Universidade Federal de Uberlândia

Instituto de Biologia

Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais

INFLUÊNCIA DOS PADRÕES ARQUITETURAIS DE TEIAS ORBICULARES SOBRE A EFICIÊNCIA DE INTERCEPTAÇÃO E RETENÇÃO DE PRESAS

Gabriel Máximo Xavier

2020

Gabriel Máximo Xavier

INFLUÊNCIA DOS PADRÕES ARQUITETURAIS DE TEIAS ORBICULARES SOBRE A EFICIÊNCIA DE INTERCEPTAÇÃO E RETENÇÃO DE PRESAS

Tese apresentada à Universidade Federal de Uberlândia, como parte das exigências para a obtenção do título de Doutor em Ecologia e Conservação de Recursos Naturais.

Orientador
Prof. Dr. Marcelo de Oliveira Gonzaga

UBERLÂNDIA

Janeiro – 2020

Ficha Catalográfica Online do Sistema de Bibliotecas da UFU
com dados informados pelo(a) próprio(a) autor(a).

X3
2020

Xavier, Gabriel Máximo, 1991-
INFLUÊNCIA DOS PADRÕES ARQUITETURAIS DE TEIAS ORBICULARES SOBRE A EFICIÊNCIA DE INTERCEPTAÇÃO E RETENÇÃO DE PRESAS [recurso eletrônico] / Gabriel Máximo Xavier. - 2020.

Orientador: Marcelo de Oliveira Gonzaga.
Tese (Doutorado) - Universidade Federal de Uberlândia, Pós-graduação em Ecologia e Conservação de Recursos Naturais.
Modo de acesso: Internet.
Disponível em: http://doi.org/10.14393/ufu.te.2020.145
Inclui bibliografia.

1. Ecologia. I. Gonzaga, Marcelo de Oliveira,1974-, (Orient.). II. Universidade Federal de Uberlândia. Pós-graduação em Ecologia e Conservação de Recursos Naturais. III. Título.

CDU: 574

Bibliotecários responsáveis pela estrutura de acordo com o AACR2:
Gizele Cristine Nunes do Couto - CRB6/2091
Nelson Marcos Ferreira - CRB6/3074

UNIVERSIDADE FEDERAL DE UBERLÂNDIA
Coordenação do Programa de Pós-Graduação em Ecologia e Conservação de Recursos Naturais
Av. Pará, 1720, Bloco 2D, Sala 26 - Bairro Umuarama, Uberlândia-MG, CEP 38405-320
Telefone: (34) 3225-8641 - www.ppgeco.ib.ufu.br - ecologia@umuarama.ufu.br

ATA DE DEFESA - PÓS-GRADUAÇÃO

Programa de Pós-Graduação em:	Ecologia e Conservação de Recursos Naturais				
Defesa de:	Tese, número 68, PPGECRN				
Data:	três de março de dois mil e vinte	Hora de início:	14:00	Hora de encerramento: 17:25	17:25
Matrícula do Discente:	11613ECR007				
Nome do Discente:	Gabriel Máximo Xavier				
Título do Trabalho:	Influência dos padrões arquiteturais de teias orbiculares sobre a eficiência de interceptação e retenção de presas				
Área de concentração:	Ecologia				
Linha de pesquisa:	Ecologia comportamental e de interações				
Projeto de Pesquisa de vinculação:	Ecologia comportamental e cuidado parental em Arachnida				

Reuniu-se na Sala 14A, Bloco 2D, Campus Umuarama, da Universidade Federal de Uberlândia, a Banca Examinadora, designada pelo Colegiado do Programa de Pós-graduação em Ecologia e Conservação de Recursos Naturais, assim composta: Professores Doutores: Vanessa Stefani Sul Moreira - INBIO/UFU; Jamir Afonso do Prado Júnior - INBIO/UFU; Yuri Fanchini Messas - Unicamp; Thiago Gechel Kloss - UEMG; Marcelo de Oliveira Gonzaga - INBIO/UFU, orientador(a) do(a) candidato(a).

Iniciando os trabalhos o(a) presidente da mesa, Dr(a). Marcelo de Oliveira Gonzaga, apresentou a Comissão Examinadora e o candidato(a), agradeceu a presença do público, e concedeu ao Discente a palavra para a exposição do seu trabalho. A duração da apresentação do Discente e o tempo de arguição e resposta foram conforme as normas do Programa.

A seguir o senhor(a) presidente concedeu a palavra, pela ordem sucessivamente, aos(às) examinadores(as), que passaram a arguir o(a) candidato(a). Ultimada a arguição, que se desenvolveu dentro dos termos regimentais, a Banca, em sessão secreta, atribuiu o resultado final, considerando o(a) candidato(a):

Aprovado(a).

Esta defesa faz parte dos requisitos necessários à obtenção do título de Doutor.

O competente diploma será expedido após cumprimento dos demais requisitos, conforme as normas do Programa, a legislação pertinente e a regulamentação interna da UFU.

Nada mais havendo a tratar foram encerrados os trabalhos. Foi lavrada a presente ata que após lida e achada conforme foi assinada pela Banca Examinadora.

Documento assinado eletronicamente por **Marcelo de Oliveira Gonzaga**, **Presidente**, em 03/03/2020, às 17:27, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do Decreto nº 8.539, de 8 de outubro de 2015.

Documento assinado eletronicamente por **Jamir Afonso do Prado Junior**, **Membro de Comissão**, em 03/03/2020, às 17:28, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do Decreto nº 8.539, de 8 de outubro de 2015.

Documento assinado eletronicamente por **Yuri Fanchini Messas**, **Usuário Externo**, em 03/03/2020, às 17:30, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do Decreto nº 8.539, de 8 de outubro de 2015.

Documento assinado eletronicamente por **Vanessa Stefani Sul Moreira**, **Membro de Comissão**, em 03/03/2020, às 17:31, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do Decreto nº 8.539, de 8 de outubro de 2015.

Documento assinado eletronicamente por **Thiago Gechel Kloss**, **Usuário Externo**, em 03/03/2020, às 17:53, conforme horário oficial de Brasília, com fundamento no art. 6º, § 1º, do Decreto nº 8.539, de 8 de outubro de 2015.

A autenticidade deste documento pode ser conferida no site https://www.sei.ufu.br/sei/controlador_externo.php?acao=documento_conferir&id_orgao_acesso_externo=0, informando o código verificador **1845587** e o código CRC **84E621CC**.

ÍNDICE

AGRADECIMENTOS 1
RESUMO GERAL 2
GENERAL ABSTRACT 3
INTRODUÇÃO GERAL 4
CAPÍTULO 1 8
Resumo 8
Introdução 9
Métodos 14
Resultados 19
Discussão 20
Literatura citada 23
Figura 1. 27
Figura 2. 28
Figura 3 29
Figura 4 30
Tabela 1 31
Tabela 2 32
CAPÍTULO 2 33
Resumo 33
Introdução 34
Métodos 37
Resultados 42
Discussão 45
Literatura citada 50
Figura 1. 56
Figura 2. 57
Figura 3. 58
Tabela 1 60
Tabela 2 61
Tabela 3 64
Tabela 4 65
Tabela 5 66
Material suplementar 67
CAPÍTULO 3 71
Resumo 71

Introdução 72
Métodos.. 76
Resultados 78
Discussão... 80
Literatura citada 85
Figura 1. 91
Figura 2. 92
Tabela 1. 93
Tabela 2.. 95
Material suplementar.. 97
CONSIDERAÇÕES FINAIS 104

AGRADECIMENTOS

Agradeço,

Ao Prof. Marcelo O. Gonzaga, por sua atenção, orientação e apoio ao longo de meu doutorado que foram fundamentais para a conclusão desta tese e para meu desenvolvimento como pesquisador.

A todos os colaboradores do Laboratório de Aracnologia por terem fornecido indispensável apoio ao longo destes quatro anos. Devo destacar que Adilson Quero, Felipe A. Meira, Camila Vieira e Rafael R. Moura possuem colaboração direta em meus capítulos.

Aos professores e pesquisadores que gentilmente cederam tempo e atenção para avaliar e revisar esta tese: Jamir A. do Prado Júnior, Vanessa Stefani, Thiago G. Kloss, Yuri F. Messas, Vinícius L.G. Brito e Natália O. Leiner.

Aos meus familiares, em especial os meus pais, Altamiro e Vilma, e meu irmão Guilherme, pelo imenso incentivo e apoio ao longo de meus estudos.

Ao Programa de Pesquisas Ecológicas de Longa Duração - PELD, que por meio de uma chamada CAPES-CNPq-FAPEMIG (Proc. 88887.136318/2017) me concedeu uma bolsa de doutorado para a realização desta tese.

Muito obrigado!

RESUMO GERAL

Neste estudo investigamos dois grandes aspectos da ecologia de aranhas construtoras de teias orbiculares: a captura de presas e o comportamento de construção. Além disso, como as teias mediam estas questões, dedicamos também um capítulo (Capítulo 1) a aprimorar estimadores do comprimento total de fios pegajosos em teias orbiculares, uma vez que esta variável é importante para esta linha de pesquisa. Assim, por meio de um raciocínio matemático simples chegamos a duas novas fórmulas. Estas fórmulas produziram estimativas acuradas e, assim, poderão ser usadas em conjunto em trabalhos que nesta linha de pesquisa. Quando investigamos (Capítulo 2), a influência de diferentes comportamentos e características arquiteturais das teias sobre a captura de presas, vimos que a área de captura da teia e o período das interações possuem poder preditivo sobre o tamanho dos insetos capturados. Estas variáveis, então, são discutidas como características funcionais que determinam as interações entre aranhas e suas presas. Finalmente, investigamos (Capítulo 3) o poder explicativo de tradicionais hipóteses para as decisões comportamentais das aranhas ao construir teias orbiculares. Então, aqui conduzimos uma investigação em busca de uma explicação simplificada e generalizável para os comportamentos de construção de teias de modo a corrigir estes erros analíticos provenientes de estudos prévios. Ao final vimos que, embora plausíveis, as explicações tradicionais possuem poder explicativo limitado. A necessidade de compensar o maior tempo de chegada até a presa interceptada, por sua vez, demonstra ser importante o suficiente para determinar amplamente qual é a maneira ótima de distribuir fios pegajosos ao longo da teia.

Palavras-chave: geometria, interações biológicas, aranhas, teias.

GENERAL ABSTRACT

We investigated two great issues on orb-web spiders' ecology: the prey capture and the building behaviour. As the webs mediate these issues, we also dedicate a chapter (Chapter 1) to improve the capture threads length' estimators since this variable is important to this research field. Thus, by means of a simplified mathematical reasoning, we proposed two new formulae. These formulae produced accurate estimates and, then, can be used in this type of investigation. When we assessed (Chapter 2) the influence of distinct spider behaviours and many orb-web architectural traits over the prey capture, we verified the web capture area and period of the interactions exert predictive power over the captures of insects of different sizes. Then, these variables were discussed as functional features determining the interactions between spiders and prey. Finally, we investigated (Chapter 3) the predictive power of traditional hypotheses to behavioural decisions in orb web building. Thus, we conducted an assessment in order to find a simplified and generalizable explanation to these behaviours in such way to correct analytical problems from previous studies. Ultimately, we found that, despite plausible, some of the traditional explanations have limited application. The need to compensate the greater spent time to achieve the intercepted prey, in its turn, proves to be important enough to widely which is the optimal manner to distribute the sticky threads along the web.

Keywords: geometry, biological interactions, spiders, webs.

INTRODUÇÃO GERAL

Em Ecologia, o interesse em utilizar aranhas como modelo para investigação de questões científicas abrangentes, como padrões comportamentais ligados à seleção sexual e forrageamento, evolução, padrões de riqueza e diversidade e funções desempenhadas em agroecossistemas, entre várias outras, já remonta algumas décadas (*e.g.* Wise 1993). Entretanto, a viabilidade em abordar tais questões depende muito de um conhecimento científico preliminar desenvolvido com o grupo. Hoje, entretanto, esse conhecimento adquirido e acumulado, fornece uma base mais sólida e encoraja os pesquisadores a abordarem as mais diferentes questões, desde a evolução de comportamentos particulares de determinados grupos até padrões globais de distribuição. É possível, por exemplo, estimar o papel de todo o grupo taxonômico na movimentação de matéria e energia ao longo dos ecossistemas terrestres com base em dados da literatura existente (Nyffeler & Birkhofer 2017). Além disso, filogenias (*e.g.* Scharff *et al*. 2019), padrões comportamentais gerais (*e.g.* Eberhard 2014), padrões globais de biodiversidade (*e.g.* Cardoso *et al*. 2011), interações biológicas com predadores e parasitoides (*e.g.* Eberhard & Gonzaga 2019), bem como com suas populações de presas (*e.g.* Nyffeler & Birkhofer 2017, Ludwig *et al*. 2018) são assuntos emergentes.

As diferentes famílias de aranhas construtoras de teias orbiculares constituem considerável parte da biodiversidade total de aranhas (WSC 2019), são amplamente distribuídas (Cardoso *et al.* 2011), e a forma de suas teias (Blackledge *et al.* 2011) as tornam especialmente interessantes como organismos modelo em estudos ecológicos. De fato, grande parte literatura científica sobre o grupo é dedicada a estas famílias (Foelix 2011), e tentativas de solucionar diversas questões em ecologia de aranhas tem utilizado preferencialmente este grupo como modelo, tal como a solução de *trade-offs* energéticos e comportamentais (*e.g.* Venner & Casas 2005, Blackledge 2011).

Apesar disso, grandes questões da ecologia comportamental de aranhas orbitelas, bem como a influência de padrões arquiteturais de suas teias sobre as interações com as presas, ainda permanecem em aberto. Na ecologia comportamental, por exemplo, diversas hipóteses alternativas disputam o posto de melhor explicação para os valores adaptativos e influência de restrições incidentais sobre o comportamento de construção de teias (Eberhard 2014, Xavier *et al*. 2017). Além disso, as teias orbiculares carregam mais variação estrutural e mecânica do que aparentam possuir (Blackledge *et al*. 2011). Cada tipo de fio utilizado para tecer a armadilha possui formação molecular e propriedade física específica (Harmer *et al*. 2011). Uma vez que o investimento em cada tipo de fio e sua disposição arquitetural varia na teia, intra e interespecificamente, diferentes combinações destas características devem ser capazes de determinar quais tipos de presas são mais eficientemente capturadas por cada aranha (Blackledge & Zevenbergen 2006). Entretanto, a avalição sobre estas relações ainda é preliminar e inconclusiva (Ludwig *et al*. 2018).

Portanto, a essência de minha tese está na tentativa de responder a estas amplas questões que visam esclarecer como as interações com presas são determinadas pelos padrões arquiteturais das teias (Capítulo 2) e como o comportamento de construção destas armadilhas são determinadas por diferentes valores funcionais (Capítulo 3). Justamente por trabalhar com questões abrangentes, que envolveram diversos *taxa* e com a necessidade de amostragem considerável, surgiu também a necessidade elaborar métodos mais eficientes para a coleta de dados. Se as teias orbiculares intermediam todas as nossas questões, grande parte de nosso esforço se concentrou em quantificar suas características. Por isso, antes de tudo, dedico um texto (Capítulo 1) a elaborar novos cálculos para a quantificação de características importantes das teias orbiculares. A construção desses novos cálculos surge devido às limitações impostas a este tipo de coleta de dados, tais como as computacionais e de mensuração de teias danificadas em campo. Dessa forma, apresento nas páginas a seguir estes três capítulos em formato de artigos científicos. Espero que estes novos estudos sejam de ampla utilização para outros pesquisadores e ajudem a esclarecer temas que ainda permanecem em aberto.

LITERATURA CITADA

Cardoso, P., Pekár S., Jocqué, R. & Coddington, J.A. 2011. Global Patterns of Guild Composition and Functional Diversity of Spiders. *PLoS ONE*. 6, e21710. DOI: doi.org/10.1371/journal.pone.0021710

Blackledge, T.A. 2011. Prey capture in orb weaving spiders: are we using the best metric? *Journal of Arachnology*. 39. 205-210. DOI: doi.org/10.1636/Chi10-52.1

Blackledge, T.A., Kuntner, M. & Agnarsson, I. 2011. The form and function of spider orb webs: evolution from silk to ecosystems. Pp. 175–262. In Advances in Insect Physiology (J. Casas, ed.). Burlington, Academic Press.

Blackledge, T.A. & Zevenbergen, J.M. 2006. Mesh width influences prey retention in spider orb webs. *Ethology*. 112, 1194-1201. DOI: doi.org/10.1111/j.1439-0310.2006.01277.x

Eberhard, W.G. 2014. A new view of orb webs: multiple trap designs in a single structure. *Biological Journal of the Linnean Society*. 111, 437-449. DOI: doi.org/10.1111/bij.12207

Eberhard, W.G. & Gonzaga, M.O. 2019. Evidence that *Polysphincta*-group wasps (Hymenoptera: Ichneumonidae) use ecdysteroids to manipulate the web-construction behaviour of their spider hosts. *Biological Journal of the Linnean Society*. 127 (2), 429-471. DOI: doi.org/10.1093/biolinnean/blz044

Harmer, A.M.T., Blackledge, T.A., Madin, J.S. & Herberstein, M.E. 2011. High-performance spider webs: integrating biomechanics, ecology and behaviour. *Journal of The Royal Society Interface*. 8, 457-471. DOI: doi.org/10.1098/rsif.2010.0454

Ludwig, L., Barbour, M.A., Guevara, J., Avilés, L., & González, A.L. 2018. Caught in the web: Spider web architecture affects prey specialization and spider–prey stoichiometric relationships. *Ecology and Evolution*. 8, 1-14. DOI: doi.org/10.1002/ece3.4028

Nyffeler, M. & Birkhofer, K. 2017. An estimated 400–800 million tons of prey are annually killed by the global spider community. *The Science of Nature*. 104, 30. DOI: doi.org/10.1007/s00114-017-1440-1

Venner, S., Casas, J. 2005. Spider webs designed for rare but lifesaving catches. *Proceedings of the Royal Society B*. 272, 1587-1592. DOI: doi.org/10.1098/rspb.2005.3114

Wise, D. H. 1993. Spiders in Ecological Webs. Cambridge University Press.

World Spider Catalog. 2019. World Spider Catalog, version 20.0. Natural History Museum. Bern. Accessed 09 June 2019. http://wsc.nmbe.ch

Xavier, G.M., Moura, R.R. & Gonzaga, M.O. 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. DOI: doi.org/10.1636/JoA-S-17-001.1

CHAPTER 1

TOWARDS SIMPLICITY AND ACCURACY: ASSESSING TRADITIONAL AND NEW ESTIMATORS OF ORB-WEB CAPTURE THREAD LENGTH

ABSTRACT

Before using estimators, it is essential to consider their efficiency in order to avoid bias in results. Due to the architectural and structural complexity of spider webs, some important variables involved in prey capture are usually estimated based on a few measurements obtained from photographs. One of these variables is the capture thread length (CTL), which can provide valuable information on foraging behaviours and the energetic investment in prey capture. However, many of the webs found in the field are damaged, and there is no automatic method to measure the CTL. Therefore, the determination of a simple and accurate estimator of this variable is important to several studies involving spider foraging strategies. In this study, we assessed the accuracy of traditional and new CTL estimators and their vulnerability to web shape and asymmetry. Our results validated the accuracy of the previous estimators. However, we also presented a simple new estimator that can be even more accurate, irrespective of whether the webs exhibit circular shapes or asymmetry in thread investment between superior and inferior web parts. Moreover, we presented an accurate CTL estimator for non-circular orb webs, for which the traditional ones are not applicable.

Keywords: animal behaviour; spider; ecology calculus; orb; web; geometry

1. INTRODUCTION

Scientific realism relies on our ability to acquire and assess high-quality empirical data (Popper 1959; Godfrey-Smith 2016). However, it is not always possible to directly measure some biological structures due to methodological and logistical limitations. Thus, estimators can be used as a proxy once they prove to be reliable and optimally minimize these limitations. In studies on spider behaviour and ecology, the measurement of orb web architecture is an example of such a challenge because of the constraints to properly measure some structures.

Much of the efforts dedicated to acquiring data on the ecology of orb-web spiders is focused on the quantification of specific web features. It is relevant because the orb web mediates the interactions between the spider and its prey (Blackledge & Zevenbergen 2006) and involves energetic and material costs (Coslovsky & Zschokke 2009). Three basic steps are involved in the prey catching process. First, the web must intercept prey. The area occupied by the orb is associated with the probability to intercept flying insects (Sandoval 1994, Blackledge & Eliason 2007). Second, after the interception, the web must stop the prey. The non-adhesive radial threads (Fig. 1) have the mechanical properties to absorb the prey's kinetic energy (Sensenig et al. 2012). Lastly, the web must retain the prey on the sticky capture threads (Fig. 1) long enough for the spider to move from its resting site, reach the interception point, immobilize the prey, and transport and consume the prey. The spider investment in sticky capture threads is crucial to increased prey retention because prey can break threads and escape (Blackledge & Zevenbergen 2006). Since the biomaterial to produce silk is limited, the spider must optimize the architecture of its web to achieve these three goals (e.g. Sandoval 1994, Tso *et al*. 2007, Blamires *et al*. 2011). Thus, the study of orb web architecture provides valuable information to investigate the spider-prey interactions and assess how much energy is devoted to each step of prey capture (Blackledge & Zevenbergen 2006).

The investment in prey retention is assessed by measuring the sticky capture thread length (CTL), apart from the other kinds of threads in the web (Venner *et al*. 2001, Blackledge *et al*. 2011). Thereby, CTL is useful in studies on spider energetic and material expenditure (Venner *et al*. 2003, Venner & Casas 2005). The CTL estimates are also used as both predictor and response variables in statistical models to test behavioural and ecological hypotheses (Venner *et al*. 2006) and to classify the webs in groups according to their traits (Tan *et al*. 2010). For example, the CTL has been used to assess the effect of pesticides (Pasquet *et al*. 2016), urbanization levels (Dahirel *et al*. 2017), and spider aging (Anotaux *et al*. 2014, Pasquet *et al*. 2018) on the web structure and its influence over the prey capture. The CTL has been used also to assess how spiders adjust the silk investment according to the environment they are occupying or according to their building experience (Nakata & Ushimaru 2004, Pasquet *et al*. 2014). Then, given the widespread use of CTL in spider ethology and ecology, it is worthwhile to investigate the most accurate way to estimate this variable.

Currently, there is good software to access components of web geometry from photographs (*e.g.* ImageJ, National Institutes of Health, USA; and WebPlotDigitizer, Ankit Rohatgi, USA), which is the best way to increase accuracy. However, the software available does not automatically discriminate between capture threads and radii among the distinct sets of threads. Thus, the researcher must undertake a laborious task to manually select the capture threads in order to measure the exact CTL, especially when dealing with a large number of images. We performed this analytic approach by measuring the real CTL values in several photographs. The CTL can reach up to 33.2 m in some webs, requiring almost three hours to carefully measure the individual webs. An additional problem to this approach is that orb webs are usually found damaged in the field which makes direct measurement unreliable. Thus, reliable estimators using simple measurements, that can be obtained even from damaged webs, are a better approach for evaluating the CTL and will also save time and efforts by enabling access to a larger sample size.

