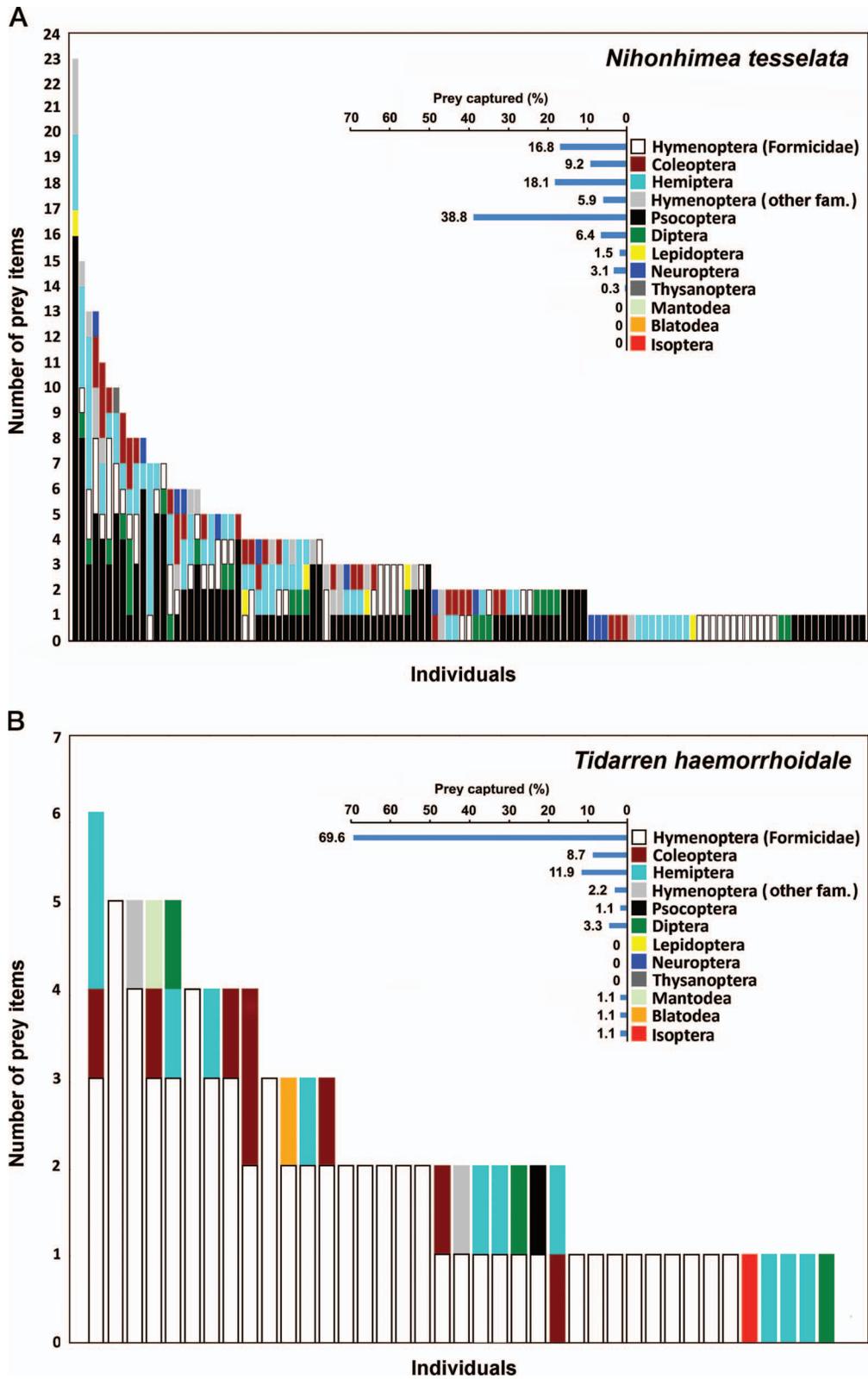


Figure 2.—Prey captured by (A) *Nihonhimea tessellata* and (B) *Tidarren haemorrhoidale*. Each color corresponds to a group of insects captured by the spiders and each vertical bar represents the diet of an individual. Horizontal bars represent the proportion of each prey type in the diet of each species.