The attempt to develop calculations to orb web traits is not recent, like capture area and mesh size estimators (Tso 1996, Herberstein & Tso 2000, Blackledge & Gillespie, 2002). The mesh size is defined as the distance between each sticky capture thread from the adjacent ones (Fig. 1). At the same way, the CTL estimators are not recent (Witt *et al*. 1968, Sherman 1994, Heiling & Herberstein 1998, Venner *et al*. 2001). These estimators can be divided into two categories: "constant mesh size" and "variable mesh size" (Venner *et al*. 2001). The constant mesh size estimators calculate the CTL by considering that the spacing between the consecutive sticky capture thread turns from the free zone (Fig. 1) to the outer edge is constant. Therefore, they assume that the CTL is approximately equal to N concentric circles. The CTL can then be estimated as the sum of the perimeter of N circles of medium diameter (D) (Venner *et al*. 2001). All these estimators arise from the following calculation: $CTL = N \pi D$, where N is the average number of spiral turns and D corresponds to the average diameter of the circles that compose the orb web, with D_i being the diameter of the innermost circle and D_o the diameter of the outermost circle (Fig. 1). The formulae can incorporate the number of N spiral turns and measurement of D in different axes: vertical (v), horizontal (h), and diagonals ($d1$ and $d2$). Venner *et al*. (2001) elaborated different formulae and suggested that the most accurate ones are CTL_{VH} and CTL_{VHD}, which are shown in equations (1) and (2). While CTL_{VH} includes information from just the vertical (v) and horizontal (h) axes, CTL_{VHD} also includes information from both diagonal axes ($d1$ and $d2$).

$$(1)\quad CTL_{VH} = \frac{\pi}{16}(N_v + N_h)(D_{o.v} + D_{i.v} + D_{o.h} + D_{i.h})$$

$$(2)\quad CTL_{VHD} = \frac{\pi}{64}(N_v + N_h + N_{d1} + N_{d2})[D_{o.v} + D_{o.h} + D_{o.d1} + D_{o.d2} + 2(D_{i.v} + D_{i.h})]$$

The variable mesh size estimators calculate the CTL by considering that there may be a consecutive increase or decrease at the spacing between the consecutive sticky capture thread turns from the free zone to the outer edge. To correct this mesh variation, these estimators separate each part of the web being considered as a calculation (upper [*up*], lower [*lo*], left [*le*], and right [*ri*]) in an innermost and outermost portion. The innermost and outermost portions are separated by a median radius (R_m), shown in equation (3).

$$(3)\quad R_m = \frac{R_o - R_i}{2} + R_i$$

In the above equation, R_o is the distance from the hub to the outer spiral turn, and R_i is the distance from the hub to the first spiral turn, delimiting the free zone (Fig. 1). Different regions of the web have their own R_m, for example the upper ($R_{m.up}$), lower ($R_{m.lo}$), left ($R_{m.le}$), and right ($R_{m.ri}$) regions (Fig. 1). The number of spiral turns (N) is then counted separately before and after the R_m. These calculations estimate separately the innermost circles (N_i), outermost circles (N_o), and their sum using the same formulae. Venner *et al*. (2001) elaborated different formulae, modifying the Heiling & Herberstein (1998) formulae, and suggested that the most accurate one is the CTL_{VHM}, shown in equation (4).

$$(4)\quad CTL_{VHM} = \frac{\pi}{4}\,[N_{i.up}(R_{i.up} + R_{m.up}) + N_{o.up}(R_{m.up} + R_{o.up}) + N_{i.lo}(R_{i.lo} + R_{m.lo}) + N_{o.lo}(R_{m.lo} + R_{o.lo}) + N_{i.ri}(R_{i.ri} + R_{m.ri}) + N_{o.ri}(R_{m.ri} + R_{o.ri}) + N_{i.le}(R_{i.le} + R_{m.le}) + N_{o.le}(R_{m.le} + R_{o.le})]$$

Some orb-web spider species let a capture area free of sticky spirals, which is called free-sector (Gregorič *et al*. 2010, Xavier *et al*. 2017). If present, this lack of spirals threads can be discounted from the CTL formulae by multiplying them by a corrective factor (1 - a) (Venner *et al*. 2001). The corrective factor is shown in equation (5), where *B* is the base length and *H* is the height of the triangle corresponding to the free-sector.

$$(5)\quad a = \frac{B\,(H/2)}{\pi\,[(D_{o.v} + D_{o.h})/4]^2}$$

These three CTL formulae (CTL_{VH}, CTL_{VHD}, and CTL_{VHM}) had a good accuracy, while the alternative ones had a clear inaccuracy estimating the real measurements (Venner *et al*. 2001). Despite these important findings, there is an alternative mathematical approach available to elaborate more accurate estimators that would be applicable across all orb-web spider species. First, we hypothesize that part of the deviation of estimates from actual measures is due to the fact that orb webs are usually not exactly circular, but more elliptical. Then, the sum of *N* entire circles can introduce some estimate error. Moreover, we hypothesize that orb-web asymmetries influence estimator accuracy (such as different numbers of threads between the orb vertical halves, Fig. 2A) and can be better controlled. Thus, a more accurate formulae must be equally efficient with both circular and elliptical orbs, as well as to more symmetrical and asymmetrical orbs. Moreover, the simplicity of the formulae must be preserved or even improved to make its use feasible even for damaged webs and save mechanical work in robust sample sizes. For example, CTL_{VHM} uses 12 measurements, 8 counts, and 4 extra calculations (R_m). We believe that the same result can be reached in a simpler way. Moreover, many spider species do not build circular webs, but rather semi-circular webs or even a fraction of the semicircle (Fig. 2B). In other scientific proceedings, we surveyed 290 orb webs in a single forest, and 85 of these were non-circular (personal observation). The traditional estimators are not applicable to these webs, which can be abundant in some surveys. Thus, we elaborated new CTL estimators and compared their accuracy with three of the most efficient traditional estimators. We also elaborated a CTL estimator for non-circular webs and tested its accuracy by expanding the test to 11 other species from different genera. Our goal is to provide empirically efficient and logistically feasible methods that can be applied in studies of orb-web spiders.

2. METHODS

2.1 Real CTL measures and spider species

In the field, we used a DSLR Nikon camera to photograph a total of 82 preserved orb webs from 11 species (Table 1) between 2017 and 2019. We used a graduated scale (in mm) parallel to the orb plane. Then, we measured the real CTL from the digital photographs using the software ImageJ (National Institutes of Health, USA). We also measured and counted all the other necessary parameters to apply the different formulae from these photos. All spiders were probably at the last three instars. Our intention was to include webs of different sizes and symmetries to allow a general assessment of the estimators' accuracy (Table 1).

2.2 Elaborating new CTL estimators

A better estimator must control different shapes of orb webs (*e.g.*, more circular or more elliptical) and their possible asymmetries (*e.g.*, different number of sticky capture thread turns at different parts of the web). Thus, we can control both problems by considering the different web parts separately in calculations.

Since asymmetries may be present both vertically and horizontally, we can account for this variation by separating each orb web into four parts, assuming the hub as the centre of the web: upper (*up*), lower (*lo*), left (*le*), and right (*ri*) (Fig. 3). Therefore, the calculation does not sum entire circles but rather a sequence of arcs from each one of the web parts. Then, we can estimate the perimeter of each arc relative to its distance from the hub. So, the arc perimeter estimate will have a consistent approximation regardless of whether we are working with semicircle or semi-ellipse arcs. Considering that arcs of same positions in different parts of the orb have different distances to the hub, the estimate of the arc perimeters will have a better approximation regardless of which part of the orb they are located in and whether they are circle or ellipse arcs.

Towards the outer edge, each arc will always be consecutively greater than the previous one, regardless of the spacing between each arc. Therefore, there will always be an arithmetic progression in which each term is an arc. Therefore, the first new estimator arises simply from four sums (to each orb part) of terms of arithmetic progressions. We call this estimator CTL_A, shown in equation (6).

$$(6) \quad CTL_A = \frac{(A_{1.up}+A_{n.up})N_{up}}{2} + \frac{(A_{1.lo}+A_{n.lo})N_{lo}}{2} + \frac{(A_{1.le}+A_{n.le})N_{le}}{2} + \frac{(A_{1.ri}+A_{n.ri})N_{ri}}{2}$$

In equation (6), *N* is the number of sticky capture thread turns that can be counted in each web sector (*up, lo, le, ri*) (Fig. 3) and CTL_A is the total number of arcs that are being summed in each arithmetic progression. The notation A_1 is the first arc perimeter (*i.e.*, first arithmetic progression term) and A_n is the last arc perimeter (*i.e.*, last arithmetic progression term). Considering that the orb is divided into four parts, each *A* perimeter can be approximated as $\pi/2*R$, where R_i is the radius of the first arc and R_o is the radius of the last arc (Fig. 1). When we do the appropriate substitutions at equation (6), we achieve equation (7), shown below.

$$(7)\quad CTL_A = \frac{1}{2}\left\{\begin{array}{l}\left[\frac{N_{up}\pi}{2}\left(R_{i.v.up}+R_{o.v.up}\right)\right]+\left[\frac{N_{lo}\pi}{2}\left(R_{i.v.lo}+R_{o.v.lo}\right)\right]\\ +\left[\frac{N_{le}\pi}{2}\left(R_{i.h.le}+R_{o.h.le}\right)\right]+\left[\frac{N_{ri}\pi}{2}\left(R_{i.h.ri}+R_{o.h.ri}\right)\right]\end{array}\right\}$$

Since *Wixia abdominalis* webs had free-sectors, we also elaborated a calculation compatible with the new estimators to discount them from the orbs, shown in equation (8).

$$(8)\quad Free-sector\ discount = \frac{N}{2}\left[\frac{\pi\alpha}{180}\left(R_i+R_o\right)\right]$$

In equation (8), α is the angle formed by the two radii that delimits the free-sector, R_i is the distance from the hub to the first spiral thread should be occupying, and R_o is the distance from the hub to the place in which the last spiral thread should be occupying. If a free-sector was present, we subtracted this discount from the values estimated by CTL_A.

Finally, as we mentioned in the introduction, the traditional estimators are not applicable to CTL estimates of non-circular orb webs, which can be common in some samples. However, using our approach, we formulated an equivalent CTL estimator that can be used for these types of webs. We call this estimator CTL_{AN}, shown in equation (9).

$$(9)\quad CTL_{AN} = \left[\frac{N_f}{2}\left(\frac{\pi\alpha}{3}/180\right)\left(R_{o.f} + R_{i.f}\right)\right] + \left[\frac{N_s}{2}\left(\frac{\pi\alpha}{3}/180\right)\left(R_{o.s} + R_{i.s}\right)\right] + \left[\frac{N_t}{2}\left(\frac{\pi\alpha}{3}/180\right)\left(R_{o.t} + R_{i.t}\right)\right]$$

In CTL_{AN}, α is the angle formed by the two segments of the bridge thread (Fig. 3B) or primary frame located closest to the hub (Fig. 3C) that delimits the capture area. The non-circular orb web is divided into three parts (f, s, and t) and α is divided by 3 (Fig. 3B and C). For each web part, we measured the number of sticky capture threads crossing it (N) and the distance of the first (R_i) and last (R_o) arc to the hub.

2.3 Measuring orb web general shape and sticky capture thread distribution asymmetry

To measure the general web shape (WS), we quantified how each orb web departs from a circle. We measured the horizontal ($D_{o.h}$) and vertical ($D_{o.v}$) diameters of each orb web, and divided the smallest measure by the largest one. Thus, WS values next to 1 (the maximum value possible) represent more circular webs and the smallest values correspond to a departure from a circular shape. The advantage of this simple ratio is the representation of the web shape regardless of the axis in which the web may be more elongated.

To measure the general asymmetry of investment in capture threads (AICT) between the web parts, we quantified the difference in sticky capture thread investment between the upper and lower half of each web. For each web, we counted the number of sticky capture threads along the vertical axis at the upper (N_{up}) and lower (N_{lo}) half, and again divided the smallest number by the largest one. Thus, AICT values close to 1 represent a symmetric investment in capture threads between the web parts regardless of which part is the greatest investment.

2.4 Assessing estimator accuracy and their sensibility to web shape and sticky capture thread distribution asymmetry

After directly measuring the CTL of the 82 orb webs, we estimated the CTL values using the estimators. As 75 of these webs are complete orbs, we estimated their CTL with CTL_{VH}, CTL_{VHD}, CTL_{VHM}, and CTL_{A}. As the seven remaining webs are non-circular orbs, we estimated their CTL with CTL_{AN}. Then, we performed linear regressions between the real CTL measurements (independent variable) and each CTL value estimated using the formulae (dependent variable). Therefore, the best estimators must produce the best adjustment at this relation, with R^2 and β values close to 1 representing a perfect accuracy.

Inevitably, even the best estimator will produce some degree of deviation from the real CTL values. However, some estimators can consistently underestimate or overestimate the real measurement. Thus, in these situations, the cumulative estimate errors produce serious bias to scientific proceedings, especially when they involve the CTL sum of many webs or when the CTL is used to assess and refine questions, such as in spider energetic spending issues. Therefore, the best estimator must also produce values which do not statistically deviate from zero because their underestimated and overestimated errors tend to annul each other. Therefore, we calculated the percentage of error for each estimated CTL value in relation to the real CTL, shown in equation (10). Negative percentages are underestimates and positive percentages are overestimates. For each estimator, we tested if the estimate errors were different from zero.

$$(10) \quad \% \, error = \frac{(CTL_{estimated} - CTL_{real\ measurement})100}{CTL_{real\ measurement}}$$

Finally, it is important to known if each estimator produces consistent or skewed estimate errors to different kinds of webs. A good estimator must produce the same estimate accuracy to all kinds of webs regardless their shapes and asymmetries. Thus, to assess the estimator accuracy consistence to different kinds of webs we performed also linear regressions between the WS values and the absolute estimate errors (equation 10, but considering all values as positive), and between the AICT values and the absolute estimate errors. Therefore, the best estimators must produce the no influence at this relation, with low R^2 values close to zero representing a good estimate consistence.

3. RESULTS

Our survey included a considerable variation of real CTLs, with values ranging from 211.74 to 3,322.39 cm, and also a variation of web shapes and asymmetries (Table 1). The relationships between the real CTLs and their respective estimated values by each formula are shown in Table 2. Clearly, all estimators had a high accuracy in approximating the real values. However, both CTL_{VHM} and CTL_A are the most refined estimators since they produced the closest values to the real measures (Table 2; R^2 and β values closer to 1 in the relations between real CTL vs. estimate CTL values). CTL_A kept its estimate accuracy to all groups of web shapes and asymmetries, while CTL_{VHM} lost accuracy for webs with high AICT, just like the other traditional estimators (Table 2; relations between WS vs. estimate errors, and in AICT vs. estimate errors). Our estimator for non-circular orb webs, CTL_{AN}, also presented a high estimate accuracy and is comparable with the accuracy presented by CTL_{AN} (Table 2).

When we assessed the percentage of errors produced by each estimator, we found that these errors vary between the different formulae (Fig. 4). The estimator for non-circular orb webs, CTL_{AN}, was not compared with the others because it involved a different number of surveyed webs. In *post hoc* comparisons, CTL_{VH} and CTL_{VHD} do not differ from each other, while CTL_{VHM} and CTL_{A} do not differ in percentage of estimative errors (Figure 4). As shown in Figure 4, CTL_{VH} and CTL_{VHD} consistently underestimate the real CTL, while CTL_{VHM}, CTL_{A}, and CTL_{AN} do not deviate from zero.

4. DISCUSSION

Our results demonstrate that the new CTL_{A} estimator produces an accuracy as high as the better traditional CTL_{VHM} estimator. However, our results also reveal that the traditional CTL_{VHM} estimator was prone to accuracy loss in CTL estimates of webs that have amore asymmetric distribution of sticky capture threads. In contrast, the new CTL_{A} estimator maintained its accuracy with all kinds of webs. Therefore, in practice, the CTL_{A} estimator can exhibit an even higher accuracy than the CTL_{VHM} estimator when sampling predominantly asymmetric webs.

The second advantage of using the CTL_{VHM} and CTL_{A} estimators is that, unlike CTL_{VH} and CTL_{VHD}, the percentage of estimated errors are not statistically different from zero. This suggests that the underestimated and overestimated values of these estimators are prone to nulling each other. It is plausible to expect that even subtle accuracy improvements like these can reduce bias in results when addressing issues sensitive to error estimates. For example, CTL estimate values can be incorporated in mathematical models to evaluate the energetic costs of the web building process and spider mass loss (Venner *et al*. 2003, Venner & Casas 2005). These CTL estimate values can also be used as part of other calculations, such as to calculate the volume of the sticky capture threads (Sensenig *et al*. 2011), in which the results can highly vary according to subtle changes in the inputted CTL values. Moreover, some studies can estimate the CTL of the same individual spider many times as it replaces the threads (Venner *et al*. 2003). Thus, to evaluate the total movement and energetic cost, all CTL measures from the same individual can be summed and incorporated in mathematical models (Venner *et al*. 2003). Therefore, when the sum of CTLs is necessary, it is possible to produce a greater cumulative error if the formulae consistently underestimate or overestimate the CTL.

We should also highlight that despite of the CTL_{VHM} being the most efficient traditional estimator, the CTL_{VH} estimator has been used at scientific papers instead of the first one (Venner *et al*. 2003, Venner & Casas 2005, Nakata & Ushimaru 2004, Venner *et al*. 2006, Tan *et al*. 2010, Anotaux *et al*. 2014, Pasquet *et al*. 2014, Pasquet *et al*. 2016, Dahirel *et al*. 2017, Pasquet *et al*. 2018). Probably, this is because of the less simplicity of the CTL_{VHM} calculation (Venner *et al*. 2001). When comparing the mathematical structure of estimators, CTL_A is a much simpler formula and requires less information than CTL_{VHM} (Table 2). Besides needing more measurements, CTL_{VHM} requires extra calculations for median radii, R_m. So, after the measurements and extra calculations, the researcher must then locate the four median radii in each photograph to perform the remaining counts. This is an especially tiring process when the researcher has to spend hours performing mechanical work to measure a robust sample size and may even reduce attention throughout the measurements. Here, we demonstrate that the sum of arcs in an arithmetic progression in CTL_A eliminates the need for extra calculations to achieve the best approximations.

It is also important to note that all the traditional estimators are not applicable to non-circular orb webs. Therefore, by means of the same mathematical reasoning used for the new CTL_A estimator, we formulated the CTL_{AN} estimator for non-circular orb webs. This new formula showed a high estimate accuracy, equivalent to CTL_A, and did not produce bias to underestimate or overestimate the real CTLs. Therefore, both CTL_A and CTL_{AN} can equally be used together to estimate CTLs of different species in the same scientific work.

Finally, we must highlight that CTL estimators have been used for many different purposes in studying spider behaviour and ecology (Venner *et al*. 2003, Venner & Casas 2005, Nakata & Ushimaru 2004, Venner *et al*. 2006, Tan *et al*. 2010, Anotaux *et al*. 2014, Pasquet *et al*. 2014, Pasquet *et al*. 2016, Dahirel *et al*. 2017, Pasquet *et al*. 2018). Therefore, it is worthwhile to investigate the generality of these estimators to different species which build different kinds of orb webs. Here, we expanded this assessment to 11 other spider species.

Here, we proposed new estimators which produced more accurate results for all assessed species, web shapes and symmetries, including those non-circular orb webs for which the traditional formulae are not applicable. Therefore, we indicate the use of the new estimators, CTL_A and CTL_{AN}. The error of estimates produced by all formulae may not influence the results of some specific kinds of research, however, since the scientific method aims to minimize the bias, we have no reason to not use the best tools if they are empirically and logistically accessible. Thus, we are confident to have made two new and simple estimators with high accuracy available to other researchers.

LITERATURE CITED

Anotaux, M., Toscani, C., Leborgne, R., Châline, N. & Pasquet, A. 2014. Aging and foraging efficiency in an orb-web spider. *Journal of Ethology*. 32, 155-163. DOI: doi.org/10.1007/s10164-014-0404-6

Blackledge, T.A., Kuntner, M. & Agnarsson, I. 2011. The form and function of spider orb webs: evolution from silk to ecosystems. In J. Casas (ed.), Advances in Insect Physiology (pp. 175-262). Burlington: Academic Press.

Blackledge, T. A. & Eliason, C. M. 2007. Functionally independent components of prey capture are architecturally constrained in spider orb webs. *Biology Letters*. 3, 456-458. DOI: doi.org/10.1098/rsbl.2007.0218

Blackledge, T.A. & Zevenbergen, J.M. 2006. Mesh width influences prey retention in spider orb webs. *Ethology*. 112, 1194-1201. DOI: doi.org/10.1111/j.1439-0310.2006.01277.x

Blackledge, T.A. E Gillespie, R.G. 2002. Estimation of capture areas of spider webs in relation to web asymmetry. *Journal of Arachnology*. 30, 70-77. DOI: doi.org/10.1636/0161-8202(2002)030[0070:EOCAOS]2.0.CO;2

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. DOI: doi.org/10.1016/j.anbehav.2011.01.022

Coslovsky, M. & Zschokke, S. 2009. Asymmetry in orb-webs: an adaptation to web building costs? *Journal of Insect Behavior*. 22, 29-38. DOI: doi.org/10.1007/s10905-008-9151-2

Dahirel, M., Dierick, J., Cock, M. De, & Bonte, D. 2017. Intraspecific variation shapes community-level behavioral responses to urbanization in spiders. *Ecology*. 98, 2379-2390. DOI: doi.org/10.1002/ecy.1915

Gregorič, M., Kostanjšek, R. & Kuntner, M. 2010. Orb web features as taxonomic characters in *Zygiella*s .l. (Araneae: Araneidae). *Journal of Arachnology*. 38, 319-327. DOI: doi.org/10.1636/A09-80.1

Godfrey-Smith, P. 2016. Theory and Reality: An Introduction to the Philosophy of Science. Chicago: University of Chicago Press.

Heiling, A.M. & Herberstein, M.E. 1998. The web of *Nuctenea sclopetarius* (Araneae: Araneidae): relationship between body size and web design. *Journal of Arachnology*. 16, 295-302.

Heiling, A.M., Herberstein, M.E., & Spitzer, G., 1998. Calculation of the capture thread length in orb webs: evaluation of new formulae. *Ann. Entomol. Soc. Am*. 91, 135-138. DOI: doi.org/10.1093/aesa/91.1.135

Herberstein, M.E. & Tso, I-M. 2000. Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneoidea, Araneae). *Journal of Arachnology*. 28, 180-184. DOI: doi.org/10.1636/0161-8202(2000)028[0180:EOFTET]2.0.CO;2

Nakata, K. & Ushimaru, A. 2004. Difference in web construction behavior at newly occupied web sites between two *Cyclosa* species. *Ethology*. 110, 397-411. DOI: doi.org/10.1111/j.1439-0310.2004.00983.x

Pasquet, A., Marchal, J., Anotaux, M. & Leborgne, R. 2014. Does building activity influence web construction and web characteristics in the orb-web spider *Zygiella x-notata* (Araneae, Araneidae)? *Zoological Studies*. 53, 11. DOI: doi.org/10.1186/1810-522X-53-11

Pasquet, A., Tupinier, N., Mazzia, C. & Capowiez, Y. 2016. Exposure to spinosad affects orb-web spider (*Agalena tearedii*) survival, web construction and prey capture under laboratoryconditions. *Journal of Pest Science*. 89, 507-515. DOI: doi.org/10.1007/s10340-015-0691-x

Pasquet, A., Toscani, C., & Anotaux, M. 2018. Influence of aging on brain and web characteristics of an orb web spider. *Journal of Ethology*. 36, 85-91. DOI: doi.org/10.1007/s10164-017-0530-z

Popper, K. 1959. The Logic of Scientific Discovery. Hutchinson & Co., London.

Sandoval, C.P. 1994. Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Functional Ecology*. 8, 701-707. DOI: doi.org/10.2307/2390229

Sensenig, A.T., Agnarsson, I., & Blackledge, T.A. 2011. Adult spiders use tougher silk: ontogenetic changes in web architecture and silk biomechanics in the orb-weaver spider. *Journal of Zoology*. 285, 28-38. DOI: doi.org/10.1111/j.1469-7998.2011.00809.x

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. DOI: doi.org/10.1098/rsif.2011.0851

Sherman, P.M. 1994. The orb web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Animal Behaviour*. 48, 19-34. DOI: doi.org/10.1006/anbe.1994.1208

Tan, E.J., Seah, S.W.H., Yap, L-M.Y.L., Goh, P.M., Gan, W., Liu, F., & Li, D. 2010. Why do orb-weaving spiders (*Cyclosa ginnaga*) decorate their webs with silk spirals and plant detritus? *Animal Behaviour*. 79, 179-186. DOI: doi.org/10.1016/j.anbehav.2009.10.025

Tso, I-M. 1996. Stabilimentum of the garden spider *Argiope trifasciata*: a possible prey attractant. *Animal Behaviour*. 52, 183-191. DOI: doi.org/10.1006/anbe.1996.0163

Tso, I-M., Chiang, S-Y., & Blackledge, T.A. 2007. Does the Giant Wood Spider Nephila pilipes Respond to Prey Variation by Altering Web or Silk Properties? *Ethology*. 113, 324-333. DOI: doi.org/10.1111/j.1439-0310.2007.01318.x

Venner, S., Thevenard, L., Pasquet, A., & Leborgne, R. 2001. Estimation of the web's capture thread length in orb-weaving spiders: determining the most efficient formula. *Annals of the Entomological Society of America*. 94, 490-496. DOI: 10.1603/0013-8746(2001)094[0490:EOTWSC]2.0.CO;2

Venner, S., Bel-Venner, M-C., Pasquet, A., & Leborgne, R. 2003. Body-mass-dependent cost of web-building behavior in an orb weaving spider, *Zygiella x-notata*. *Naturwissenschaften*. 90, 269-272. DOI: 10.1007/s00114-003-0420-9

Venner, S. & Casas., J. 2005. Spider webs designed for rare but life-saving catches. *Proceedings of The Royal Society B*. 272, 1587-1592. DOI: doi.org/10.1098/rspb.2005.3114

Venner, S., Chadès, I., Bel-Venner, M-C., Pasquet, A., Charpillet, F. & Leborgne R. 2006. Dynamic optimization over infinite-time horizon: Web-building strategy in an orb-weaving spider as a case study. *Journal of Theoretical Biology*. 241, 725-733. DOI: doi.org/10.1016/j.jtbi.2006.01.008

Witt, P.N., Reed, C.F. & Peakall. D.B. 1968. A spider's web: problems in regulatory biology. New York: Springer.

Xavier, G.M., Moura, R.R. & Gonzaga, M.O. 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. DOI: doi.org/10.1636/JoA-S-17-001.1

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

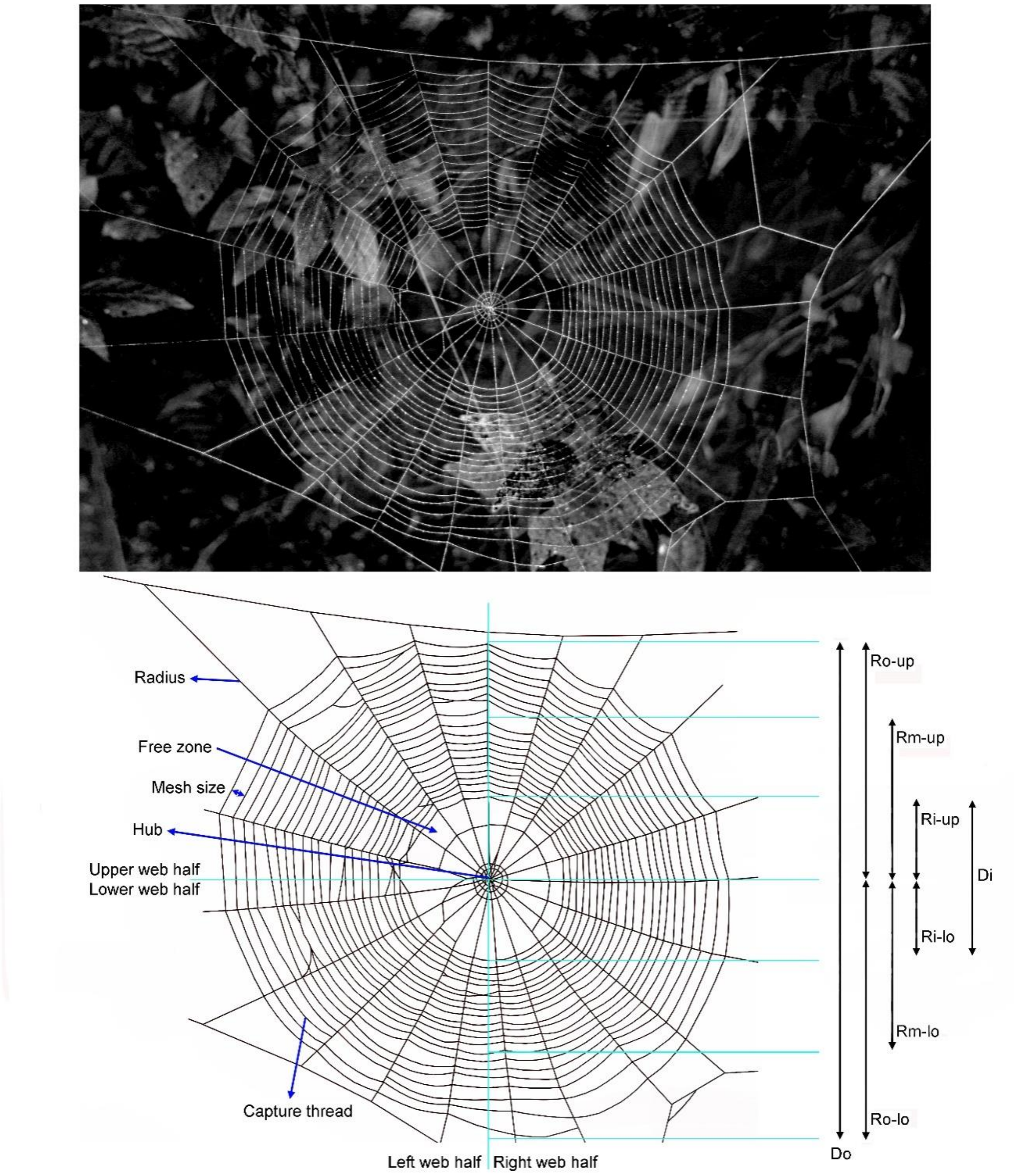


Figure 1. Main orb-web structure and components and essential measurements applied at CTL estimators. The outermost diameter (D_o), innermost diameter (D_i), outermost upper and lower radii ($R_{o.up}$ and $R_{o.lo}$), innermost upper and lower radii ($R_{i.up}$ and $R_{i.lo}$), and upper and lower median radii ($R_{m.up}$ and $R_{m.lo}$) are shown. The measurements are shown at the vertical axis, but different estimators can also incorporate the same parameters from the vertical and diagonal axes.

Figure 2. An orb web of *Araneus omnicolor* with different numbers of sticky capture threads between the web parts (A); and a non-circular orb web of *Metazygia* sp. (B).

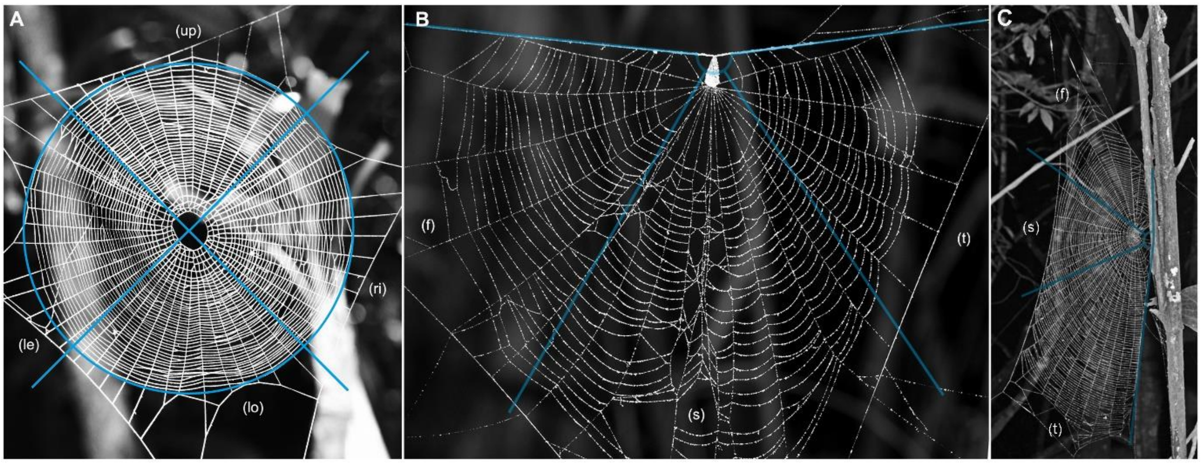


Figure 3. To use the new estimator for circular webs, *CTL_A*, each orb web is divided into four parts: upper (*up*), lower (*lo*), left (*le*), and right (*ri*) (A). This division always departs from the hub regardless the web asymmetries. To use the new estimator for non-circular webs, *CTL_{AN}*, each orb web is divided in three parts: first (*f*), second (*s*), and third (*t*) (B) and (C). The angle formed by the two segments of the bridge thread (B) or primary frame (C) located closest to the hub (see Zschokke 1999) is divided in three equal angles, delimiting the three sectors.

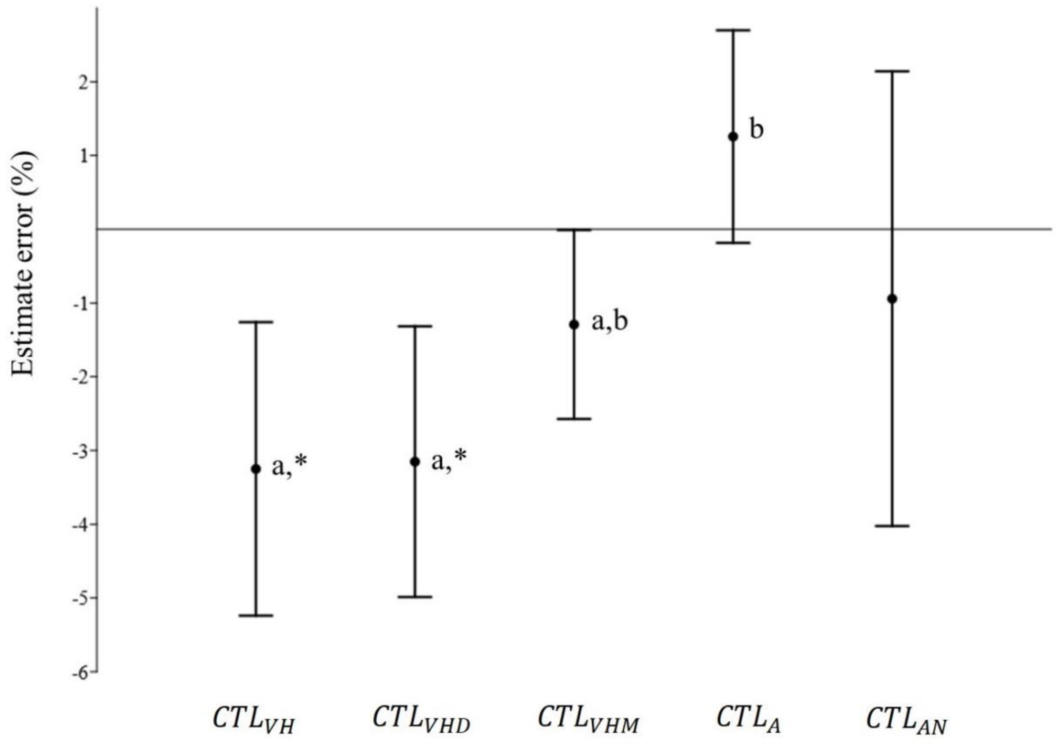


Figure 4. Comparison of estimate error percentage produced by different CTL estimators. Mean and 95% Confidence Interval. These groups differ among each other (ANOVA: $F_{3,296} = 6.2$, $P < 0.001$). The same letters were attributed to similar results in the Tukey *post hoc* tests ($P > 0.05$) and different letters to distinct results ($P < 0.05$). * corresponds to the result of a one-sample t-test in which the mean was different than zero ($P < 0.05$). The last estimator, CTL_{AN}, is proper to non-circular orb webs and its estimate errors were not compared with the other groups because it presents a very different sample size.

Table 1. Spider species and their number of photographed webs, real CTL (cm), web shape index, and asymmetry of investment in capture threads index (AICT) (mean ± SD). The geographic locations are shown in WGS84 Datum. *These are the non-circular webs; therefore, these metrics are not applied.

Species	Number of webs	Real CTL (cm)	WS	AICT	Location
Araneidae sp.1	10	918.94 ± 399.51	0.900 ± 0.053	0.492 ± 0.234	19˚10’32”S, 48˚23’38”W
Araneidae sp.2	6	954.02 ± 529.01	0.698 ± 0.194	0.641 ± 0.311	19˚10’32”S, 48˚23’38”W
Araneus omnicolor	13	1407.69 ± 474.73	0.849 ± 0.060	0.366 ± 0.094	23˚14’12”S, 46˚56’16”W
Eustala sp.	3	357.48 ± 167.91	0.740 ± 0.203	0.421 ± 0.088	23˚14’12”S, 46˚56’16”W
Leucauge sp.	5	2437.62 ± 730.37	0.947 ± 0.042	0.891 ± 0.097	23˚14’12”S, 46˚56’16”W
Micrathena swainsoni	6	708.51 ± 391.98	0.960 ± 0.020	0.965 ± 0.022	18˚45’11”S,47˚51’28”W
Micrathena sp.1	6	2041.70 ± 262.10	0.926 ± 0.040	0.959 ± 0.046	23˚14’12”S, 46˚56’16”W
Micrathena sp.2	14	1614.15 ± 345.50	0.944 ± 0.040	0.930 ± 0.101	19˚10’32”S, 48˚23’38”W
Wixia abdominalis	10	719.59 ± 523.87	0.807 ± 0.096	0.685 ± 0.163	19˚10’32”S, 48˚23’38”W
Uloborus sp.	2	170.70 and 462.59	0.775 and 0.910	0.454 and 0.714	18˚45’11”S,47˚51’28”W
Metazygia sp.	7	592.46 ± 278.11	*	*	19˚10’32”S, 48˚23’38”W

Table 2. The left columns present the linear relationship between real CTL measurements (cm) and their respective estimated values (cm) by each estimator. The right columns present the linear relationships between the estimate error (%) and web shape index (WS) (first regressions), and between the estimate error (%) and asymmetry of investment in capture threads index (AICT). The R² shows the quality of each relation. Lastly, the number of information necessary to use each estimator. * These are the non-circular webs; therefore, these relations are not applied.

Estimator	Linear function – real CTL vs. estimator values	R²	Linear functions – real CTL vs. WS, and real CTL vs. AICT	R²	Nº of measurements, counts and extra calculations
CTL_{VH}	y = 1.040x – 66.785	0.985	y = -17.496x + 21.961 y = -13.976x + 16.500	0.084 0.353	4, 2 and 0
CTL_{VHD}	y = 1.051x – 76.917	0.984	y = -20.151x + 24.346 y = -13.411x + 16.163	0.161 0.465	6, 4 and 0
CTL_{VHM}	y = 0.990x – 1.567	0.993	y = -3.021x + 7.058 y = -6.229x + 8.804	0.008 0.216	12, 8 and 4
CTL_{A}	y = 1.036x – 20.149	0.993	y = -5.259x + 9.632 y = -4.660x + 8.314	0.020 0.102	8, 4, and 0
CTL_{AN}	y = 0.998x – 7.350	0.991	*	*	7, 3, and 0

CHAPTER 2

INFLUENCE OF WEB TRAITS ON PREY CAPTURED BY ORB-WEAVER SPIDERS

ABSTRACT

Orb-webs show diversity in several traits, including silk types, architecture, physical properties, locale, and period of exposition. Then, the investigation of how specific web traits may determine the identity of intercepted prey is an important step in the evaluation of trophic niche partitioning within communities and, consequently, of local richness patterns. However, the influence of several of these traits on the composition of intercepted insects remains to be determined. In this study, we evaluated the effects of five web traits on the capture of different sizes and *taxa* of prey by orb-weaver spiders. We conducted observations of prey intercepted by the orb webs of 16 sympatric spider species and artificial webs. We found that all orb webs mainly intercepted small insects, sharing the most abundant insect families found in the study area. However, spiders that build webs with larger capture areas and show nocturnal activity capture larger insects. We discuss why these spiders are likely those that bear the tougher threads and adjust their activities to target larger prey. Other orb-web traits, such as the number of radii, density of sticky threads, and height of web placement did not influence the kind of intercepted insects. We discuss the functional, ecological implications of the two most influential traits, and why many others showed little relevance in the definition of prey types captured by orb weaver spiders.

Keywords: Orb-web design; trophic niche; predator-prey interactions.

1. INTRODUCTION

Owing to their abundance, almost ubiquitous distribution in terrestrial biomes, and diet, spiders have been postulated to be one of the most influential predators in several ecosystems (Nyffeler 2000, Nyffeler & Birkhofer 2017). Between 400 and 800 million tons of prey are consumed annually by the global spider community, possibly surpassing the mass consumed by large predators (Nyffeler & Birkhofer 2017). However, although they are usually considered generalist predators, distinct groups of spiders may exert different impacts on prey groups, depending on their specific hunting strategies (*e.g.* Sanders *et al*. 2015, Ludwig *et al*. 2018, Pitilin *et al*. 2020). Several studies have also attributed dietary preferences to nutritional requirements, microhabitat selection, web properties, and morphological traits (*e.g.* Nentwig & Wissel 1986, Hénaut *et al*. 2006, Pekár *et al*. 2012, Toft 2013).

Among the guilds of web weavers, distinct groups build either sheets, funnel-sheets, tangles, or orb webs (Vollrath & Selden 2007, Cardoso *et al*. 2011). Each category presents peculiar traits, such as the investment in silk threads and the architecture of the structure used to intercept prey, and the microhabitats in which webs are constructed (*e.g.* Vollrath & Selden 2007, Xavier *et al*. 2017, Pitilin *et al*. 2020). Indeed, studies on food webs (Ludwig *et al*. 2018) and stable isotopes (Sanders *et al*. 2015) have found that spiders using each web type (*e.g.*, tangle, sheet, or orb) consume specific kinds of prey, or similar types, but in different proportions. The quantity, proportion, and arrangement of each kind of silk in a given web can vary between species with the same web type and even between individuals of the same species, likely influencing prey capture (*e.g.* Sandoval 1994, Vollrath & Selden 2007, Eberhard 2014, Xavier *et al*. 2017). If this hypothesis is consistent, spiders using the same web type, but exhibiting differences in their web traits, would capture different sets of prey. Accordingly, web traits could be considered as functional traits, since they are morphological, physiological, or behavioral features associated with specific biotic interactions (Schmitz 2017).

Orb webs are good study models for investigating the role of web traits in foraging, mainly because the function of each type of silk thread is well known, and also due to the fact that their complex structural variations can result in the capture of distinct prey types (Sandoval 1994, Blackledge *et al.* 2011, Harmer *et al.* 2011). Orb webs evolved under selective pressure to efficiently absorb and dissipate the high kinetic energy of flying insects, and to retain that prey until the spider approaches (Sensenig *et al*. 2010). The radial threads are composed of tough polypeptide fibers that can absorb a large amount of kinetic energy before breakage (Blackledge *et al.* 2011, Harmer *et al.* 2011). Consequently, the more radii the prey contacts during the interception process, the more efficient the energy absorption (Sensenig *et al*. 2012). In contrast, the sticky capture threads contain elastic fibers which have a negligible role in absorbing and dissipating energy (Sensenig *et al*. 2012). They are responsible for retaining the prey long enough for the spider to be able to subdue it. Thus, the probability of escaping from the web depends on the number of sticky capture threads that the prey is in contact with (Blackledge & Zevenbergen 2006, Opell *et al*. 2006).

The efficiency of an orb web to capture different prey may be highly influenced by the proportions of the radii and sticky capture threads, as well their spacing and interconnectedness (Blackledge & Zevenberg 2006, Blackledge & Eliason 2007). It is expected that a spider potentializes the dampening function by investing more in radii than in sticky threads if the targeted prey is especially difficult to stop but easy to retain. The opposite pattern of investment in silk threads is expected if the targeted prey is easy to stop, but difficult to retain. Alternatively, the spider may simultaneously improve both functions by building smaller, but denser webs. Spiders may also spin larger webs with threads sparsely distributed, to increase the probability of capturing important prey that are easily stopped and held. This strategy may increase the chances of intercepting more prey. However, few studies have assessed these possibilities outside of laboratory conditions, and they are focused on only a few species (*e.g.* Sandoval 1994, Hénaut *et al*. 2006, Gregorič *et al*. 2011).

The physical properties of orb-web threads also vary among species. Large spiders usually produce tougher silk threads, implying a higher potential for stopping large prey (Sensenig *et al*. 2010). A similar pattern is generally found throughout ontogeny, in which large, more mature individuals build tougher webs (Sensenig *et al*. 2011), depending less on thread density than area to obtain heavier prey (Hénaut *et al.* 2006, Sensenig *et al*. 2010, Sensenig *et al*. 2011). Therefore, a broader assessment of the influence of web traits on prey capture should cover a considerable range of species, body sizes, and ontogenetic stages of spiders facing similar prey availability under natural conditions.

Beyond the web architecture, other web traits may have important functions in prey capture, such as the location, and the period in which a web is built. In *Leucauge venusta* (Tetragnathidae), adult spiders construct their webs at positions higher than those of juveniles, likely because high webs are more prone to intercept large insects in mid-flight (Hénaut *et al*. 2006). This type of ontogenetic segregation can also occur during different periods of the day. In a study involving six species, small spiders built their webs in the early evening, while larger spiders constructed their webs through the night (Ward & Lubin 1992). Although there was no direct record of prey interception associated with this temporal segregation, the pattern was correlated with the flying activity of large insects (Ward & Lubin 1992). Therefore, we suppose that spatial and temporal segregation of webs may influence the types of prey captured by orb-web spiders.

In this study, we investigated the effects of orb-web architecture, microhabitat choice, and foraging period on the capture of different prey types. Hereafter, we refer to these features as ‘orb-web traits’. We hypothesized that each of these orb-web traits are determining factors for prey size and *taxa*. Consequently, the expected results were that orb webs exhibiting different investments in each trait intercepted distinct sets of prey. We considered the effects on prey sizes and *taxa* because both relate to the impact absorption and retention challenges imposed on webs during the capture process, (Blackledge & Zevenbergen 2006, Gwynne *et al*. 2007), based on spatial and temporal flying activities (Ward & Lubin 1992, Hénaut *et al*. 2006). Hence, we performed extensive surveys on the frequencies of prey capture by sympatric orb-web spider species to assess these predictions. We also distributed artificial webs in three height categories to record the types of intercepted prey. This experiment allowed us to investigate the effect of height on prey capture more confidently, regardless of the residual variation found in the natural observations.