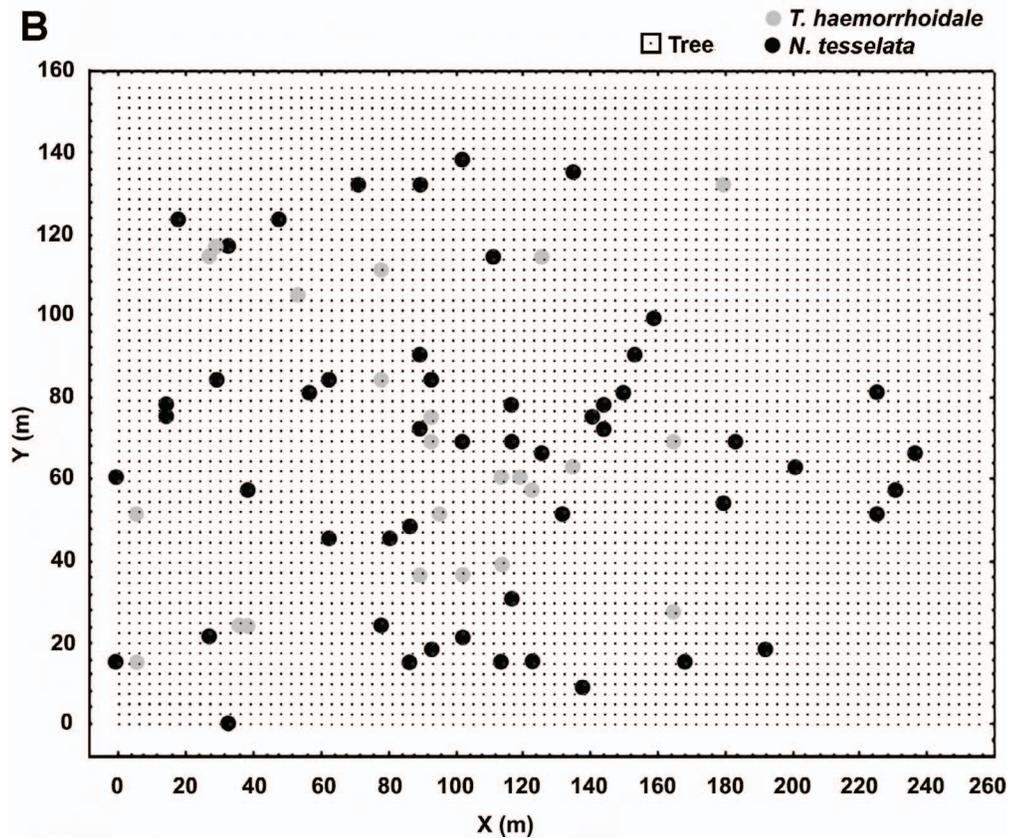


Figure 3.—Spatial distribution of trees and webs of two species. (A) *Eucalyptus* trees; (B) Bidimensional map of the distribution of webs in the scale of study area; gray dots correspond to *Tidarren haemorrhoidale* and black dots to *Nihonhimea tessellata*.

ing efficiencies for each prey type, or distinct efficiencies in the interception of each prey type by their webs. The spatial distance of webs was not correlated with diet dissimilarity in either species, indicating that intraspecific variation in prey

types is not determined by the large-scale spatial distribution of potential prey items. In the microhabitat level, the height of webs from the ground, a variable previously described as relevant for diet determination (Herberstein 1998), was similar