2. METHODS

2.1 *Surveys of natural events of prey interception*

We carried out this study at Reserva Ecológica do Panga (19°10′32″ S, 48°23′38″ W, *Datum*: WGS84), in Uberlândia, Minas Gerais, Brazil. The reserve covers 409 ha, contains both forest and savanna vegetation, and is held strictly for ecological conservation and scientific use. We sampled prey on webs found in the vegetation under the forest canopy in a semideciduous area that covers approximately 80 ha. We conducted surveys once a week for 19 weeks, from March to July 2018 (14 consecutive weeks) and from December 2018 to January 2019 (5 consecutive weeks). In each sampling expedition, two team members actively searched for orb webs along the forest between 7:30 and 10:30, and between 20:00 and 23:00. We kept the same routes during all samplings, covering as much of the 80 ha as possible. According to the Köppen-Geiger classification (Beck *et al*. 2018), the study area is part of the Tropical Savanna Climate (Aw), which has a dry season from April to September (total rainfall of 46 mm in 2018), and a rainy season from October to March (total rainfall of 376 in 2018) (Instituto Nacional de Meteorologia 2020); our survey method allowed us to capture samples from both seasons.

When we found an insect trapped in an orb web, we collected it and measured the traits of each orb web once only. After data collection, we destroyed the orb webs to avoid sampling the same webs twice. However, we used a criterion to record prey capture; the interception must have occurred prior to our arrival, and the insect was entangled and already subdued or in the process of being consumed by the spider. All interception events that occurred during our presence were disregarded to avoid attraction bias. When an interaction met the criterion, we recorded the spider species and collected the insects. We also measured the height from the ground to the orb hub (cm), and photographed the web using a DSLR Nikon camera equipped with an 18–55 mm lens, and a scale (graduated in mm) parallel to the web plane.

We identified the family of insects using the entomological identification keys included in Triplehorn (2017), and measured spider body length (mm) using a Leica 250C stereomicroscope equipped with a Leica DFC camera using the LAS Application Suite software. Voucher specimens were deposited in the collection of Laboratório de Aracnologia, Universidade Federal de Uberlândia (curator: M.O. Gonzaga).

For each photograph of an orb web, we counted the number of radii and measured the capture area (cm^2) (the area delimited by the innermost sticky capture thread turn and the outermost one). Following the method described by Xavier *et al.* (2020), we also measured 12 parameters from each photograph and calculated the sticky capture thread length (*CTL*, cm) using the CTL_A formulae for complete orbs and the CTL_{AN} formulae for non-circular orb webs. These calculations are highly accurate for estimating the *CTL* of different kinds of orb webs, despite their web shape, asymmetry, or damage (Xavier *et al*. 2020). For each web, we divided its *CTL* value by its respective capture area, obtaining a sticky capture thread density value (*CTD*, cm of sticky threads per capture area) for each web. The advantage of this method is the accurate estimate of the length of sticky thread an insect will come into contact with at the interception, which would not be possible if we only counted the number of sticky thread turns. All measurements were performed using ImageJ software (U.S. National Institutes of Health).

2.2 *Assessing the effect of orb-web traits on prey capture*

To assess the role of orb-web traits on prey size, we performed a model selection approach. First, we recorded prey length (in mm) and the corresponding web traits for each web: (i) the period of the day in which prey capture was observed (morning or night), (ii) the web height from the ground to the hub (in cm), (iii) the capture area (cm^2), (iv) the number of radii, and (v) the *CTD* (cm/cm^2). Second, we performed a set of generalized linear mixed models with gamma error distribution, using prey length as the response variable and the orb web traits as predictors. We mean-centered and scaled the predictors using the ‘scale’ function from the ‘scales’ package (Becker 1998). We included both spider species and sampling dates as random variables in all models.

We compared the adjustment of the alternative models and the null model using model selection. We considered the models with the smallest Akaike Information Criterion (AICc) values within a range of 2.0 from the smallest value (ΔAICc) to represent the best explanation(s) to the response variable (Burnham & Anderson 2002). Finally, we considered the simplest model as superior and dismissed the ones with uninformative parameters (*sensu* Arnold 2010). Lastly, when we chose the most informative model, we estimated bootstrap-based confidence intervals (95%) to the slopes of the predictors from the model (see Akdur *et al.* 2016). When a confidence interval did not include zero, this predictor was considered an informative parameter. We performed these analyses using ‘car’ (Fox & Weisberg 2011), ‘lme4’ (Bates 2015), and ‘MuMIn’ (Barton 2019) packages using R software, version 3.6.1 (R Development Core Team 2019).

We evaluated whether the prey families were affected by collection dates before assessing the influence of orb-web traits on their interceptions. We then performed a permutation multivariate analysis of variance (PERMANOVA) with the matrix as the abundance of prey families, using the collection weeks and the two seasons of expeditions as predictors. First, we calculated the Bray-Curtis dissimilarities of prey families along the temporal variables and applied 10,000 permutations using the ‘adonis2’ function from the ‘vegan’ package (Oksanen *et al.* 2019). Since there was no temporal bias (see Results), we could proceed without considering these in the next analyses. We then created three quantitative categories for each evaluated orb-web trait to assess the levels of trophic niche overlap. To classify the orb webs into these categories, we used the ‘kmeans’ function from the ‘classInt’ package (Bivand 2019). This method classifies the variable into *k* classes by grouping the values closest to the *k* means. Then, we built interaction matrices by adding the orb-web trait categories in the rows and the prey families in the columns.

To better demonstrate the levels of trophic niche overlapping, we built bipartite interaction networks using the ‘bipartite’ package (Dormann *et al*. 2008). Owing to the low number of categories on one side of the network (orb-web traits), network metrics such as modularity indexes were unreliable to quantify the segregation patterns. We applied Pianka’s (1973) overlap index to these matrices, in which ‘zero’ indicates total partitioning and ‘one’ indicates total overlapping. To assess whether the overlapping patterns were determined by the orb-web traits or as a result of stochastic processes, we performed Monte Carlo tests to determine whether the real overlapping values were less than 95% of the null distributions. Thus, for each interaction matrix, we generated a null distribution from 5,000 randomizations of the prey abundances captured by the web categories using the algorithm RA3 by Lawlor (1980). We performed these statistical analyses using the ‘EcoSimR’ package (Gotelli *et al*. 2015).

2.3 *Assessing the effect of height on prey interception using artificial webs*

To assess the effect of height on prey interception, we used standardized insect traps using wooden frames and nylon fishing lines that simulate certain orb-web features. These artificial webs had a capture area compatible with those of the surveyed natural webs of 18 × 18 cm (Fig. 1A). Fishing lines were attached to both sides of the frames, keeping 2 mm between adjacent lines. The lines had a 0.2 mm diameter and were white/semi-transparent (Mazzaferro®, Brazil). In the field, we coated the lines with a polybutene-based entomological glue (Colly Química, Brazil). In order to reduce the visual and olfactory bias, we suspended each trap with black strings that produced little contrast with the shaded understory environment, and covered the frames with dried leaves using adhesive tape (Fig. 1B). Based on the range of orb webs observed in the study area, we distributed the traps at three different heights, determined as the distance between the ground and the base of the web: low (40 cm), medium (110 cm), and high (180 cm) (Fig. 1C). We used eight triads of these traps (a total of 24 traps): four triads in June, and four triads in July 2018. Each triad was placed more than 80 m apart, while the traps in each triad were approximately 3 m apart. We aimed to evenly distribute the trap triads over the forest. We installed all traps between 12:00 and 13:00 and collected them 24 h later. All trapped insects were measured using the same procedure as previously described.

We performed a general linear mixed model with the insect length (mm) as the response variable, the categories of trap height (low, medium, and high) and the month of installation (first and second) as predictor variables, and the trap triad identity as a random variable. We graphically investigated the normality and homoscedasticity of the residuals. To compare subgroup differences, we conducted a Tukey's HSD *post hoc* test. We performed statistical analysis using 'lme4' (Bates *et al*. 2015) and 'car' packages (Fox & Weisberg 2011).

3. RESULTS

3.1 *Insect interceptions on natural webs*

We observed 269 natural prey capture events involving 37 insect families and 16 spider species. However, the number of events was asymmetrically distributed between the spider species, likely due to the relative abundance of each species in the study area (Table 1).

The largest number of insects was intercepted on *Metazygia* sp. webs (Table 1). This spider builds non-circular orb webs (Xavier *et al*. 2020) and remains hidden in a retreat placed on twigs or trunks located close to the web. When an insect is intercepted on the web, the spider leaves the retreat and subdues the prey. Webs of this species remain exposed during day and night.

Webs of *Parawixia audax* intercepted the second largest number of insects (Table 1). This solitary spider species builds circular orb webs at night. This is the largest spider species included in the samples and, consequently, exhibited the largest orb web and the highest variation of capture area and *CTD* (Table 1).

We also observed several insect interceptions on the webs of *Micrathena plana* (Table 1). This species builds circular orbs that remain exposed only during the daytime. Webs of *M. plana* are smaller than those of *P. audax*. They are similar in size to those constructed by *Metazygia* sp., but denser, presenting higher values for *CTD* and the number of radii (Table 1). The remaining events of insect interceptions were distributed between 13 other spider species, and involve diverse web sizes and thread densities.

3.2 *The effect of orb-web traits on prey capture*

Our model selection resulted in the seven alternative models with the best predictive power for the captured prey sizes (Table 2). Among these seven, the third model had the best parsimony, using only the capture area and the periods of the day (diurnal and nocturnal) as predictors (Table 2). Moreover, the inclusion of one additional predictor on this parsimonious model had a weak impact on the model weight (ω_i, Table

2). In this model, the estimated confidence intervals for both predictors did not include zero (Table 2, Fig. 2). The results showed that spiders building larger webs during the night were more prone to capture larger prey, despite small prey being frequently found in all types of webs (Fig. 2). Since an exceptionally large web was present in this model (Fig. 2), we performed another generalized linear model removing this outlier, and verified that the capture area and the period of the day retained their predictive effects on prey sizes (Table 3).

We found that neither the weeks of collections nor the seasons of expedition produced differences in insect families, explaining only 6% and 8% of the dissimilarities among these temporal variables, respectively (PERMANOVA: week – $F = 1.19$, $R^2 = 0.06$, d.f. = 1, $P = 0.28$; season of expedition – $F = 1.60$, $R^2 = 0.08$, d.f. = 1, $P = 0.07$; d.f. residuals = 16). When we tested whether orb-web traits influence the capture of different prey families, we considered only the three most abundant spider species: *Metazygia* sp., *P. audax*, and *M. plana*. We illustrated the interaction networks considering the foraging periods and capture area categories (Fig. 3). The remaining interaction networks in relation to the other orb-web traits can be found in the Supplementary Material. All situations produced intermediate levels of niche overlap, with Pianka’s indices around 0.5 (Table 4). However, these values did not differ from 95% of the values produced in random distributions.

3.3 *The effect of height on prey interception with the artificial webs*

In the artificial web experiment, the number of insects intercepted in each height category was similar: low (39), medium (43), and high (42). However, both the height categories and the temporal factors produced differences in terms of the captured prey size (Table 5). The second month presented larger insects than the first, without the interaction effect of the height category predictors (Fig. 1D, Table 5); therefore, we reconducted the comparisons for each. The sizes of insects captured by all height categories were not different in the first month of installation. However, they were different in the second one, with only the medium height category capturing smaller insects than the high height category (Fig. 1D, Table 5).

4. DISCUSSION

In this study, we hypothesized that orb-web traits, which include both architectural traits and temporal-spatial placement, would influence prey capture. Thus, different investments in each feature would result in distinct prey types. However, when we used a survey of natural prey interceptions by orb webs with a diversity of designs, we found that only two of these features influenced prey size. Orb webs with greater capture areas and nocturnal foraging activities were more likely to result in the interception of large insects, while small insects were frequently captured in all web types and periods. However, when considering the taxonomic identity of prey, we found that all types of orb webs were frequently intercepting prey from the same families.

Owing to the physical properties of radial threads, the function of the kinetic energy dampening exerted by the orb webs is primarily determined by radii. Ideally, the more radii the prey contacts during the interception, the more efficient the energy absorption (Sensenig *et al*. 2012). For this reason, we expected to find a higher frequency of large prey in webs with a larger number of radial threads. Instead, the orb-web capture area was the trait determining the higher frequency of large insects. This raises the question: why does the capture area explain the interception of larger insects, whereas the number of radii does not? It is known that in general, larger webs are produced by spider species with larger individuals (Blackledge *et al*. 2011, Harmer *et al*. 2011), which have relatively sizable silk glands able to produce a large number of denser threads (Mayntz *et al.* 2009). At the same time, it is known that these larger spiders are more likely to produce tougher threads, giving them the best potential for trapping prey (Sensenig *et al*. 2010, Sensenig *et al*. 2011). Therefore, it is plausible to suppose suggest that, in our survey, larger webs have the toughest threads.

The physical properties of threads can be more decisive to the stopping function than the number of radii in the web. Spiders that produce tougher silk (usually larger ones) (Sensenig *et al*. 2010, Sensenig *et al*. 2011) should not need a high density of radii to stop large prey, while spiders that produce weaker threads should compensate for their stopping limitations by increasing this density. Indeed, there are reports of younger spiders with weaker threads in their orb webs, producing more radii and more compact webs than larger individuals (Barrantes *et al.* 2017). In this study, *M. plana*, *Mangora* sp., and *Cyclosa* sp. had dense webs with a higher number of radii, and there is evidence that these genera have silk threads in the weaker classes of stopping potential (Sensenig *et al*. 2010). Contrastingly, *P. audax* and *Wagneriana* sp. had larger webs and presented a small number of radii. Moreover, there is evidence that longer radial threads are better suited for absorbing the prey impact than shorter ones, even if the silk properties are the same (Harmer *et al.* 2015). Therefore, only evaluating the number of radii is not sufficient to explain the stopping potential for large prey, when considering the physical properties of threads and their role in this process. Instead, the capture area can be a good proxy for the stopping potential of orb webs. However, given the limited number of sampled species in this study, expanding this investigation to future studies would better clarify this relationship. Nevertheless, considering this relation (the greater the capture area, the greater the stopping potential) as a possibility, spider species with a wide range of growth should capture a greater diversity of prey sizes along their life cycle. Indeed, in a stable isotope assessment, a positive relationship was verified between body-size range and niche size (Sanders *et al*. 2015).

The remaining web trait, the capture thread density (*CTD*), did not influence the size of intercepted insects. It is known that contact with a large number of sticky threads by the prey reduces the risk of escape (Blackledge & Zevenbergen 2006, Opell *et al*. 2006). However, insect behavior after interception, and escaping abilities based on morphological features, such as the presence of scales in the wings of moths also affect this risk (Blackledge & Zevenbergen 2006, Gwynne *et al*. 2007). The absence of a relationship between *CTD* and prey size may be explained by the theory that prey size is independent of prey escaping abilities. We suppose that a large insect body can have both positive and negative influences on the likelihood of escaping. A large individual can contact several sticky threads, but it may be stronger than smaller prey, and therefore able to physically break more lines to escape. Thus, escaping abilities may depend more on behavioral traits, such as insect body adherence, prey threat level, and even spider speed and subduing abilities. The second possible cause is related to the intrinsic physical properties of the threads. Webs with different *CTDs* can have compatible retention abilities if the low densities of capture threads are compensated for by high stickiness.

Considering the height of the web placement and the foraging period (nocturnal or diurnal), only the latter trait affected the capture of differently sized prey. Webs exposed at night were more likely to capture large prey. There is some evidence that larger spiders, which are more likely to subdue large prey, adjust their web building behavior to match longer insect activity periods (Ward & Lubin 1992). Therefore, given that the larger webs included in this study were recorded at night, it is quite possible that the spider’s temporal activities reflect their optimal foraging abilities. The height of the web building, however, did not explain differences in the capture of insects of different sizes, considering natural capture events. This result does not corroborate the hypothesis that higher web heights are more likely to intercept larger insects in mid-flight (Hénaut *et al*. 2006). Sanders *et al*. (2015) found that spiders building webs near to the ground present peculiar, nitrogen, isotopic signatures in relation to spiders with webs placed at higher sites. However, these low webs were not orb webs and were capturing ground-dwelling invertebrates, such as springtails (Sanders *et al*. 2015). Here, we controlled these architectural features using artificial webs. We found no relationship between height class and prey catching ability, as statistical differences emerged, and only the high and medium categories differed from each other in a specific month of installation. Hénaut *et al*. (2006) verified a correlation between web size and web height, which can plausibly explain the capture of large insects, assuming that large webs are more likely to stop prey. In our study, however, we did not observe such a web size-web height correlation.

Finally, although we observed that the size of the intercepted prey was influenced by the capture area and by the period of foraging activity, prey composition was independent of all orb-web traits and placements. Despite this, we reported a partial overlap in prey composition for each of the traits included in this study. This occurs because some insects are intercepted only by some types of web categories. For example, considering the temporal classification, most of the Formicidae, Chrysomellidae, and Cicadellidae were captured at night, while almost all Aleyrodidae and Pseudocaecilidae were captured in webs exposed during the day. However, some of the most frequently captured insect groups, such as Cecidomyiidae and Aphididae, were observed to be intercepted in both periods. Therefore, in general, all spiders captured the same set of the main families of prey, despite some specific types of prey being exclusively intercepted by some web categories. As in other surveys (Sanders *et al*. 2015, Ludwig *et al*. 2018), our results showed that spiders exhibit generalist prey consumption patterns, suggesting that even if a group of webs were capturing predominantly smaller or larger insects, the spiders were not targeting a specific range of prey families.

It is hypothesized that large prey can be especially important for spider nutrition and reproduction (Venner & Casas 2005, Blackledge 2011). However, more recent assessments suggest that the energetic value of these large prey has been overestimated (Eberhard 2013), and they are captured so infrequently that the spider biomass acquisition relies more on the frequency of interception of common, relatively small prey than on the consumption of large and rare prey (Harmer *et al.* 2015). The design of our survey is not suitable to properly assess the energetic contribution of each prey size to the spiders. It is beyond the scope of our research. However, we verified that some orb webs are more prone to capture larger prey, and possibly the biomass content of these prey may be more relevant to some spiders, likely the larger ones. Thus, future research on prey capture should clarify whether the specific energetic demands drive differential investment in each web trait. Much work must be done to understand the patterns of interactions between orb-web spiders and prey. We investigated some assumptions, which were traditionally tested in the laboratory or were restricted to a few species, in a wider field examination. The web size and the daily period of web placement appeared to be good candidates for functional traits (see Schmitz 2017) affecting the orb-web, spider-prey interactions, which future research may address.

LITERATURE CITED

Akdur, H.T.K., Özonur, D. & Bayrak, H. 2016. Comparison of Confidence Interval Methods of Fixed Effect in Nested Error Regression Model. *Journal of Natural and Applied Sciences*. 20, 167-175.

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management*. 74, 1175-1178.

Cardoso, P., Pekár S., Jocqué, R. & Coddington, J.A. 2011. Global Patterns of Guild Composition and Functional Diversity of Spiders. *PLoS ONE*. 6, e21710. DOI: doi.org/10.1371/journal.pone.0021710

Barrantes, G., Triana, E. & Sánchez-Quiróz, C. 2017. Functional changes in web design along the ontogeny of two orb-weavers. *Journal of Arachnology*. 45, 152-159. DOI: doi.org/10.1636/JoA-S-16-026.1

Barton, K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.10.

Bates, D., Mächler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. 67, 1-48. DOI: 10.18637/jss.v067.i01

Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A. & Wood, E.F. 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. *Scientific Data*. 5, 180214. DOI: 10.1038/sdata.2018.214

Becker, R.A., Chambers, J.M. & Wilks, A.R. 1988. *The New S Language*. Wadsworth & Brooks/Cole.

Bivand, R. 2019. classInt: Choose Univariate Class Intervals. R package version 0.4-2.

Blackledge, T.A. 2011. Prey capture in orb weaving spiders: are we using the best metric? *Journal of Arachnology*. 39, 205-210. DOI: doi.org/10.1636/Chi10-52.1

Blackledge, T.A., Kuntner, M. & Agnarsson, I. 2011. The form and function of spider orb webs: evolution from silk to ecosystems. *Advances in Insect Physiology* (ed. J. Casas), pp. 175-262. Academic Press, Burlington.

Blackledge, T.A. & Eliason, C.M. 2007. Functionally independent components of prey capture are architecturally constrained in spider orb webs. *Biology Letters*. 3, 456-458. DOI: doi.org/10.1098/rsbl.2007.0218

Blackledge, T.A. & Zevenbergen, J.M. 2006. Mesh width influences prey retention in spider orb webs. *Ethology*. 112, 1194-1201. DOI: doi.org/10.1111/j.1439-0310.2006.01277.x

Burnham, K.P. & Anderson, D.R. 2002. *Model selection and multimodel inference a practical information: Theoretic approach*, 2nd Edition. Springer-Verlag New York Inc., New York.

Dormann, C.F., Gruber, B. & Fruend, J. (2008) Introducing the bipartite Package: Analysing Ecological Networks. *R news*. (8/2), 8-11.

Eberhard, W.G. (2013) The rare large prey hypothesis for orb web evolution: a critique. *Journal of Arachnology*. 41, 76-80. DOI: doi.org/10.1636/B12-34.1

Eberhard, W.G. 2014. A new view of orb webs: multiple trap designs in a single structure. *Biological Journal of the Linnean Society*. 111, 437-449. DOI: doi.org/10.1111/bij.12207

Foelix, R.F. 2011. *Biology of spiders,* 3rd edition. Oxford University Press, Oxford.

Fox, J. & Weisberg, S. 2011. *An {R} Companion to Applied Regression*. Sage, Thousand Oaks.

Gregorič, M., Agnarsson. I., Blackledge, T.A. & Kuntner, M. 2011. Darwin's bark spider: giant prey in giant orb webs (*Caerostris darwini*. Araneae: Araneidae)? *Journal of Arachnology*. 39, 287-295. DOI: doi.org/10.1636/CB10-95.1

Gotelli, N.J., Hart, E.M. & Ellison, A.M. 2015. EcoSimR: Null model analysis for ecological data. DOI: doi.org/10.5281/zenodo.16636

Harmer, A.M.T., Blackledge, T.A., Madin, J.S. & Herberstein, M.E. 2011. High-performance spider webs: integrating biomechanics, ecology and behaviour. *Journal of The Royal Society Interface*. 8, 457-471. DOI: doi.org/10.1098/rsif.2010.0454

Harmer, A.M.T., Clausen, P.D., Wroe, S. & Madin, J.S. 2015. Large orb-webs adapted to maximise total biomass not rare, large prey. *Scientific Reports*. 5, 14121. DOI: doi.org/10.1038/srep14121

Hénaut, Y., García-Ballinas, J.A. & Alauzet, C. 2006. Variations in web construction in *Leucauge venusta* (Araneae. Tetragnathidae). *Journal of Arachnology*. 34, 234-240. DOI: doi.org/10.1636/S02-65.1

Hothorn, T., Bretz, F. & Westfall, P. 2008. Simultaneous Inference in General Parametric Models. *Biometrical Journal*. 50, 346-363. DOI: doi.org/10.1002/bimj.200810425

Instituto Nacional de Meteorologia. 2020. Ministério da Agricultura, Pecuária e Abastecimento. https://portal.inmet.gov.br/dadoshistoricos

Lawlor, L.R. 1980. Overlap, similarity, and competition coefficients. *Ecology*. 61, 245-251. DOI: doi.org/10.2307/1935181

Ludwig, L., Barbour, M.A., Guevara, J., Avilés, L. & González, A.L. 2018. Caught in the web: Spider web architecture affects prey specialization and spider–prey stoichiometric relationships. *Ecology and Evolution*. 8, 1-14. DOI: doi.org/10.1002/ece3.4028

Mayntz, D., Toft, S. & Vollrath, F. 2009. Nutrient balance affects foraging behaviour of a trap-building predator. *Biology Letters*. 5, 735-738. DOI: doi.org/10.1098/rsbl.2009.0431

Nentwig, W. 1987. The prey of spiders. *Ecophysiology of Spiders* (ed. W. Nentwig), pp. 251. Springer-Verlag, Berlin.

Nyffeler, M. 2000. Ecological impact of spider predation: a critical assessment of Bristowe's and Turnbull's estimates. *Bulletin of the British Arachnological Society*. 11, 367-373.

Nyffeler, M. & Birkhofer, K. 2017. An estimated 400–800 million tons of prey are annually killed by the global spider community. *The Science of Nature*. 104, 30. DOI: doi.org/10.1007/s00114-017-1440-1

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., & Wagner, H. 2019. vegan: Community Ecology Package. R package version 2.5-6.

Pekár, S., Coddington, J. & Blackledge, T. 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. DOI: doi.org/10.1111/j.1558-5646.2011.01471.x

Pianka, E.R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics*. 4, 53-74. DOI: doi.org/10.1146/annurev.es.04.110173.000413

Pitilin, R.B., Moura, R.R. & Gonzaga, M.O. 2020. Population and individual trophic niche breadths of two sympatric cobweb spiders, *Nihonhimea tesselata* and *Tidarren haemorrhoidale* (Araneae: Theridiidae). *Journal of Arachnology*. 48, 59-66. DOI: doi.org/10.1636/0161-8202-48.1.59

R Development Core Team. 2019. R: A language and environment for statistical computing.

Sanders, D., Vogel, E. & Knop, E. 2015. Individual and species-specific traits explain niche size and functional role in spiders as generalist predators. *Journal of Animal Ecology*. 84, 134-142. DOI: doi.org/10.1111/1365-2656.12271

Sandoval, C.P. 1994. Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Functional Ecology*. 8, 701-707. DOI: doi.org/10.2307/2390229

Schmitz, O. 2017. Predator and prey functional traits: understanding the adaptive machinery driving predator-prey interactions. *F1000Research*. 6, 1767. DOI: doi.org/10.12688/f1000research.11813.1

Sensenig, A., Agnarsson, I. & Blackledge, T.A. 2010. Behavioural and biomaterial coevolution in spider orb webs. *Journal of Evolutionary Biology*. 23, 1839-1856. DOI: doi.org/10.1111/j.1420-9101.2010.02048.x

Sensenig, A., Agnarsson, I. & Blackledge, T.A. 2011. Adult spiders use tougher silk: ontogenetic changes in web architecture and silk biomechanics in the orb-weaver spider. *Journal of Zoology*. 285, 28-38. DOI: doi.org/10.1111/j.1469-7998.2011.00809.x

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. DOI: doi.org/10.1098/rsif.2011.0851

Toft, S. 2013. Nutritional aspects of spider feeding. *Spider Ecophysiology* (ed. W. Nentwig). Springer-Verlag.

Triplehorn, C.A. & Johnson, N.F. 2017. *Borror and Delong's introduction to the study of insects*. Thompson Brooks/Cole, Belmont.

Venner, S., & Casas, J. 2005. Spider webs designed for rare but life-saving catches. *Proceedings of the Royal Society B*. 272, 1587-1592. DOI: doi.org/10.1098/rspb.2005.3114

Vollrath, F. & Selden, P. 2007. The Role of Behavior in the Evolution of Spiders, Silks, and Webs. *Annual Review of Ecology, Evolution, and Systematics*. 38, 819-846. DOI: doi.org/10.1146/annurev.ecolsys.37.091305.110221

Ward, D. & Lubin, Y. 1992. Temporal and spatial segregation of web-building in a community of orb-weaving spiders. *Journal of Arachnology*. 20, 73-87.

Wickham, H. & Seidel, D. 2019. scales: Scale Functions for Visualization. R package version 1.1.0.

Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge.

World Spider Catalog. 2019. World Spider Catalog. version 20.5. Natural History Museum. Bern. Accessed 17 Dezember 2019. http://wsc.nmbe.ch

Xavier, G.M., Moura, R.R. & Gonzaga, M.O. 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. DOI: doi.org/10.1636/JoA-S-17-001.1

Xavier, G.M., Moura, R.R. & Gonzaga, M.O. 2020. Towards simplicity and accuracy: assessing traditional and new estimators of orb-web capture thread length. *Behavioural Processes*. 173, 104086. DOI: doi.org/10.1016/j.beproc.2020.104086

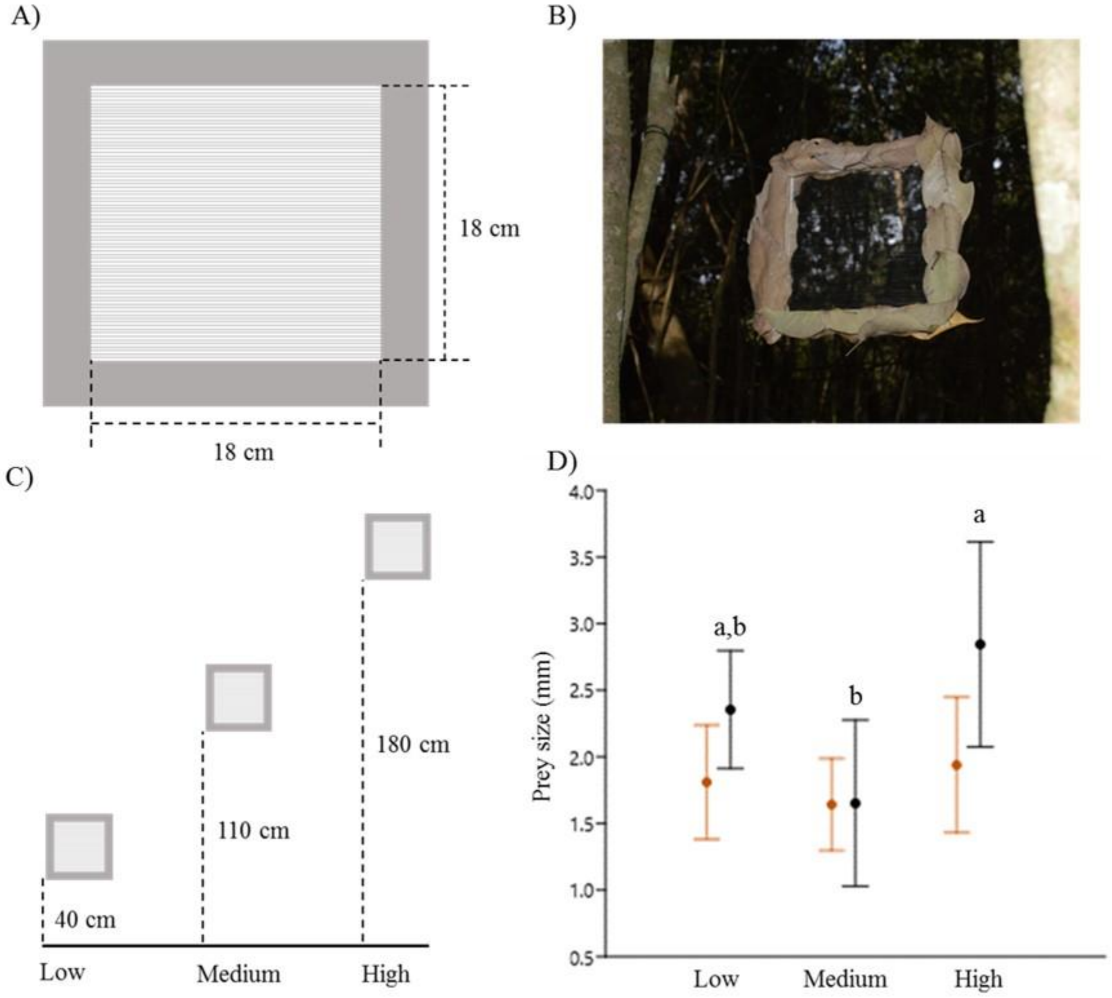


Figure 1. (A) The basic structure of artificial webs. (B) Artificial web installed in the field. (C) The three height categories used for web placement. (D) Means and 95% confidence intervals of the sizes (mm) of the captured prey by each height category. Different letters indicate statistical differences between the categories. Orange indicate the first month of installation and black the second month.

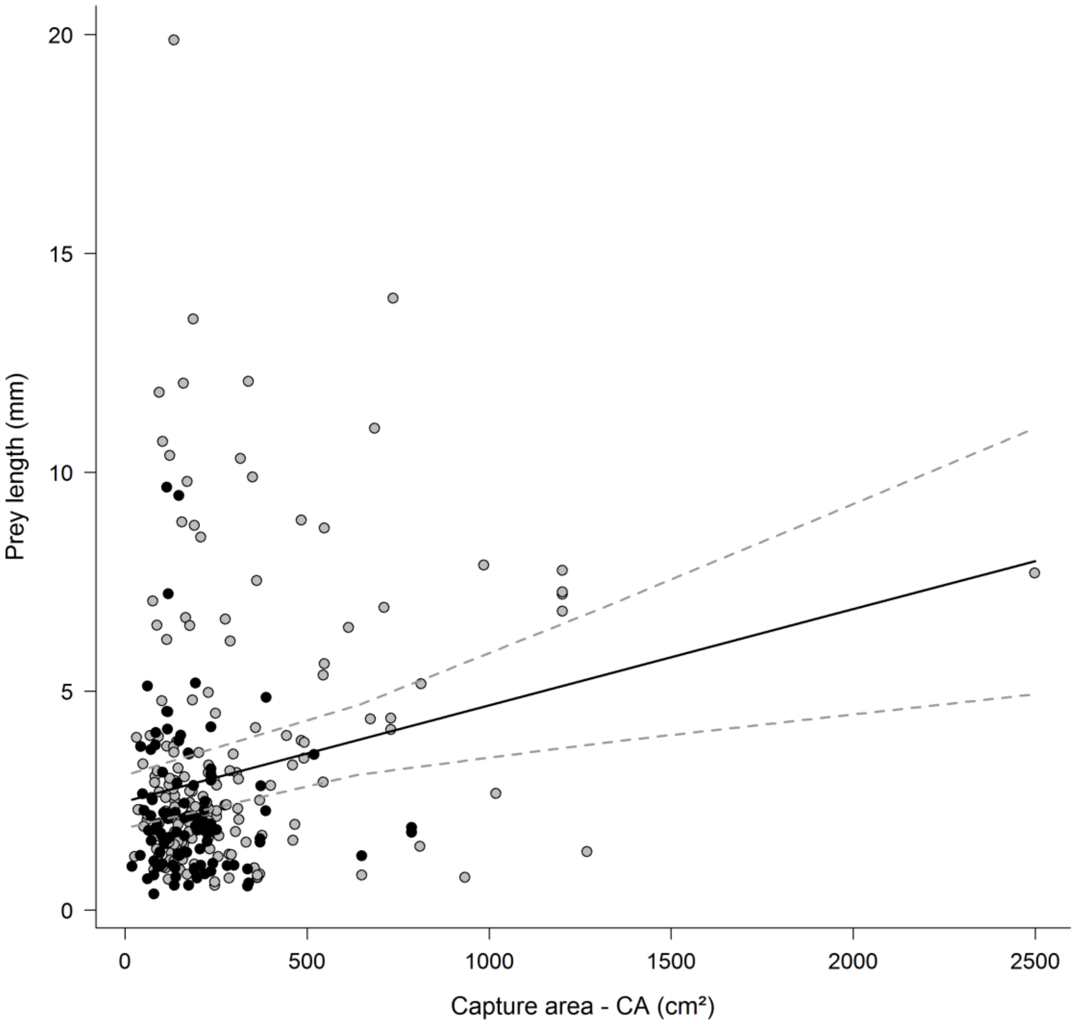


Figure 2. The selected parsimonious model, with a 95% confidence interval (Table 2). This model includes the effects of the webs' capture area and the period of interception (night in grey, and day in black) over the prey length. Nocturnal and larger webs intercepted larger prey.

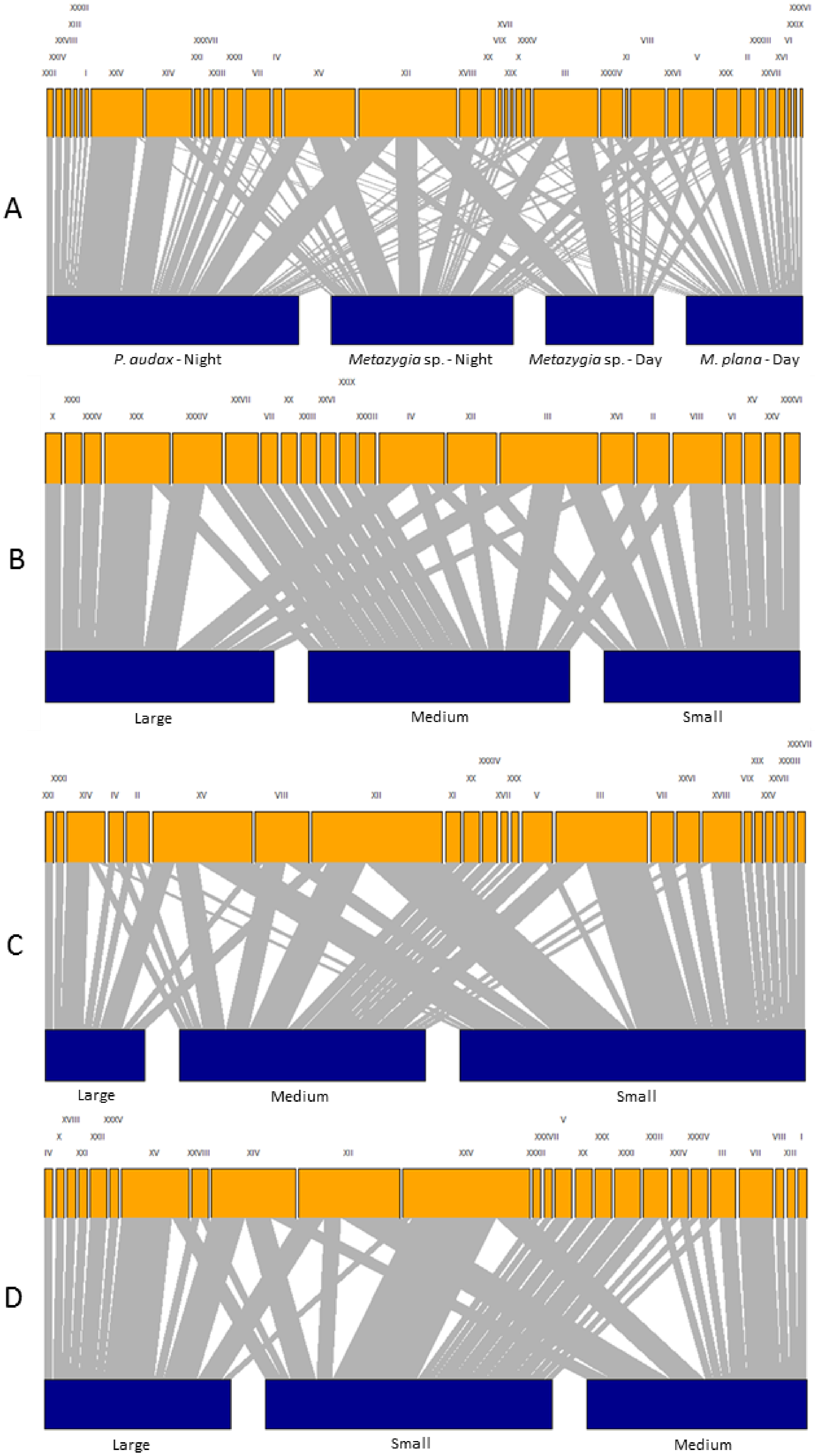

A
P. audax - Night
Metazygia sp. - Night
Metazygia sp. - Day
M. plana - Day
B
Large
Medium
Small
C
Large
Medium
Small
D
Large
Small
Medium

Figure 3. Bipartite interaction networks between spiders (blue) and prey families (orange). (A) The three most abundant orb-web spiders are categorized considering the interaction period (night and day). (B-D) The three most abundant orb-web spiders are categorized considering the capture areas: (B) *Micrathena plana*, (C) *Metazygia* sp., and (D) *Parawixia audax*. Categories and insect families are disposed according interaction similarities. The interaction networks for the other web traits are shown in the Supplementary Material. Insect groups: I-Acalyptratae (1 individual), II-Aleyrodidae (5), III-Aphidiae (21), IV-Apidae (3), V-Asilidae (10), VI-Bibionidae (1), VII-Bostrichidae (8), VIII-Brachonidae (11), IX-Brochidae (9), X-Buprestidae (2), XI-Caecilidae (1), XII-Cecidomyiidae (32), XIII-Chalcididae (1), XIV-Chrysomellidae (15), XV-Cicadellidae (23), XVI-Cinipidae (2), XVII-Coccinellidae (1), XVIII-Curculionidae (6), XIX-Dolichopodidae (1), XX-Drosophilidae (5), XXI-Elateridae (2), XXII-Empidiae (2), XXIII-Eurytomidae (4), XXIV-Flatidae (2), XXV-Formicidae (winged) (17), XXVI-Fulgoridae (4), XXVII-Ichneumonidae (3), XXVIII-Lycidae (2), XXIX-Miriidae (1), XXX-Pseudocaeciliidae (7), XXXI-Psocidae (5), XXXII-Psychodidae (1), XXXIII-Pteromalidae (2), XXXIV-Sciaridae (7), XXXV-Simuliidae (2), XXXVI-Staphylinidae (1), XXXVII-Vespidae (2).

Table 1. Descriptive features of behavioural and web architectural traits of each recorded spider species. Mean ± SD and Variation coefficient are shown to each web trait, except for rare records (≤ 5. just the mean is shown). The N represents exclusively nocturnal interactions and D exclusively diurnal interactions; 'D and N' represents spiders that capture activities cross both periods while 'D or N' represents spiders that can choose one of these periods to build webs.

Spider species	Number of interactions	Capture area (cm²)	*CTD* (cm/cm²)	Height (cm)	Number of radii	Activity
Metazygia sp.	90	175.96 ± 90.62, 51.50	4.86 ± 1.78, 36.62	125.32 ± 44.4, 35.42	31.32 ± 8.04, 25.67	D and N
Parawixia audax	82	366.04 ± 300.16, 82.00	4.61 ± 2.62, 56.83	96.81 ± 43.43, 44.86	21.82 ± 3.78, 17.32	N
Micrathena plana	42	163.95 ± 60.37, 36.82	10.58 ± 3.18, 30.05	95.29 ± 40.38, 42.37	61.70 ± 5.70, 9.23	D
Wagneriana sp.	9	271.10 ± 122.63, 45.23	5.02 ± 1.31, 26.09	114.44 ± 43.33, 37.86	20.55 ± 3.00, 14.59	D or N
Wixia abdominalis	7	135.55 ± 25.60, 18.88	5.97 ± 0.60, 10.05	91.14 ± 63.76, 69.95	28 ± 3.69, 13.17	N
Alpaida sp.1	7	151.42 ± 59.05, 38.99	4.55 ± 0.92, 20.21	92.92 ± 37.39, 40.23	17.83 ± 1.83, 10.26	D or N
Alpaida sp.2	5	266.79	5.92	45.6	25.06	D
Mangora sp.	5	130.42	17.47	98.4	52.4	D or N
Araneidae sp.1	4	556.1	3.07	92.37	21.25	D or N
Araneidae sp.2	4	502.72	3.01	112.75	17.05	D or N
Araneidae sp.3	4	70.15	9.17	159.87	24.75	D or N
Araneidae sp.4	4	165.24	7.20	125.5	43.75	D or N
Cyclosa sp.	2	71.95	12.49	102.5	51.5	D and N
Uloborus sp.	2	168.54	3.39	98	42.5	D
Leucauge sp.	1	47.1	13.78	131	40	D
Araneus sp.	1	2498.24	1.95	202	38	N

Table 2. Results of a model selection procedure to investigate the prediction of different orb-web traits over the size of the intercepted insects: period of the interception (day or night), web height, capture area (cm^2), capture threads density (*CTD*, cm/cm^2), and number of radii. The alternative models are ranked according to their Akaike Information Criterion (AICc) values. The best models are shaded in grey (ΔAICc ≤ 2) and the most parsimonious model is in bold. ΔAICc is the difference between the AICc value of each model and the AICc value of the most parsimonious model; K is the number of parameters; $\boldsymbol{\omega_i}$ = AICc weight of each model.

Model' intercept	Coefficients' estimates					K	AICc	ΔAICc	ωi
	Period	Height	Capture area	*CTD*	Nº of radii				
2.248	+		0.570		0.227	7	1082.2	0	0.204
2.263	+		0.666	0.197		7	1082.9	0.71	0.143
2.243	**+**		**0.563**			**6**	**1083**	**0.74**	**0.141**
2.301	+	0.130	0.605		0.218	8	1083	0.8	0.136
2.355	+	0.148	0.700	0.214		8	1083.3	1.1	0.117
2.33	+	0.135	0.587			7	1083.7	1.52	0.095
2.245	+		0.625	0.103	0.167	8	1083.8	1.54	0.094
2.296	+	0.138	0.668	0.120	0.149	9	1084.4	2.18	0.068
2.227	+					5	1095.7	13.49	0
2.13	+				0.153	6	1096.3	14.12	0
2.818		0.219	0.711			6	1097	14.73	0
2.222	+	0.091				6	1097.3	15.03	0
2.133	+			-0.111	0.233	7	1097.4	15.21	0
2.219	+			-0.037		6	1097.7	15.48	0
2.147	+	0.070			0.148	7	1098.1	15.88	0
2.748			0.639			5	1098.4	16.13	0
2.803		0.216	0.736	0.046		7	1099	16.73	0
2.808		0.214	0.703		-0.053	7	1099	16.74	0
2.217	+	0.096		-0.049		7	1099.2	16.97	0
2.155	+	0.062		-0.107	0.226	8	1099.3	17.05	0
2.733			0.686	0.077		6	1100.2	17.95	0

2.743		0.634		-0.085	6	1100.3	18.02	0
2.777	0.206	0.746	0.086	-0.100	8	1100.8	18.59	0
2.715		0.709	0.128	-0.148	7	1101.8	19.57	0
2.691					4	1112.7	30.46	0
2.679	0.169				5	1112.7	30.51	0
2.719	0.180		-0.173		6	1112.9	30.69	0
2.719			-0.156		5	1113.2	30.98	0
2.69				-0.114	5	1114.5	32.25	0
2.676	0.167			-0.109	6	1114.5	32.31	0
2.714	0.178		-0.169	-0.052	7	1115	32.73	0
2.719			-0.151	-0.064	6	1115.2	32.97	0

Table 3. Since an exceptionally large web was present the selected model (Fig. 2), we performed a generalized linear model with a Gamma error distribution removing this outlier, and verified that the capture area and periods of interaction keep their predictive effects on prey size.

	Coefficient' estimate	Standard error	*t* value	*P*
Intercept	2.243	0.327	6.853	< 0.001
Capture area	0.563	0.169	3.321	< 0.001
Period	1.224	0.307	3.985	< 0.001

Table 4. Chances to acquire the observed Pianka's overlap values randomly with Monte Carlo tests to each interaction network. The probability *P* of the observed values being greater than 5% of the smaller values of the null distribution is shown.