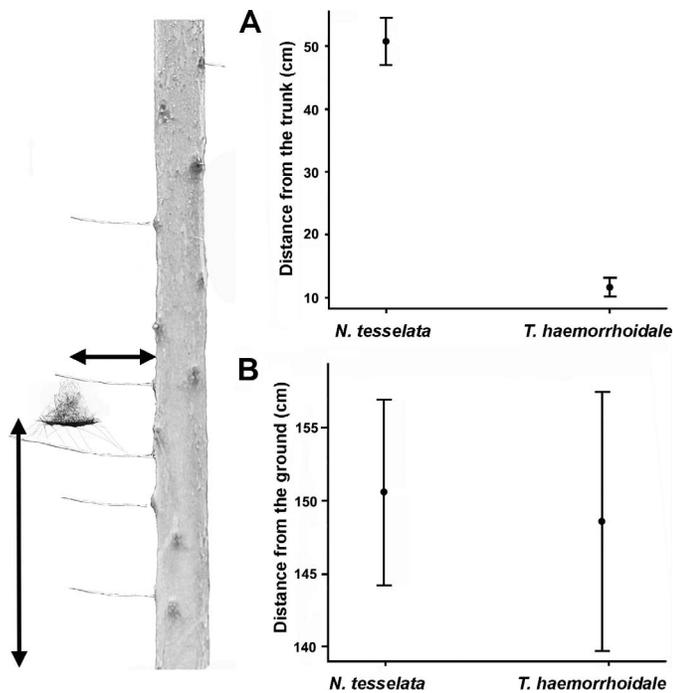


Figure 4.—Comparison between webs of spiders in relation to the distance from the *Eucalyptus* trunks (A) and from the ground (B) in a microhabitat scale. The dots represent the means, and bars the standard errors.

between species. However, there was a difference in microhabitat selection based on the distance from the tree trunks. Thus, distinctions in web design and microhabitat selection between species are likely to promote the capture of distinct types of prey. We discuss how these conditions affect prey capture and compare our findings with those on other theridiid species.

Nihonhimea tessellata captured mainly Psocoptera and winged insects, and the sum of these categories represented 83% of all prey items collected in *N. tessellata* webs. These cobweb spiders establish their webs in positions far from trunks, attached to thin branches of trees. Their webs act as traps for flying insects, and jumpers that reach the top mesh fall on the sheet and are attacked by the spider (Eberhard 1972; Barrantes & Weng 2006). Spiders from other closely related genera, such as *Cryptachaea cinnabarina* (Levi, 1963) and *Latrodectus hesperus* Chamberlin & Ivie, 1935, however, use both sheets and anchored gumfooted threads attached to the ground and nearby vegetation to capture their prey. These hunting tactics allow the interception of both flying and cursorial insects (Japyassú & Jotta 2005; Zevenberger et al. 2008). Variation in prey capture strategies within the Theridiidae is broad, including prey interception based on the construction of web structures completely covered by viscid silk, such as in *Helvibis longicauda* Keyserling, 1891 and *Chryso intervales* Gonzaga, Leiner & Santos, 2006 (Gonzaga et al. 2006), and others in which prey interception is based on a few points of viscid glue positioned in the attachment points of threads to the vegetation (gumfooted threads), which seems to be the case with *T. haemorrhoidale*. The position and architecture of webs of *T. haemorrhoidale* favor the spiders

to intercept insects that walk on tree trunks. Such insects, especially ants, represented more than 70% of this species' diet. A similar result was found for *T. haemorrhoidale* in cacao plantations in Mexico (Moreno-Mendoza et al. 2012) where the ants were captured at an even higher frequency than in our study.

Web design and microhabitat selection in *Eucalyptus* plantation by *T. haemorrhoidale* promoted the predominance of ants in its diet. However, environmental variation in prey availability may change the types of prey captured by this species. In cotton plantations, for example, *T. haemorrhoidale* has been previously reported to build webs at a lower position, between herbaceous plants (Nyffeler et al. 1988). In this situation, individuals captured mainly aphids that are abundant in the agroecosystem (Nyffeler et al. 1988). Thus, *T. haemorrhoidale* appears able to exploit distinct food resources based on their availability, being restricted by some web traits, such as the adhesive components located only in gumfooted threads. Web designs and distribution of viscid elements, however, seem to vary within the genus. For example, *Tidarren sisypoides* (Walckenaer, 1842) build their webs on plants with large leaves, and the web is composed of a dense and irregular tangle situated above a dome-shaped sheet, which is connected to the substrate. Viscid globules are present on threads of the dome and in the horizontal sheet. The upper tangle functions to knock down jumping and flying insects, which are then restrained by viscid elements in the dome-shaped sheet (Madrigal-Brenes & Barrantes 2009).