Interaction network	Orb-web trait categories	Observed Pianka's index	Mean of simulated Pianka's index	5% threshold of smaller values of the null distribution	*P*
Period of interactions		0.58	0.28	0.22	0.998
Metazygia sp.	Capture area	0.65	0.35	0.23	0.99
Parawixia audax		0.46	0.28	0.17	0.97
Micrathena plana		0.47	0.43	0.32	0.70
Metazygia sp.	*CTD*	0.73	0.37	0.26	0.99
Parawixia audax		0.49	0.31	0.20	0.97
Micrathena plana		0.35	0.38	0.27	0.32
Metazygia sp.	Web height	0.81	0.37	0.26	0.99
Parawixia audax		0.63	0.33	0.23	0.99
Micrathena plana		0.30	0.34	0.23	0.33
Metazygia sp.	Number of radii	0.74	0.33	0.21	0.99
Parawixia audax		0.20	0.23	0.12	0.44
Micrathena plana		0.23	0.32	0.19	0.13

Table 5. General linear mixed models with Gaussian error distributions testing the influence of the height categories (low, medium, high) and installation months of artificial webs over the captured prey sizes. As the month of installation shows a significative effect without interaction in the complete model, we conduct separate tests to first and second installation months with Tukey *post hoc* tests. *significance with a α = 0.05.

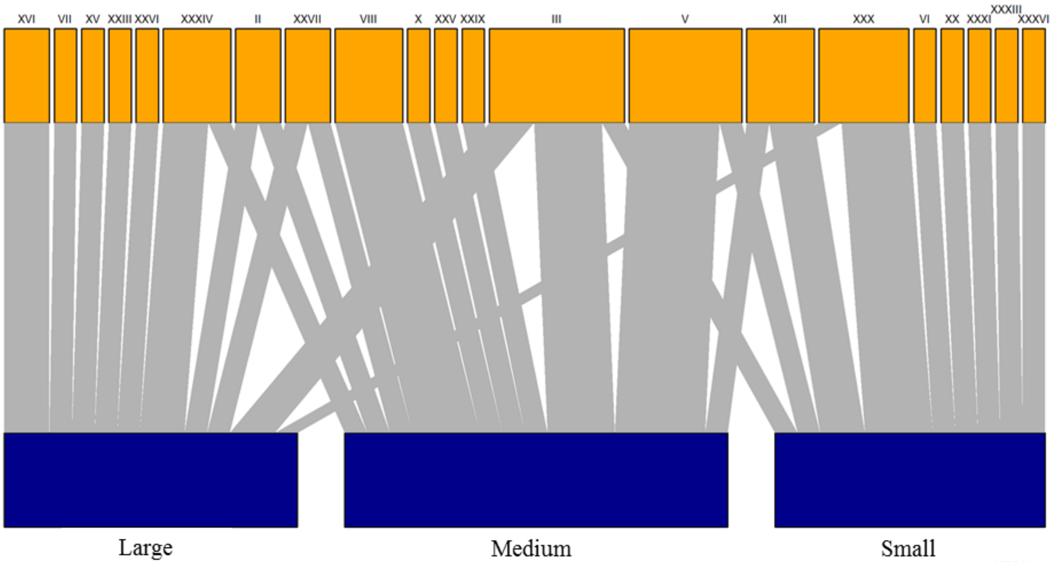
GLMM	Predictor	F	d.f.	d.f. residuals	*P*
Complete	Height category	3.83	2	117.58	0.02*
	Month	4.26	1	117.27	0.04*
	Height category * Month	1.19	2	116.35	0.30
First installation month	Height category	0.45	2	55	0.63
Second installation month	Height category	3.56	2	63	0.03*
Tukey's HSD *post hoc* tests	low vs. high				0.55
	medium vs. high				0.02*
	low vs. medium				0.28

SUPPLEMENTARY MATERIAL

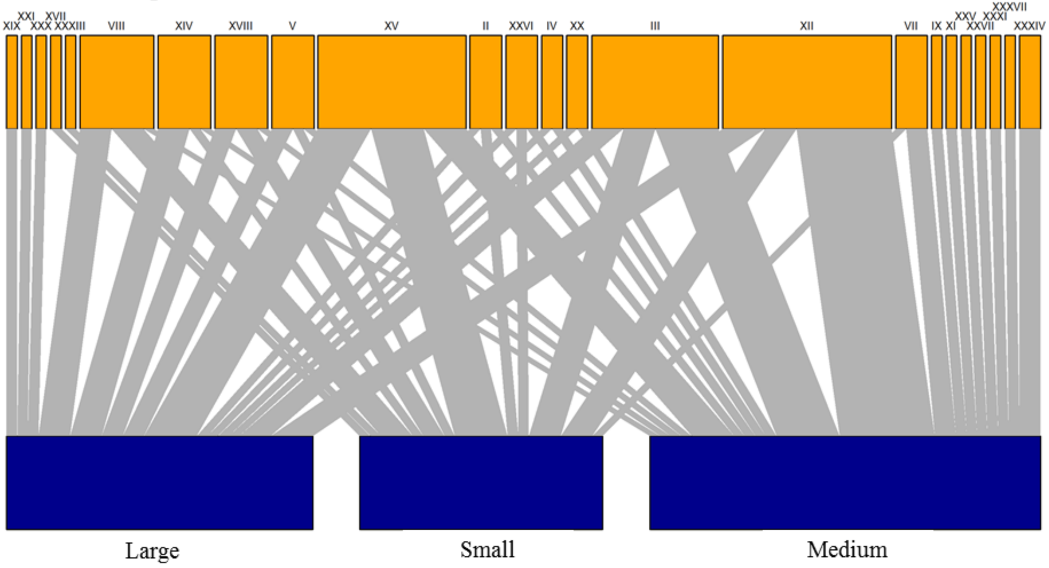
CHAPTER 2

At the following pages we show the remaining bipartite interaction networks between spiders (blue) and prey families (orange) from which we assess the niche overlapping analyses (Table 4). The three most abundant orb-web spiders (blue) are categorized in relation to the web height (E, F, G), *CTD* (H, I, J), and number of radii in their webs (K, L, M). The order of the spider specied from top to bottom spiders to each trait is: *Micrathena plana*, *Metazygia* sp., and *Parawixia audax*. Categories and insect families are disposed according interaction similarities. The interaction networks for the other web traits are shown at the Supplementary Material. Insect groups: I-Acalyptratae, II-Aleyrodidae, III-Aphidiae, IV-Apidae, V-Asilidae, VI-Bibionidae, VII-Bostrichidae, VIII-Brachonidae, IX-Brochidae, X-Buprestidae, XI-Caecilidae, XII-Cecidomyiidae, XIII-Chalcididae, XIV-Chrysomellidae, XV-Cicadellidae, XVI-Cinipidae, XVII-Coccinellidae, XVIII-Curculionidae, XIX-Dolichopodidae, XX-Drosophilidae, XXI-Elateridae, XXII-Empidiae, XXIII-Eurytomidae, XXIV-Flatidae, XXV-Formicidae (winged), XXVI-Fulgoridae, XXVII-Ichneumonidae, XXVIII-Lycidae, XXIX-Miriidae, XXX-Pseudocaeciliidae, XXXI-Psocidae, XXXII-Psychodidae, XXXIII-Pteromalidae, XXXIV-Sciaridae, XXXV-Simuliidae, XXXVI-Staphylinidae, XXXVII-Vespidae.

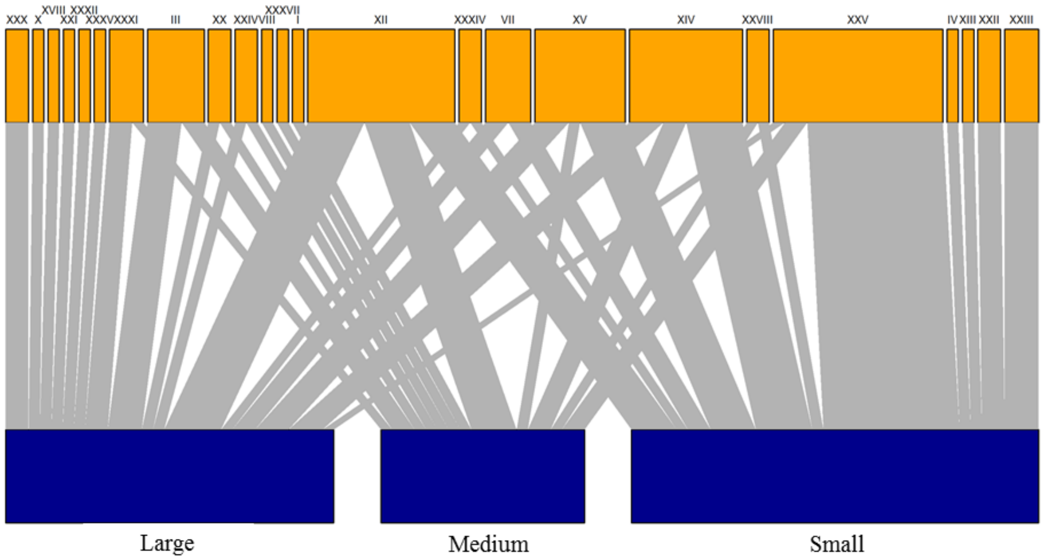
E


XVI
VII
XV
XXIII
XXVI
XXXIV
II
XXVII
VIII
X
XXV
XXIX
III
V
XII
XXX
VI
XX
XXXI
XXXIII
XXXVI
Large
Medium
Small

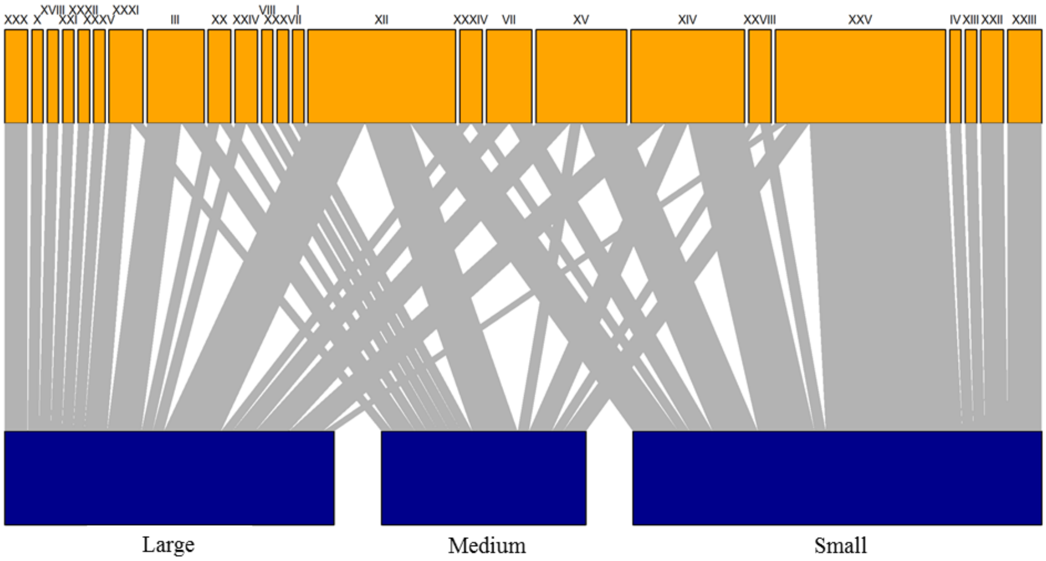
F


XIX
XXI
XXX
XVII
XXXIII
VIII
XIV
XVIII
V
XV
II
XXVI
IV
XX
III
XII
VII
IX
XI
XXV
XXVII
XXXI
XXXVII
XXXIV
Large
Small
Medium

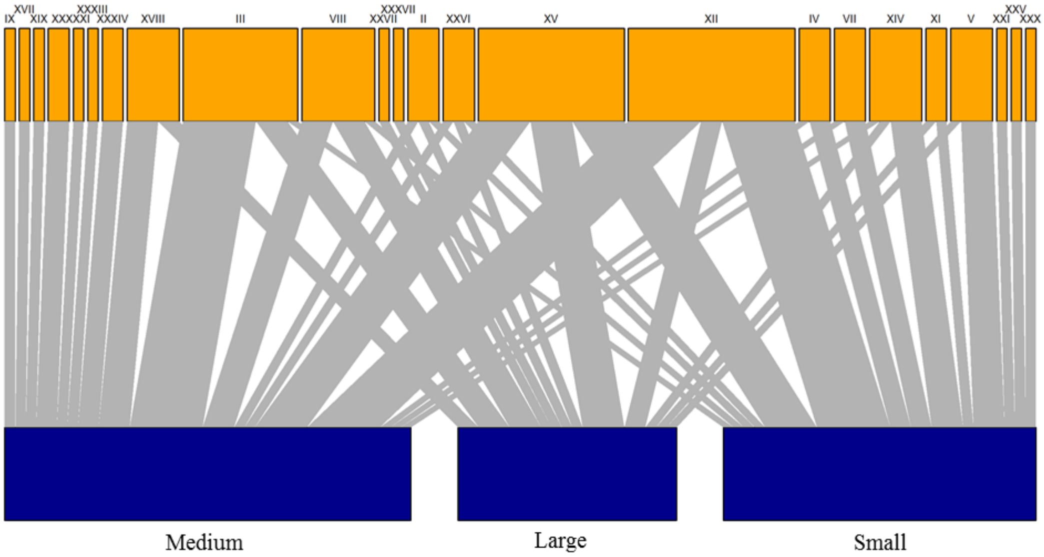
G


XXX
X
XVIII
XXI
XXXII
XXXV
XXXI
III
XX
XXIV
VIII
XXXVII
I
XII
XXXIV
VII
XV
XIV
XXVIII
XXV
IV
XIII
XXII
XXIII
Large
Medium
Small

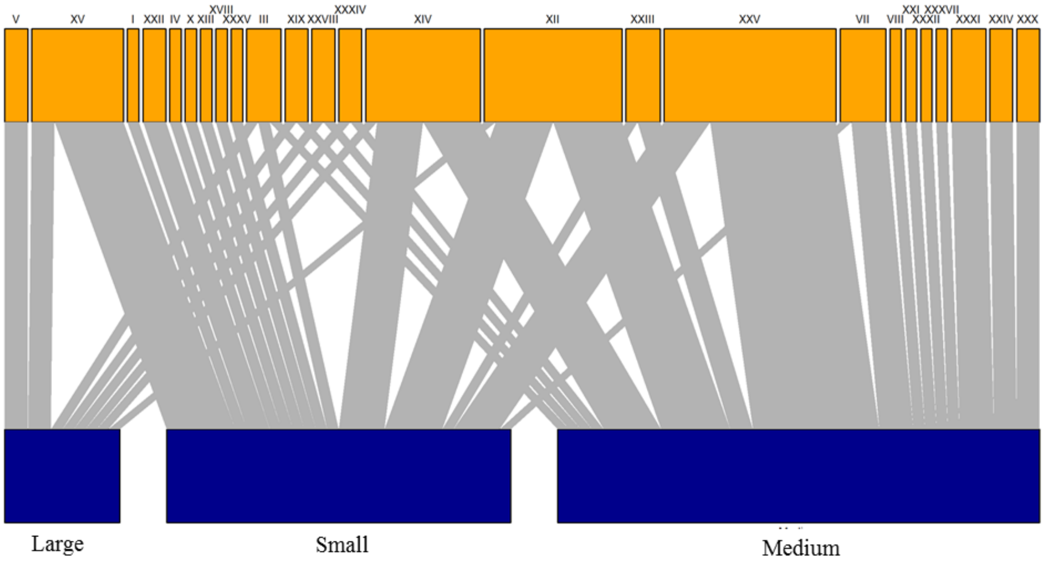
H

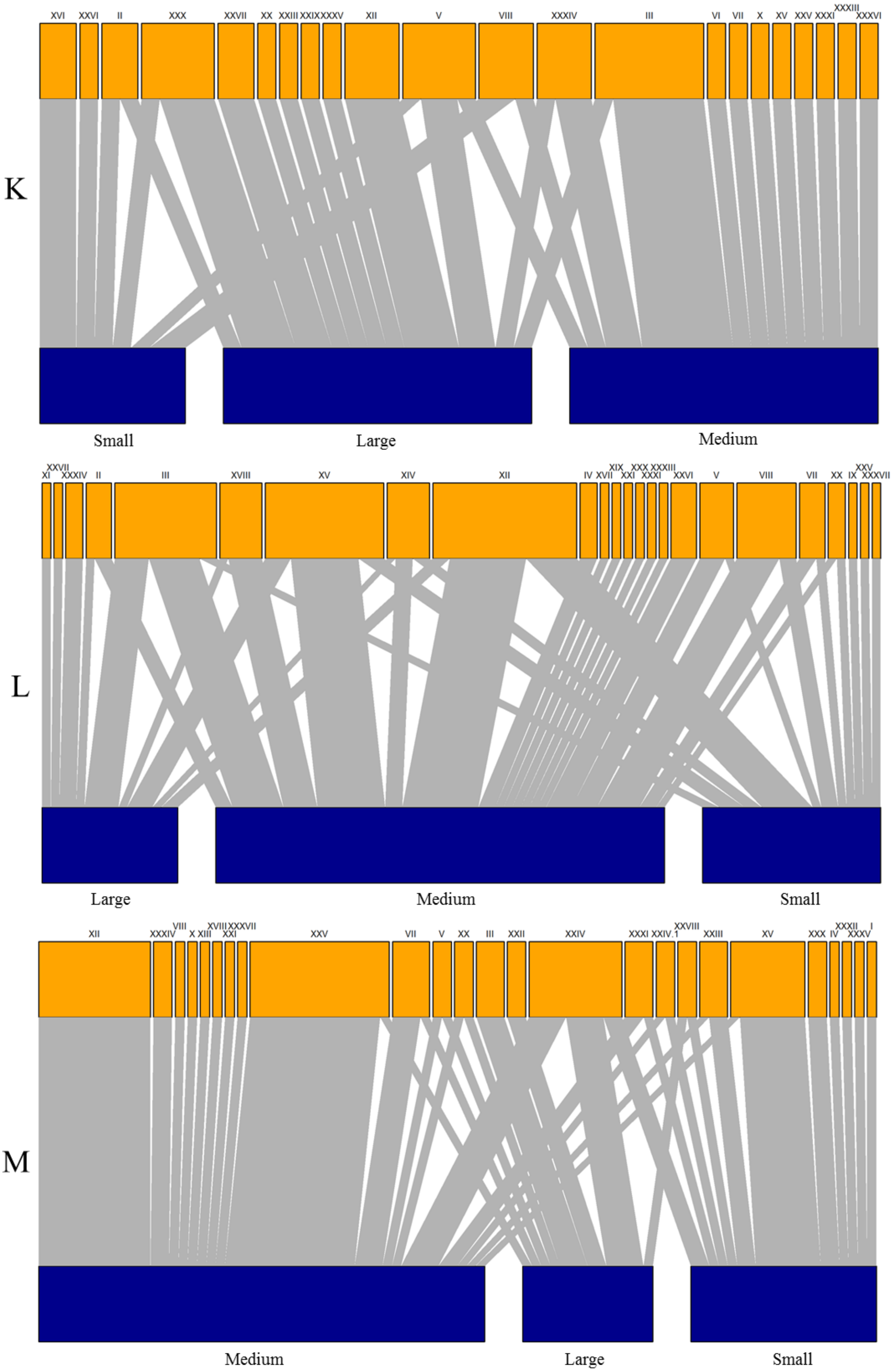

XXX
X
XVIII
XXI
XXXII
XXXV
XXXI
III
XX
XXIV
VIII
XXXVII
I
XII
XXXIV
VII
XV
XIV
XXVIII
XXV
IV
XIII
XXII
XXIII
Large
Medium
Small

I


IX
XVII
XIX
XXXXXI
XXXIII
XXXIV
XVIII
III
VIII
XXVII
XXXVII
II
XXVI
XV
XII
IV
VII
XIV
XI
V
XXI
XXV
XXX
Medium
Large
Small

J


V
XV
I
XXII
IV
X
XIII
XVIII
XXXV
III
XIX
XXVIII
XXXIV
XIV
XII
XXIII
XXV
VII
VIII
XXI
XXXII
XXXVII
XXXI
XXIV
XXX
Large
Small
Medium


K
XVI
XXVI
II
XXX
XXVII
XX
XXIII
XXI
XXXV
XII
V
VIII
XXXIV
III
VI
VII
X
XV
XXV
XXXI
XXXIII
XXXVI
Small
Large
Medium
L
XI
XXVII
XXXIV
II
III
XVIII
XV
XIV
XII
IV
XVII
XIX
XXI
XXX
XXXI
XXXIII
XXVI
V
VIII
VII
XX
IX
XXV
XXXVII
Large
Medium
Small
M
XII
XXXIV
VIII
X
XIII
XVIII
XXI
XXXVII
XXV
VII
V
XX
III
XXII
XXIV
XXXI
XXIV.1
XXVIII
XXIII
XV
XXX
IV
XXXII
XXXV
I
Medium
Large
Small

CHAPTER 3

OPTIMIZATION OF WEB ARCHITECTURE IN RESPONSE TO RESTING POSITIONS OF ORB-WEAVER SPIDERS

ABSTRACT

The distribution of the different types of threads in orb webs is highly variable between species and individuals. Several hypotheses have been proposed to explain the causality of these architectural patterns. Previous studies have favoured hypotheses that predict that the optimal distribution of sticky capture threads depends on the density of the impact-absorbing radial threads and the speed at which the spider reaches the location of prey interception. However, these studies have been conducted with some analytical limitations. To mitigate these issues, we undertook a new analytical approach involving multiple species. Our results suggest that some of the previous hypotheses have limited predictive power to be considered a broad rule influencing web designs. However, we verified that compensatory mechanisms involved in prey retention have the potential to be important enough to widely influence the design of orb webs. We observed that when the trajectory to reach the potential prey is longer, such as in situations in which the spiders rest out of the orb web holding a signalling thread, the distances between sticky threads consistently formed uniform meshes towards the web edge.

Keywords: spider; building behaviour; orb web; behavioural patterns.

1. INTRODUCTION

An orb web is the result of successive stereotyped behaviours, based on which we can track most of the spider trajectory during the construction and its investment decisions in several distinct tasks. The distribution of silk threads in an orb web is crucial for defining the outcomes of spider-prey interactions because each web thread exhibits different functions during the prey capture process. Radii contain tougher fibres, which are responsible for absorbing and dissipating the kinetic energy of prey during the impact (Sensenig *et al*., 2012). The sticky capture threads, on the other hand, are elastic fibres with a negligible capacity to absorb and dissipate kinetic energy (Sensenig *et al*., 2012). However, their adhesivity is responsible for retaining the prey for an interval that allows the spider to approximate and perform prey immobilisation (Blackledge & Zevenbergen, 2006). Nevertheless, when examining these webs more closely, we can clearly verify that the behavioural repertoire employed during web construction rarely results in a symmetric distribution of threads (*e.g.*, Zschokke & Nakata, 2015). For example, it is usual to observe a larger area below the hub of the orb, with more sticky capture threads and radii closer to a parallel distribution than in the upper part (*e.g.*, Eberhard, 2014; Zschokke & Nakata, 2015). It is also common to observe an uneven distribution of sticky threads between web portions. The inner parts (close to the hub) and the bottom half of the orb usually have a denser mesh than the outer portions and the upper half of the web, respectively (*e.g.*, Herberstein & Heiling, 1999; Eberhard, 2014; Xavier *et al*., 2017). Nevertheless, no general rule was observed, and many exceptions have been reported (*e.g.*, Nakata & Zschokke, 2010; Nakata, 2012). Moreover, the asymmetries can vary greatly between species and even between ontogenetic stages (Hesselberg, 2010). If the basic function of all orb webs is prey capture in mid-flight, why are the threads distributed unevenly in the orb and why is there such variation between species?