Diet was independent of the large-scale spatial distribution for both species, indicating that all insect groups consumed are evenly distributed in *Eucalyptus* plantation. Another possibility that explains this pattern is that insects may be attracted to the webs, but chemicals or specific web structures that may be involved in prey attraction are unknown in these genera. In the Theridiidae, as far as we know, the only previously described case of prey attraction involves the modified web of *Phoroncidia studio* Levi, 1964, which may attract Cecidomyiidae (Diptera) (Eberhard 1981). Within the homogenous habitat, individuals of *N. tessellata* probably select suitable microhabitats to intercept aerial insects (on the extremities of thin *Eucalyptus* branches), while individuals of *T. haemorrhoidale* select sites close to tree trunks to attach their gumfooted threads to trap ants effectively. Selection of specific microhabitats in relatively homogeneous habitats was also observed in the Linyphiidae (Harwood et al. 2001, 2003). In this case, comparison of abundances of potential prey between web construction sites and other unoccupied locations within wheat fields showed that webs are significantly more likely to be found in areas of higher prey density, around the bases of wheat stems. Thus, microhabitat selection was an important factor associated with web design to determine the prey type captured by the theridiid species.

In this study, we concluded that although *T. haemorrhoidale* and *N. tessellata* construct their webs in the same environment, they capture different prey, segregating their trophic niches, which might be important to allow the coexistence of large populations of these species in disturbed habitats, such as *Eucalyptus* monocultures. These species have differences in the position of their webs in a microhabitat level and very distinct web architectures, which probably are determining factors to

explain the interception of different types of insects. Supporting these findings, the prey type was found to be independent of the large-scale spatial distribution of webs.

ACKNOWLEDGMENTS

We thank Dr. Adalberto José dos Santos for the identification of spider species, and Dra. Vanessa Stefani Sul Moreira and Dra. Camila Vieira for many suggestions on the manuscript. Special thanks to Dr. Marcos Vinicius Sampaio for the identification of the insects. This project was supported by Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG: Proc. APQ-02984-17), Programa de Pesquisas Ecológicas de Longa Duração (CAPES-CNPq-PELD: Proc. 88887.136318/2017), Fundação de Amparo à Pesquisa do Estado de São Paulo (São Paulo Research Foundation, FAPESP: Proc. 2017/14196-5), Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES: Finance Code 001), and Conselho Nacional de Desenvolvimento Científico e Tecnológico (Proc. 300295/2016-2, Proc. 441225/2016-0, Proc. 311823/2017-3).

LITERATURE CITED

- Barrantes, G. & J.L. Weng. 2006. The prey attack behavior of *Achaearanea tessellata* (Araneae, Theridiidae). *Journal of Arachnology* 34:456–466.
- Benjamin, S.P. & S. Zschokke. 2003. Webs of theridiid spiders: construction, structure and evolution. *Biological Journal of the Linnean Society* 78:293–305.
- Blackledge, T.A. 2011. Prey capture in orb weaving spiders: are we using the best metric? *Journal of Arachnology* 39:205–210.
- Blackledge, T.A. & C.M. Eliason. 2007. Functionally independent components of prey capture are architecturally constrained in spider orb webs. *Biology Letters* 3:456–458.
- Blackledge, T.A. & J.M. Zevenbergen. 2006. Mesh width influences prey retention in spider orb webs. *Ethology* 112:1194–1201.
- Blackledge, T.A., M. Kuntner & I. Agnarsson. 2011. The form and function of spider orb webs: evolution from silk to ecosystems. *Advances in Insect Physiology* 41:175–262.
- Blackledge, T.A., A.P. Summers & C.Y. Hayashi. 2005. Gumfooted lines in black widow cobwebs and the mechanical properties of spider capture silk. *Zoology* 108:41–46.
- Costa-Pereira, R. & J. Pruitt. 2019. Behaviour, morphology and microhabitat use: what drives individual niche variation. *Biology Letters* 15:20190266.
- Diaz, C., A. Tanikawa, T. Miyashita, A. Dhinojwala & T.A. Blackledge. 2018. Silk structure rather than tensile mechanics explains web performance in the moth-specialized spider, *Cyrtarachne*. *Journal of Experimental Zoology Part A: Ecological and Integrative Physiology* 329:120–129.
- Eberhard, W.G. 1972. Observations on the biology of *Achaearanea tessellata* (Araneae: Theridiidae). *Psyche* 79:209–212.
- Eberhard, W.G. 1975. The ‘inverted ladder’ orb web of *Scoloderus* sp. and the intermediate orb of *Eustala* (?) sp. (Araneae: Araneidae). *Journal of Natural History* 9:93–106.
- Eberhard, W.G. 1980. The natural history and behavior of the bolas spider, *Mastophora dizzydeani* sp. n. (Araneae). *Psyche* 87:143–170.
- Eberhard, W.G. 1981. The single line web of *Phoroncidia studo* Levi (Araneae, Theridiidae): a prey attractant? *Journal of Arachnology* 9:229–232.
- Eberhard, W.G., I. Agnarsson & H.W. Levi. 2008. Web forms and the phylogeny of theridiid spiders (Araneae: Theridiidae): chaos from order. *Systematics and Biodiversity* 6:415–475.
- Gonzaga, M.O., N.O. Leiner & A.J. Santos. 2006. On the stick cobwebs of two theridiid spiders (Araneae: Theridiidae). *Journal of Natural History* 40:293–306.
- Goslee, S.C. & D.L. Urban. 2007. The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software* 22:1–19.
- Gotelli, N.J., E.M. Hart & A.M. Ellison. 2015. EcoSimR: Null model analysis for ecological data. R package version 0.1.0
- Guevara, J., M.O. Gonzaga, J. Vasconcellos-Neto & L. Avilés. 2011. Sociality and resource use: insights from a community of social spiders in Brazil. *Behavioral Ecology* 22:630–638.
- Han, S.I., H.C. Astley, D.D. Maksuta & T.A. Blackledge. 2019. External power amplification drives prey capture in a spider web. *Proceedings of the National Academy of Sciences* 116(24) doi:10.1073/pnas.1821419116.
- Harmer, A.M.T., T.A. Blackledge, J.S. Madin & M.E. Herberstein. 2011. High-performance spider webs: integrating biomechanics, ecology and behaviour. *Journal of The Royal Society Interface* 8:457–471.
- Harwood, J.D., K.D. Sunderland & W.O.C. Symondson. 2001. Living where the food is: web location by linyphiid spiders in relation to prey availability in winter wheat. *Journal of Applied Ecology* 38:88–99.
- Harwood, J.D., K.D. Sunderland & W.O.C. Symondson. 2003. Web-location by linyphiid spiders: prey-specific aggregation and foraging strategies. *Journal of Animal Ecology* 72:745–756.
- Henaut, Y., J.A. Garcia-Ballinas & C. Alauzet. 2006. Variation in web construction in *Leucauge venusta* (Araneae, Tetragnathidae). *Journal of Arachnology* 34:234–240.
- Herberstein, M.E. 1998. Implications of microhabitat selection on prey capture for the web spider *Nerienne radiata* (Walckenaer) (Araneae: Linyphiidae). Pp. 197–202. *In Proceedings of the 17th European Colloquium of Arachnology*. (P.A. Selden, ed.). Edinburgh.
- Herberstein, M. & A.M. Heiling. 1998. Does mesh height influence prey length in orb-web spiders (Araneae)? *European Journal of Entomology* 95:367–371.
- Higgins, L. & C. Goodnight. 2010. *Nephila clavipes* females have accelerating dietary requirements. *Journal of Arachnology* 38:150–152.
- Japyassú, H.F. & E.G. Jotta. 2005. Forrageamento em *Achaearanea cinnabarina* Levi 1963 (Araneae, Theridiidae) e evolução da caça em aranhas de teia irregular. *Biota Neotropica* 5:1–15.
- Jörger, K.M. & W.G. Eberhard. 2007. Web construction and modification by *Achaearanea tessellata* (Araneae, Theridiidae). *Journal of Arachnology* 34:511–523.
- Li, D. & R.R. Jackson. 1996. Prey preferences of *Portia fimbriata*, an araneophagic, web-building jumping spider (Araneae: Salticidae) from Queensland. *Journal of Insect Behavior* 9:613–642.
- Madrigal-Brenes, R. & G. Barrantes. 2009. Construction and function of the web of *Tidarren sisypheoides* (Araneae: Theridiidae). *Journal of Arachnology* 37:306–311.
- Moreno-Mendoza, S.D., G. Ibarra-Núñez, E.R. Chamé-Vázquez & F.J. Valle-Mora. 2012. Gama de presas capturadas por cuatro especies de arañas tejedoras (Arachnida: Araneae) en un agroecosistema de cacao en Chiapas, México. *Tropical and Subtropical Agroecosystems* 15:457–469.
- Moura, R.R., L.C. Leal & T.G. Kloss. 2016. Does nutritional status constrain adoption of more costly and less risky foraging behaviour in an Amazonian shelter-building spider? *Journal of Natural History* 50:2829–2837.
- Murakami, Y. 1983. Factors determining the prey size of the orb-web spider, *Argiope amoena* (L. Koch) (Argiopidae). *Oecologia* 57:72–77.
- Nentwig, W. 1985. Social spiders catch larger prey: a study of