Incidental hypotheses, which attribute these variations to behavioural and energetic constraints during web building, have failed to explain many web designs (Eberhard, 2014). Given the high diversity of insects with distinct kinetics and escape abilities (Blackledge & Zevenbergen, 2006), and the variety of spider silks (Blackledge *et al*., 2011), it is reasonable to expect that orb webs result from a balance of different foraging demands. Further, it is unlikely that any simplified explanation will be able to predict the variation in the orb web architectures. Indeed, different functional hypotheses have been proposed to explain the observed web designs (Heiling & Herberstein, 1998; Eberhard, 2014; Xavier *et al*., 2017). However, these hypotheses have had certain analytical limitations, which we will discuss further, and these investigations still require additional tests and empirical pieces of evidence.

The “radii-density hypothesis” (Zschokke, 2002) states that the spider invests more sticky threads in the web where there is the greatest capacity to stop prey. Consequently, it predicts that the distribution of sticky capture threads in an orb web is dependent on the radii density. This hypothesis has provided acceptable explanations for the predominant tendency to have a denser mesh of sticky threads near the hub and also in the lower portions of the orbs, where the radii are usually more parallel (Eberhard, 2014; Xavier *et al*., 2017). However, these same asymmetries are equally well explained by another functional hypothesis, the “attack-time hypothesis” (Heiling & Herberstein, 1998). This hypothesis states that the larger investment in sticky threads will be at segments where the spider can reach faster, consequently prioritising retention where there is less chance for the prey to escape. Therefore, it also predicts the greatest investment in sticky threads near the hub and at the bottom half of webs, since orb-web spiders usually rest facing downwards and run faster in this direction (Heiling & Herberstein, 1998). Likewise, spiders that rest facing upward would increase the investment in sticky threads in the upper part of webs (Nakata & Zschokke, 2010). Both "radii-density" and "attack-time" hypotheses fit well to most orb-web designs, consequently leading to multifunctional explanations (Eberhard, 2014). However, there are three analytical problems in these investigations, and it would be cursory to take these explanations as equally predictive.

The first analytical problem is that these previous approaches were unable to dissociate the tests of both hypotheses, merging cause and effect relationships. These studies attributed the spacing patterns of sticky capture threads to these hypotheses, mainly due to intra-web differences. For example, if the bottom half of a web from a given species had a greater radii density and a greater investment in sticky threads, the hypotheses were considered acceptable. However, there were no direct assessments of the influence of radii densities or distances to reach the prey over the measured spacing patterns of sticky threads.

The second analytical problem from previous studies is that these hypotheses fail to explain many exceptions in orb web architecture. Some spiders distribute the sticky threads from the edge to the hub uniformly (de Crespigny *et al.*, 2001; Eberhard, 2014; Zschokke & Nakata, 2015; Xavier *et al.*, 2017), contradicting both hypotheses because they are investing in retention far from their resting position and where radii concentration is reduced. Then, alternative explanations come into play. The "prey-tumbling hypothesis" (de Crespigny *et al.*, 2001) states that smaller spaces between sticky thread loops at the outermost area below the hub of the webs of some spider species could increase capture success when prey tend to escape by tumbling in vertical orb webs (*e.g.*, Zschokke *et al.*, 2006). Also, Xavier *et al.* (2017) proposed the "compensation hypothesis". The authors reported a case with the araneid *Wixia abdominalis* O. Pickard-Cambridge, 1882, in which some individuals build orb webs with free-sectors and wait for prey interception on a twig situated out of the web, holding a signal line. These individuals, unlike those that wait in the hub, show a uniform investment in sticky threads along the bottom half of the web. This suggests that spiders can invest in retention capacity according to the time spent to arrive at the intercepted prey. Here, we report similar cases involving two other araneid species, *Araneus omnicolor* (Keyserling, 1893) and *Metazygia* sp. F. O. Pickard-Cambridge, 1904 (their web architectures are reported in Xavier *et al*., 2020). These species can build orbs of similar size or even larger webs than those constructed by *W. abdominalis*, suggesting that this pattern is not a simple result of a dense mesh of threads in small webs.

Finally, the third analytical problem from previous studies is that current information on the radii function was not considered. Experimental proceedings demonstrated that the more radii the prey contacts during the impact with the web, the more efficient is the energy absorption and smaller is the chance to damage the web (Sensenig *et al*., 2012). However, the physical properties of radii vary greatly between species, with toughness ranging more than 20-fold (Agnarsson *et al*., 2010; Sensenig *et al*., 2010). Consequently, webs with tougher threads can achieve higher stopping performances without a large number of radii. These tougher threads usually compose large webs, since they are mostly spun by the larger spider species and larger individuals (Sensenig *et al*., 2010, 2011; Harmer *et al*., 2011). Indeed, in natural observations, the number of radii alone does not explain the capture of large prey when different spider species are analysed, while the web size does (unpubl. data). Therefore, the radii-density hypothesis may have limited explanation for the design of orb webs with tougher silks.

In this study, we aimed to assess the adjustment of each functional hypothesis, mitigating these analytical problems from previous studies by means of a different statistical approach. If the radii-density hypothesis is a consistent and broad rule of orb-web designs, we expect that (i) the distribution of the sticky capture threads will change according to the density of radii in each measured web, regardless of the web size. If the attack-time hypothesis is a broad rule, we expect (ii) to find a sparser mesh of sticky capture threads far from where the spider rests. This prediction should be consistent, regardless of the radii density in each measured web, the spider resting position (hub or outside the web), and the web size. If the prey tumbling hypothesis is a broad rule, we expect to (iii) find a closer mesh of sticky threads towards the lower edge as a common trait. Finally, if the compensation hypothesis explains the web designs, we expect (iv) to find uniform dispositions of sticky threads along the web when the spider rests outside the web and needs to cover a long trajectory to achieve a prey, irrespective of all the other web features.

2. METHODS

2.1 *Orb-web design measurement*

Between April 2016 and February 2019, we photographed 200 orb webs of 17 spider species belonging to Araneidae and Tetragnathidae families, in the field (Table 1). We used a DSLR Nikon camera equipped with 18–55 mm lens, and a scale (graduated in mm) parallel to the orb web plane. Using digital photos and the ImageJ software, version 1.52 (National Institute of Health, USA), we measured the following predictor variables for each orb web: (i) the number of radii and (ii) the number of sticky threads' turns, both on the bottom half of the web (below the hub), (iii) the capture area (cm^2), and (iv) the resting position of the spider species (on the hub or outside the web, or even they were alternating these positions between day and night time). It is important to clarify that the variable (ii) was included to assess if spiders adjust the disposition of sticky threads along the orb controlling the number of sticky threads or just their spacing patterns. We then measured (vi) the pattern of retention investment as the response variable. For this, we measured the distances between all consecutive sticky threads from the edge to the hub (Fig. 1), always along the most vertical radius below the hub. Since orb webs have different sizes and numbers of spacings between the sticky thread loops, we standardised these values after the measurements to make comparisons feasible. The distances between the sticky threads were standardised by dividing each measurement by the median value of the distances on that radius. The standardised measure of distance between spiral loops was plotted against the relative distance to the hub, defined as the fraction of the number of spaces between loops attached to that radius. The value of one was closest to the hub (Fig. 1) (see Eberhard, 2014). Therefore, each orb web produced a linear relationship between the relative distance to the hub and the standardised sticky thread distances (Fig. 1). If this relationship results in an inclination close to zero, the spider is investing in retention uniformly along the web. If this relation is negative, the spider is investing in more retention next to the hub because the mesh is tight there (Fig. 1). Therefore, we can assess the influence of the predictors (i-iv) on these retention investment patterns.

2.2 *Assessing the adjust of the functional hypotheses to the observed web designs*

To assess the adjustment of the functional hypotheses to the observed web designs, we performed a model selection approach. We aimed to assess the effect of the (i) number of radii, (ii) number of sticky threads' turns, (iii) the capture area, and (iv) the spider resting position, over the relationship between (vi) the distance to the hub and the standardised sticky thread distances (uniform or decreasing). Thus, we built a set of generalised linear mixed models with Gamma error distribution, using these web variables (i-iv) and their interactions with the relative distance to the hub as the predictors and the standardised sticky thread distances as the response. We included both spider species and individuals as random variables in all models. After building the alternative models, we conducted the selection procedure to choose the models with the best adjustments. We considered the models with the smallest Akaike Information Criterion (AICc) values within a range of 2.0 (ΔAICc) from the smallest value to represent the best explanation(s) of the response variable (Burnham & Anderson, 2002). Finally, we considered the simplest model as the best one and dismissed the others with uninformative parameters (*sensu* Arnold, 2010). This is plausible because we are looking for a broad explanation of the web architectures between many alternative hypotheses. Lastly, we calculated the confidence intervals (95%) of the predictor(s) included in the best model (see Akdur *et al*., 2016). When these confidence intervals did not include ‘zero’, this predictor was considered as an informative parameter. We performed statistical analysis using ‘car’ (Fox & Weisberg, 2011), ‘lme4’ (Bates *et al*., 2015), ‘MuMIn’ (Barton, 2019) packages in software R, version 3.6.1 (R Development Core Team, 2019).

Voucher specimens have been deposited in the arachnological collection of Universidade Federal de Minas Gerais (curator A. J. Santos).

3. RESULTS

The values of the predictors to test the functional hypotheses and the distribution pattern of sticky threads are summarised in Table 1. This survey involved nine spider species that wait for prey interception exclusively on the web hub (H), two species that stay waiting for prey interception out of the web (O), one species in which individuals may adopt both behaviours (H or O), and five species which alternate these positions according the daily period, where all of them stay out of the web during the day and go to the hub at the night time (A) (Table 1). Most species exhibited a distribution pattern of sticky threads with a closer mesh towards the hub or a nearly uniform pattern of distribution. This is because the inclinations (β values) produced by the linear relations between the relative distances to the hub and the standardised spacing of the sticky threads were negative or close to zero, respectively (Table 1). Only one species, *Verrucosa arenata* (Walckenaer, 1841), clearly exhibited webs with a closer mesh towards the web edge (high and positive β value).

At a first glance, these patterns of sticky thread distribution do not seem to be related to the number of radii or the web size, nor depend of the number of sticky threads turns below the hub. Indeed, our model selection procedure corroborates this observation. The model selection resulted in four alternative models with the best predictive power of the pattern of sticky thread distribution (with ΔAICc lower than 2.0) (Table 2). Between these four alternative models, the first one had the best parsimony, with just the spider resting position (hub, outside, or alternating) and the relative distance to the hub as predictors (Table 2). We then considered this model as the best one also due to the fact that the inclusion of one more predictor in this parsimonious model reduced the model weight (ω_i) (Table 2). The coefficients of this model did not include zero within 95% confidence intervals, and were considered as informative parameters (Table 2). Thus, this model demonstrates a general tendency of increasing distances between consecutive sticky threads towards the orb edge (see the additive effect of the relative distances of spacings to hub 'Dist.'). However, despite this tendency, spiders that rest outside the web were more prone to build webs with a uniform distribution of sticky threads, while spiders that rest on the web hub or rest there only at night time were more prone to build webs with closer mesh next to the hub (Fig. 2). When we compared these resting categories in our selected generalized linear model, we verified that they differ from each other (‘hub’ vs. ‘outside’: $\chi^2 = 183.05$, $p < 0.01$; ‘alternating positions’ vs. ‘outside’: $\chi^2 = 37.97$, $p < 0.01$; ‘alternating positions’ vs. ‘hub’: $\chi^2 = 12.66$, $p < 0.01$).

4. DISCUSSION

In this study, we aimed to assess the adjustment of each of the functional hypotheses about orb-web architectures. We have also mitigated the analytical problems from previous studies. Hence, we recorded orb webs encompassing different species, web sizes, radii numbers, sticky threads’ turns, and resting positions. Sticky thread distributions were not influenced by web traits, but were affected by the spider resting position. Spiders waiting for prey interception out of the web were more prone to build a uniform mesh of sticky threads along the bottom half of the orbs, while the others were more prone to build relatively more spaced meshes towards the web edge. Since these patterns were independent of the number of sticky threads’ turns below the hub of webs, the spiders are controlling the uniformity of meshes without necessarily add much threads.

These results contradict the expectations for the radii-density hypothesis (Zschokke, 2002), suggesting that the pattern of sticky thread distribution does not depend on the radii number. However, it is important to highlight that these results do not mean that the retention function is not influenced by the stopping function. The greater the number of radii in a given web, the greater are the chances that a given prey touches two or more radii during the impact with the orb web. This effect indeed improves the kinetic energy absorption and reduces the chances of web disruption (Sensenig *et al.*, 2012). Moreover, if larger insects indeed constitute an especially important source of energy for spiders (*e.g.*, Venner & Casas, 2005), an optimal stopping function becomes even more important. However, the stopping function is also highly influenced by the physical properties of radii (Sensenig *et al*., 2010; Sensenig *et al*., 2011; Harmer *et al*., 2011). Thus, spiders with tougher and high-quality radii would not need a large number of radii to stop prey with high kinetic energy because the contact with one thread during the impact would be enough to successfully dampen the kinetic energy (Sensenig *et al*., 2010; Sensenig *et al*., 2011). Indeed, in an experimental setup, orb-web spiders feeding on prey with high kinetic energy produced tougher silk fibres without increasing the number of radii in the webs (Tso *et al*., 2007). Moreover, the number of radii in webs did not explain the capture of large prey in natural observations, but their quality probably did (unpubl. data).

Therefore, the radii-density hypothesis is possibly an explanation limited to some spiders with weaker threads. Indeed, there are cases of younger individuals, with weaker threads in their orb webs, producing more radii and more compact orb webs than larger ones (Barrantes *et al*., 2017). Since the webs surveyed in this study involved spider genera with diverse and even contrasting levels of thread toughness (*e.g. Micrathena* and *Araneus*) (Swanson *et al*., 2007; Agnarsson, 2010; Sensenig, 2010), this effect became more evident than in previous studies (Eberhard, 2014; Xavier *et al*., 2017). Similar contradictions to the radii-density hypothesis were found by Eberhard (2014) in orb webs of *Trichonephila clavipes* (Linnaeus, 1767) and *Metepeira* sp. F. O. Pickard-Cambridge, 1903, exhibiting uniform or closer sticky threads mesh toward the lower edge of the orbs. However, these species also exhibit auxiliary structures in their webs, which increase the absorption of the kinetic energy of insects intercepted far from the hub. These structures include auxiliary non-adhesive spiral threads, divided radii (radii that duplicate before reaching the orb edge forming a ‘Y’, which increase the radii density toward the edges of the web), and frontal barrier lines (which dampen the prey’s kinetic energy before to reach the orb) (Eberhard, 2014). However, only individuals of *Eustala perfida* Mello-Leitão, 1947, usually included one or two divided radii in their webs in this study, making our conclusion consistent.

Similarly, the prediction of the attack-time hypothesis (Heiling & Herberstein, 1998) was not corroborated because spiders did not invest in more sticky capture threads near locations where they reached faster. This was contradicted by the predominantly uniform distribution of sticky threads in webs of five species (*A. omnicolor*, *W. abdominalis*, *Metazygia* sp., *E. perfida*, and *E. taquara*) and by the closer meshes towards the bottom edge of *Verrucosa arenata* webs. In such cases, spiders invested in retention far from their resting position, especially when they remained outside the web. In these cases, the spiders usually rest above the web within a retreat, such as *A. omnicolor* and *Metazygia* sp., or remain cryptically positioned on a twig, like *W. abdominalis*. After the detection of a prey interception, the spider departs from its resting position to the hub, and then approaches the entangled prey, by means of the vibrational patterns of the threads. Prey capture in these cases demands longer and more elaborate repertoires. Therefore, our results are much more congruent with the compensation hypothesis. Spiders that wait for interceptions on the hub do not need to increase the investment in sticky capture threads next to the bottom edges of the web because they are prompt to reach there at the first vibrational signal. The group of spiders that alternates the resting positions according to daily period presented different patterns of meshes. This produced an intermediary level between the uniform and the crescent towards the orb edge in the statistical model. These spiders stay outside the web during daytime, but can capture prey in any moment if it is opportune. Thus, a uniform mesh of sticky threads may be especially profitable to some of these species.

The compensation hypothesis predicts that sticky thread investment of spiders will depend on their resting position on or outside the orb web. Otherwise, the prey tumbling hypothesis requires the presence of progressively closer meshes of sticky capture threads towards the bottom edge of the web, but not of an evenly distributed investment in sticky threads along the web (de Crespigny *et al*., 2001). Insects have many strategies to escape when entangled in a web (*e.g.*, Blackledge & Zevenbergen, 2006; Zschokke *et al*., 2006). Some of them can struggle until they break the threads or move intensively to propel themselves out of the web. Then, the chances to escape are lesser if there are more sticky threads in contact with the insect body (Blackledge & Eliason, 2007). Thus, uniform patterns of sticky thread spacings indicate that the retention potential will be the same despite the prey being entangled next to or further from the hub.

Contrasting this, a closer mesh towards the bottom edge will be especially important in situations in which the prey presents a higher escape capacity by tumbling continuously, which can vary widely among insects (Zschokke *et al*., 2006). Moths, for example, tend to escape by tumbling because the ‘wing scales’ are easily broken (Stowe, 1978). Consequently, webs of spiders specialised in capturing moths present specific designs to reduce the prey-tumbling effect (Stowe, 1978). In our survey, *V. arenata* met the expectations of the prey tumbling hypothesis. The peculiar behavioural trait of *V. arenata* compared to the other sampled species was that the spider stayed on the hub facing upwards (Rao *et al.*, 2011). If turning down to locate the intercepted prey at the bottom of the web can be considerably expensive in terms of time, this design can also be a compensation mechanism. Moreover, these spiders have a peculiar behaviour during prey capture; reeling, a behaviour, in which they pull the threads to themselves while running to the intercepted insect (Rao *et al.*, 2019). Thus, this may be a special case where the prey-tumbling mitigation is important enough for the natural selection of special behaviours.

Refined information about the differences in physical properties of sticky threads along the web has been reported (Opell & Stellwagen, 2019). For example, since spiders begin to spin the sticky threads from the edge and they move in a spiral trajectory to the hub, the supply of proteins and glycoproteins in silk glands can change during the process. Consequently, in *Argiope trifasciata* (Forsskål, 1775), the first turns of threads are stickier because they have a greater volume of glue droplets, aqueous material, and glycoproteins (Opell & Stellwagen, 2019). Controlling this adhesive heterogeneity may be an important task for spiders, which must cover a longer trajectory to reach their prey. We believe that broadly measuring this feature in different species can be crucial in understanding the optimal placement of sticky threads in each situation. For now, we do not have such quantification. Despite this, our analytical approach allowed us to verify that the previous radii-density and attack-time hypotheses probably have limited predictive power to be considered as general rules influencing spider building behaviours, despite the prey stopping potential and the fast detention of escaping prey being important mechanisms in spider-prey interactions. Several selective pressures must be acting over the web designs, which must represent a complex trade-off solution. Consequently, the search for a simplified and general rule that explains the orb web designs led to the proposition of many alternative or complementary hypotheses. Here, however, we were able to demonstrate that compensatory mechanisms in prey retention have the potential to be important enough to widely influence the building behaviours of orb-web spiders.

LITERATURE CITED

Agnarsson I., Kuntner M., & Blackledge. T.A. 2010. Bioprospecting Finds the Toughest Biological Material: Extraordinary Silk from a Giant Riverine Orb Spider. *PLoS One*. 5, e11234. DOI: 10.1371/journal.pone.0011234

Akdur H.T.K., Özonur D., & Bayrak H. 2016. Comparison of Confidence Interval Methods of Fixed Effect in Nested Error Regression Model. *Journal of Natural and Applied Sciences*. 20, 167-175.

Arnold T.W. 2010. Uninformative parameters and model selection using Akaike’s Information Criterion. *Journal of Wildlife Management*. 74, 1175-1178.

Barrantes G., Triana E., & Sánchez-Quiróz C. 2017. Functional changes in web design along the ontogeny of two orb-weavers. *Journal of Arachnology*. 45, 152-159.

Barton K. 2019. MuMIn: Multi-Model Inference. R package version 1.43.10.

Bates D, Mächler M, Bolker B, & Walker S. 2015. Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*. 67, 1-48. DOI: doi.org/10.18637/jss.v067.i01

Blackledge T.A., Kuntner M., & Agnarsson I. 2011. The form and function of spider orb webs: evolution from silk to ecosystems. In: Casas J., ed. *Advances in Insect Physiology*. Burlington: Academic Press, 175-262.

Blackledge T.A. & Eliason C.M. 2007. Functionally independent components of prey capture are architecturally constrained in spider orb webs. *Biology Letters*. 3, 456-458. DOI: doi.org/10.1098/rsbl.2007.0218

Blackledge T.A. & Zevenbergen J.M. 2006. Mesh width influences prey retention in spider orb webs. *Ethology*. 112, 1194-1201. DOI: doi.org/10.1111/j.1439-0310.2006.01277.x

Blackwall J. 1863. Description of newly discovered spiders captured in Rio de Janeiro, by John Gray and the Rev. Hamlet Clark (continued). *Annals and Magazine of Natural History*. 11, 29-45.

Burnham K.P. & Anderson D.R. 2002. *Model selection and multimodel inference a practical information: Theoretic approach.* New York: Springer-Verlag New York Inc.

Clerck C. 1757. *Aranei Svecici. Svenska spindlar, uti sina hufvud-slågter indelte samt under några och sextio särskildte arter beskrefne och med illuminerade figurer uplyste.* Stockholmiae: Literis Laur.

de Crespigny F.E.C., Herberstein M.E. & Elgar M.A. 2001. The effect of predator-prey distance and prey profitability on the attack behaviour of the orb-web spider *Argiope keyserlingi* (Araneidae). *Australian Journal of Zoology*. 49, 213-221. DOI: doi.org/10.1071/ZO00074

Eberhard W.G. 2014. A new view of orb webs: multiple trap designs in a single structure. *Biological Journal of the Linnean Society*. 111, 437-449. DOI: doi.org/10.1111/bij.12207

Forsskål P. 1776. *Icones rerum naturalium, quas in itinere orientali depingi curavit Petrus Forskål.* Hauniae.

Fox J. & Weisberg S. 2011. *An R Companion to Applied Regression*. Thousand Oaks: SAGE publications.

Harmer A.M.T., Blackledge T.A., Madin J.S. & Herberstein M.E. 2011. High-performance spider webs: integrating biomechanics, ecology and behaviour. *Journal of The Royal Society Interface*. 8, 457-471. DOI: doi.org/10.1098/rsif.2010.0454

Heiling A.M. & Herberstein M.E. 1998. The web of *Nuctenea sclopetaria* (Araneae, Araneidae): relationship between body size and web design. *Journal of Arachnology*. 26, 91-96.

Herberstein M.E. & Heiling A.M. 1999. Asymmetry in spider orb webs: a result of physical constaints? *Animal Behaviour*. 58, 1241-1246. DOI: 10.1006/anbe.1999.1255

Hesselberg T. 2010. Ontogenetic changes in web design in two orb-web spiders. *Ethology*. 116, 535-545. DOI: 10.1111/j.1439-0310.2010.01760.x

Keyserling E. 1892. Die Spinnen Amerikas. Epeiridae. *Bauer & Raspe, Nürnberg*. 4, 1-208.

Keyserling E. 1893. Die Spinnen Amerikas. Epeiridae. *Bauer & Raspe, Nürnberg*. 4, 209-377.

Koch C.L. 1839. *Die Arachniden getreu nach der Natur abgebildet und beschrieben*. Nürnberg: C. H. Zeh'schen Buchhandlung.