- Anelosimus eximius* (Araneae: Theridiidae). Behavioral Ecology and Sociobiology 17:79–85.
- Nentwig, W. 1987. The prey of spiders. Pp. 251–255. In Ecophysiology of Spiders (W. Nentwig, ed.). Springer-Verlag, Berlin.
- Nentwig, W. & C. Wissel. 1986. A comparison of prey lengths among spiders. Oecologia 68:595–600.
- Nyffeler, M., D.A. Dean & W.L. Sterling. 1988. Prey records of the web-building spiders *Dictyna segregata* (Dictynidae), *Theridion australe* (Theridiidae), *Tidarren haemorrhoidale* (Theridiidae), and *Frontinella pyramitela* (Linyphiidae) in a cotton agroecosystem. Southwestern Naturalist 33:215–218.
- Oksanen, J., F.G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn et al. 2019. vegan: Community Ecology Package. R package version 2.5–4.
- Pekár, S., J. Coddington & T. Blackledge. 2012. Evolution of stenophagy in spiders (Araneae): evidence based on the comparative analysis of spider diets. Evolution: International Journal of Organic Evolution 66:776–806.
- R Development Core Team, R. 2019. R: A language and environment for statistical computing.
- Sandoval, C. 1994. Plasticity in web design in the spider *Parawixia bistriata*: A response to variable prey type. Functional Ecology 8:701–707.
- Sensenig, A., I. Agnarsson & T.A. Blackledge. 2010. Behavioural and biomaterial coevolution in spider orb webs. Journal of Evolutionary Biology 23:1839–1856.
- Souza, A.L.T., M.O. Gonzaga & J. Vasconcelos-Neto. 2007. Prey capture behaviour in the social spider *Anelosimus eximius* (Araneae: Theridiidae): responses to prey size and type. Ethology 113:856–861.
- Toft, S. 2013. Nutritional aspects of spider feeding. Pp. 373–384. In Spider Ecophysiology (W. Nentwig, ed.). Springer-Verlag.
- Watanabe, T. 2001. Effects of web design on the prey capture efficiency of the uloborid spider *Octonoba sybotides* under abundant and limited prey conditions. Zoological Science 18:585–590.
- World Spider Catalog. 2019. WSC Version 20.0. Natural History Museum, Bern. Online at <http://wsc.nmbe.ch>
- Xavier, G.M., R.R. Moura & M.O. Gonzaga. 2017. Orb web architecture of *Wixia abdominalis* O. Pickard-Cambridge, 1882 (Araneae: Araneidae): intra-orb variation of web components. Journal of Arachnology 45:160–165.
- Yeargan, K.V. 1988. Ecology of a bolas spider, *Mastophora hutchinsoni*: phenology, hunting tactics, and evidence for aggressive chemical mimicry. Oecologia 74:524–530.
- Yoshida, H. 2016. *Parasteatoda*, *Campanicola*, *Cryptachaea* and two new genera (Araneae: Theridiidae) from Japan. Bulletin of the Yamagata Prefectural Museum 34:13–30.
- Zevenbergen, J.M., N.K. Schneider & T.A. Blackledge. 2008. Fine dining or fortress? Functional shifts in spider web architecture by the western black widow *Latrodectus hesperus*. Animal Behaviour 76:823–829.

Manuscript received 18 July 2019, revised 22 November 2019.