Linnaeus C. 1767. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus differentiis, synonymis, locis*. Stockholm: Laurentius Salvius.

Mello-Leitão CF. 1943. Catálogo das aranhas do Rio Grande do Sul. *Arquivos do Museu Nacional do Rio de Janeiro*. 37, 147-245.

Mello-Leitão CF. 1947. Aranhas do Paraná e Santa Catarina, das coleções do Museu Paranaense. *Arquivos do Museu Paranaense*. 6, 231-304.

Nakata K. 2012. Plasticity in an extended phenotype and reversed up-down asymmetry of spider orb webs. *Animal Behaviour*. 83, 821-826. DOI: 10.1016/j.anbehav.2011.12.030

Nakata K. & Zschokke S. 2010. Upside-down spiders build upside-down orb webs - web asymmetry, spider orientation and running speed in *Cyclosa*. *Proceedings of the Royal Society B: Biological Sciences*. 277, 3019-3025. DOI: 10.1098/rspb.2010.0729

Opell B.D. & Stellwagen S.D. 2019. Properties of orb weaving spider glycoprotein glue change during *Argiope trifasciata* web construction. *Scientific Reports*. 9, 20279. DOI: 10.1038/s41598-019-56707-1

Perty M. 1833. Arachnides Brasilienses. In: de Spix JB., Martius FP, eds. *Delectus animalium articulatorum quae in itinere per Braziliam ann. 1817 et 1820 colligerunt.* Monachii: Impensis Editoris.

Pickard-Cambridge F.O. 1903. *Arachnida - Araneida and Opiliones. Biologia Centrali-Americana, Zoology*. London 2, 425-464.

Pickard-Cambridge, F.O. 1904. *Arachnida - Araneida and Opiliones. Biologia Centrali-Americana, Zoology*. London 2, 465-560.

Pickard-Cambridge O. 1882. On new genera and species of Araneidea. *Proceedings of the Zoological Society of London*. 50, 423-442.

Pickard-Cambridge O. 1889. *Arachnida. Araneida. Biologia Centrali-Americana, Zoology*. London 1, 1-56.

Rao D., Fernandez O.C., Castañeda-Barbosa E. & Díaz-Fleischer F. 2011. Reverse positional orientation in a neotropical orb-web spider, *Verrucosa arenata*. *Naturwissenschaften*. 98, 699-703. DOI: 10.1007/s00114-011-0811-2

Rao D., Tapia-McClung H. & Narendra A. 2019. Reeling in the prey: fishing behaviour in an orb web spider. *Journal of Experimental Biology*. 222, jeb213751. DOI: 10.1242/jeb.213751

R Development Core Team. 2019. R: A language and environment for statistical computing.

Sensenig A., Agnarsson I. & Blackledge T.A. 2010. Behavioural and biomaterial coevolution in spider orb webs. *Journal of Evolutionary Biology*. 23, 1839-1856. DOI: doi.org/10.1111/j.1420-9101.2010.02048.x

Sensenig A., Agnarsson I. & Blackledge T.A. 2011. Adult spiders use tougher silk: ontogenetic changes in web architecture and silk biomechanics in the orb-weaver spider. *Journal of Zoology*. 285, 28-38. DOI: doi.org/10.1111/j.1469-7998.2011.00809.x

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. DOI: doi.org/10.1098/rsif.2011.0851

Stowe M.K. 1978. Observations of two nocturnal orb weavers that build specialized web: *Scoloderus cordatus* and *Wixia ectypa* (Araneae, Araneidae). *Journal of Arachnology* 6: 141-146.

Strand E. 1908. Diagnosen neuer aussereuropäischer Argiopiden. *Zoologischer Anzeiger*. 33, 1-4.

Swanson B.O., Blackledge T.A. & Hayashi C.Y. 2007. Spider Capture Silk: Performance Implications of Variation in an Exceptional Biomaterial. *Journal of Experimental Zoology*. 307, 654-666. DOI: doi.org/10.1002/jez.420

Tso I-M., Chiang S-Y., Blackledge T.A. 2007. Does the Giant Wood Spider *Nephila pilipes* Respond to Prey Variation by Altering Web or Silk Properties? *Ethology*. 113, 324-333. DOI: doi.org/10.1111/j.1439-0310.2007.01318.x

Venner S. & Casas J. 2005. Spider webs designed for rare but lifesaving catches. *Proceedings of the Royal Society B*. 272, 1587-1592. DOI: doi.org/10.1098/rspb.2005.3114

Vollrath F. & Selden P. 2007. The Role of Behavior in the Evolution of Spiders, Silks, and Webs. *Annual Review of Ecology, Evolution, and Systematics*. 38, 819-846. DOI: doi.org/10.1146/annurev.ecolsys.37.091305.110221

Walckenaer C.A. 1841. *Histoire naturelle des Insects. Aptères.* Paris: Librairie encyclopédique de Roret.

Xavier G.M., Moura R.R. & Gonzaga M.O. 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. DOI: doi.org/10.1636/JoA-S-17-001.1

Xavier G.M., Moura R.R. & Gonzaga M.O. 2020. Towards simplicity and accuracy: assessing traditional and new estimators of orb-web capture thread length. *Behavioural Processes*. 173, 104086. DOI: doi.org/10.1016/j.beproc.2020.104086

Zschokke S. & Nakata K. 2015. Vertical asymmetries in orb webs. *Biological Journal of the Linnean Society*. 114, 659-672. DOI: doi.org/10.1111/bij.12456

Zschokke S., Hénaut Y., Benjamin S.P. & García-Ballinas J.A. 2006. Prey-capture strategies in sympatric web-building spiders. *Canadian Journal of Zoology*. 84, 964-973. DOI: doi.org/10.1139/Z06-074

Zschokke S. 2002. Form and function of the orb-web. In: Toft S, Scharff, N, eds. *European Arachnology 2000*. Aarthus: Aarthus University Press, 99-106.

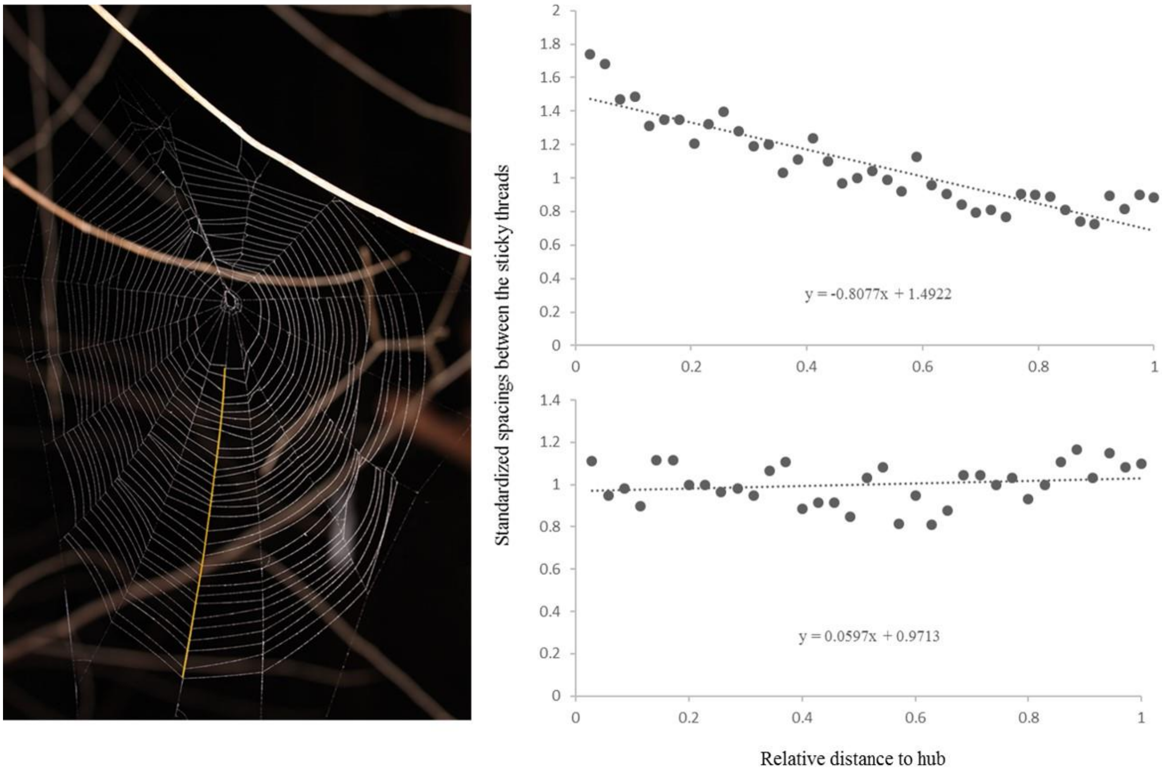


Figure 1. For each orb web, we measured the consecutive spacings between the sticky threads from the edge to the hub, always along the most vertical and less disturbed radius (see the yellow line at the photograph). Each measurement produced, then, a linear relation between the standardized values of these spacing and their relative distance to hub (1 is closest value to hub). The two individual examples show a decreasing pattern towards the web edge (upper plot) and a uniform pattern (lower plot).

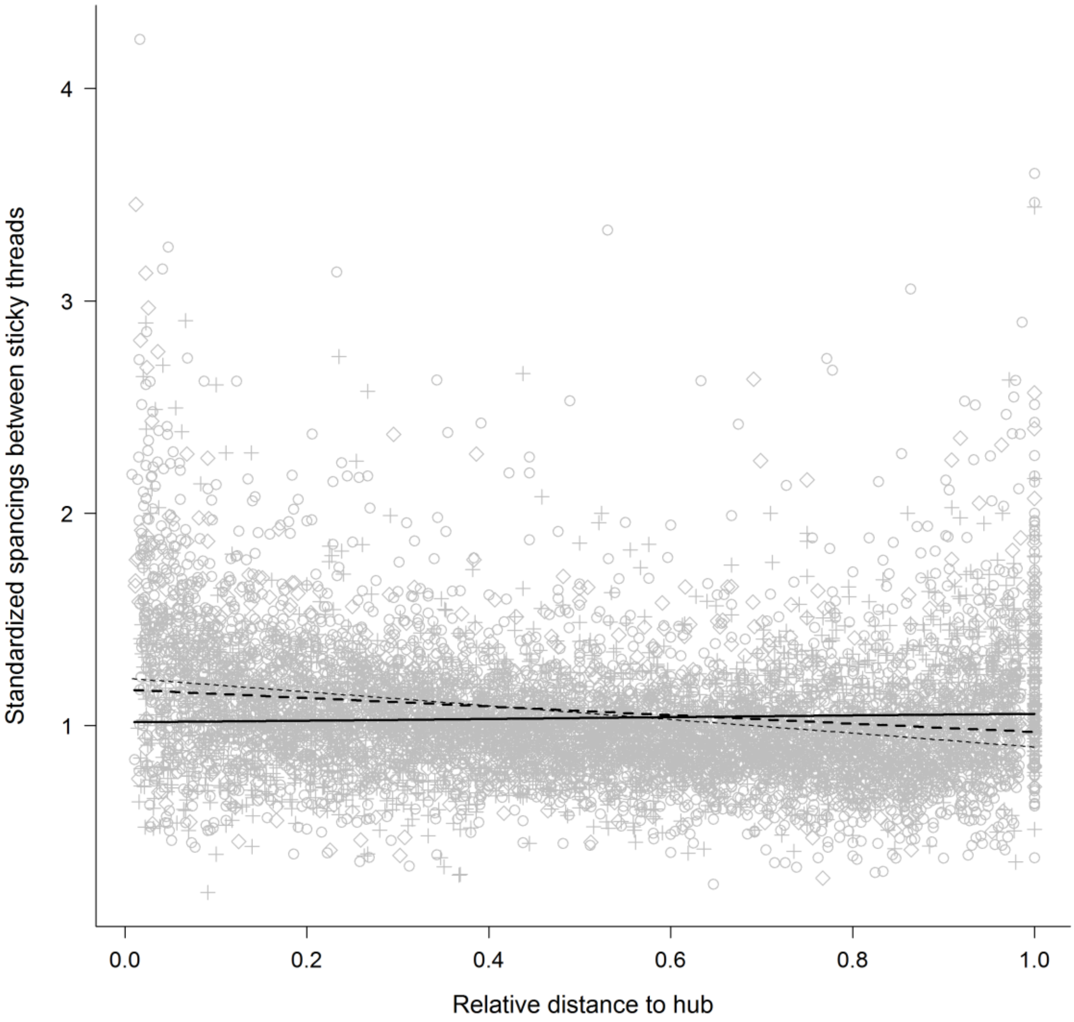


Figure 2. The parsimonious selected model (Table 1). Orb web spiders that wait for prey interception out of the web (○, continuous line) are more prone to dispose uniformly the sticky threads along the lower of webs than the spiders that wait on the hub (+, short-dashed line) and spiders that alternate the resting positions according the daily period (◊, long-dashed line).

Table 1. Number of surveyed orb webs of each spider species, their respective resting position (hub, H; out of web, O; or alternating according to the period, A), number of radii and sticky threads' turns at lower portion of webs, and capture area (cm^2) of the orbs (mean ± s.d.). The inclinations (β values) produced by the linear relations between the relative distances to hub and the standardized spacing of the sticky threads. The geographic locations are shown in WGS84 Datum.

Spider species	Number of webs	Spider resting position	Number of radii in the lower half of web	Capture area (cm²)	Sticky threads' turns in the lower half of web	β values	Geographic location
Metazygia sp. F. O. Pickard-Cambridge, 1904	32	O	19 ± 4.35	145.65 ± 99.99	45.5 ± 12.26	0.026	19˚10'32"S, 48˚23'38"W
Parawixia audax (Blackwall, 1863)	31	H	13 ± 4.33	287.56 ± 293.12	34.5 ± 9.81	-0.249	19˚10'32"S, 48˚23'38"W
Araneus omnicolor (Keyserling, 1893)	20	O	21 ± 3.57	516.29 ± 165.07	40 ± 8.29	0.116	23˚14'12"S, 46˚56'16"W
Micrathena nigrichelis Strand, 1908	20	H	33 ± 5.28	336.02 ± 117.73	48 ± 8.83	-0.450	23˚14'12"S, 46˚56'16"W
Micrathena swainsoni (Perty, 1833)	16	H	21 ± 3.86	130.06 ± 74.50	30 ± 7.71	-0.052	18˚45'11"S, 47˚51'28"W
Mangora strenua (Keyserling, 1893)	13	H	31 ± 5.63	440.19 ± 194.56	62 ± 22.29	-0.420	23˚14'12"S, 46˚56'16"W
Wixia abdominalis O. Pickard-Cambridge, 1882	9	H	15 ± 3.83	335.05 ± 562.89	32 ± 6.83	-0.285	18˚45'11"S, 47˚51'28"W
Wixia abdominalis O. Pickard-Cambridge, 1882	9	O	17 ± 3.60	117.61 ± 45.29	31 ± 5.59	-0.120	18˚45'11"S, 47˚51'28"W
Leucauge roseosignata Mello-Leitão, 1943	9	H	18 ± 1.11	478.03 ± 241.40	47 ± 5.19	-0.564	23˚14'12"S, 46˚56'16"W
Eustala perfida Mello-Leitão, 1947	6	A	21 ± 3.50	254.34 ± 76.62	75.5 ± 12.67	-0.040	23˚14'12"S, 46˚56'16"W
Eustala taquara (Keyserling, 1892)	6	A	14 ± 2.80	305.71 ± 135.25	28.5 ± 7.65	-0.074	23˚14'12"S, 46˚56'16"W
Eustala sagana (Keyserling, 1893)	5	A	13 ± 1.48	148.26 ± 121.99	39 ± 6.04	-0.585	23˚14'12"S, 46˚56'16"W
Parawixia sp. F. O. Pickard-Cambridge, 1904	5	H	13 ± 1.64	580.40 ± 390.49	30 ± 8.39	-0.334	23˚14'12"S, 46˚56'16"W
Alpaida sp. 1 O. Pickard-Cambridge, 1889	5	H	12 ± 1.51	332.04 ± 308.04	23 ± 3.03	-0.277	19˚10'32"S, 48˚23'38"W
Alpaida sp. 2 O. Pickard-Cambridge, 1889	4	A	15 ± 1.5	237.81 ± 113.62	22 ± 6.05	0.259	23˚14'12"S, 46˚56'16"W
Araneus sp. Clerck, 1757	4	A	13.5 ± 2.16	344.50 ± 173.16	62 ± 16.13	-0.432	23˚14'12"S, 46˚56'16"W
Wagneriana transitoria (C. L. Koch, 1839)	3	H	15 ± 2.30	284.48 ± 75.63	34 ± 5.68	-0.293	18˚45'11"S, 47˚51'28"W
Verrucosa arenata (Walckenaer, 1841)	3	H	18 ± 4.163	1064.9 ± 695.19	41 ± 4.58	0.416	23˚14'12"S, 46˚56'16"W

Table 2. The ten best combinations of variables of the model selection procedure to investigate the prediction of different orb-web traits over the patterns of sticky treads distribution. The complete table is in Supporting Information (Table S1). The variables are: capture area (CA, cm^2), number of radii (NR) and sticky threads' turns (NT) on the lower portion of webs, spider resting position (Posit.: hub, out of the web, or alternating the resting positions according to the daily period), and relative distances of spacings to hub (Dist.). The alternative models are ranked according to their Akaike Information Criterion (AICc) values. The best models are shaded in grey (ΔAICc ≤ 2). ΔAICc is the difference between the AICc value of each model and the AICc value of the most parsimonious model; K is the number of parameters; $\boldsymbol{\omega_i}$ = AICc weight of each model; and "×" denotes interactions between variables.

Model' intercept	Coefficients' parameters									K	AICc	ΔAICc	ωi
	Dist.	CA	NR	NT	Posit.	CA×Dist.	NR×Dist.	NT×Dist.	Posit.×Dist.				
1.149	**-0.16942**				**+**				**+**	**9**	**2691.8**	**0.0**	**0.234**
1.153	-0.16932	-0.00001			+				+	10	2693.4	1.6	0.105
1.144	-0.16951		0.00032		+				+	10	2693.6	1.8	0.095
1.143	-0.16928			0.00012	+				+	10	2693.6	1.9	0.092
1.158	-0.17932	-0.00003			+	0.00003			+	11	2694.7	2.9	0.054
1.153	-0.18625		-0.00023		+		0.00102		+	11	2695.0	3.2	0.047
1.158	-0.19510			-0.00013	+			0.00045	+	11	2695.0	3.2	0.047
1.145	-0.16918	-0.00001		0.00015	+				+	11	2695.1	3.4	0.043
1.147	-0.16940	-0.00001	0.00034		+				+	11	2695.1	3.4	0.043
1.143	-0.16943		0.00025	0.00005	+				+	11	2695.5	3.8	0.035

SUPPORTING INFORMATION

Supporting Table 1. The complete model selection procedure to investigate the prediction of different orb-web traits over the patterns of sticky treads distribution. The variables are: capture area (CA, cm²), number of radii (NR) and sticky threads' turns (NT) on the lower portion of webs, spider resting position (Posit.: hub, out of the web, or alternating the resting positions according to the daily period), and relative distances of spacings to hub (Dist.). The alternative models are ranked according to their Akaike Information Criterion (AICc) values. The best models are shaded in grey (ΔAICc ≤ 2). ΔAICc is the difference between the AICc value of each model and the AICc value of the most parsimonious model; K is the number of parameters; $\boldsymbol{\omega_i}$ = AICc weight of each model; and "×" denotes interactions between variables.

Model' intercept	Coefficients' parameters									K	AICc	ΔAICc	ωi
	Dist.	CA	NR	NT	Posit.	CA×Dist.	NR×Dist.	NT×Dist.	Posit.×Dist.				
1.149	**-0.16942**				**+**				**+**	**9**	**2691.8**	**0.0**	**0.234**
1.153	-0.16932	-0.00001			+				+	10	2693.4	1.6	0.105
1.144	-0.16951		0.00032		+				+	10	2693.6	1.8	0.095
1.143	-0.16928			0.00012	+				+	10	2693.6	1.9	0.092
1.158	-0.17932	-0.00003			+	0.00003			+	11	2694.7	2.9	0.054
1.153	-0.18625		-0.00023		+		0.00102		+	11	2695.0	3.2	0.047
1.158	-0.19510			-0.00013	+			0.00045	+	11	2695.0	3.2	0.047
1.145	-0.16918	-0.00001		0.00015	+				+	11	2695.1	3.4	0.043
1.147	-0.16940	-0.00001	0.00034		+				+	11	2695.1	3.4	0.043
1.143	-0.16943		0.00025	0.00005	+				+	11	2695.5	3.8	0.035
1.151	-0.17932	-0.00003		0.00016	+	0.00003			+	12	2696.5	4.7	0.022
1.153	-0.17927	-0.00003	0.00035		+	0.00003			+	12	2696.5	4.7	0.022
1.160	-0.19475	-0.00001		-0.00010	+			0.00044	+	12	2696.5	4.8	0.022
1.156	-0.18598	-0.00001	-0.00022		+		0.00102		+	12	2696.6	4.8	0.021

1.157	-0.19518		0.00026	-0.00020	+			0.00045	+	12	2696.9	5.1	0.018
1.152	-0.18615		-0.00031	0.00005	+		0.00103		+	12	2697.0	5.2	0.017
1.145	-0.16922	-0.00001	0.00020	0.00010	+				+	12	2697.1	5.3	0.016
1.163	-0.19691	-0.00003	-0.00023		+	0.00003	0.00105		+	13	2697.9	6.1	0.011
1.163	-0.20132	-0.00003		-0.00007	+	0.00003		0.00040	+	13	2698.0	6.2	0.010
1.150	-0.17927	-0.00003	0.00022	0.00010	+	0.00003			+	13	2698.4	6.7	0.008
1.159	-0.19480	-0.00001	0.00022	-0.00016	+			0.00044	+	13	2698.5	6.7	0.008
1.154	-0.18595	-0.00001	-0.00031	0.00008	+		0.00098		+	13	2698.5	6.7	0.008
1.158	-0.19539		-0.00006	-0.00012	+		0.00057	0.00029	+	13	2698.8	7.1	0.007
1.160	-0.19629	-0.00003	-0.00035	0.00009	+	0.00003	0.00103		+	14	2699.8	8.1	0.004
1.163	-0.20140	-0.00003	0.00021	-0.00013	+	0.00003		0.00040	+	14	2699.9	8.2	0.004
1.159	-0.19494	-0.00001	-0.00009	-0.00007	+		0.00056	0.00029	+	14	2700.4	8.6	0.003
1.163	-0.20180	-0.00003	-0.00017	-0.00002	+	0.00003	0.00072	0.00019	+	15	2701.8	10.0	0.002
1.141	-0.17321									5	2863.5	171.7	0.000
1.130	-0.14753	0.00003				-0.00007				7	2863.9	172.2	0.000
1.114	-0.13023		0.00131				-0.00203			7	2864.8	173.1	0.000
1.133	-0.17316			0.00019						6	2865.1	173.3	0.000

1.145	-0.17323	-0.00001							6	2865.2	173.4	0.000
1.137	-0.17321		0.00024						6	2865.3	173.6	0.000
1.104	-0.10736	0.00003	0.00128			-0.00007	-0.00194		9	2865.5	173.8	0.000
1.122	-0.14761	0.00003		0.00020		-0.00007			8	2865.5	173.8	0.000
1.126	-0.14758	0.00003	0.00025			-0.00007			8	2865.8	174.0	0.000
1.152	-0.17285				+				7	2866.3	174.5	0.000
1.117	-0.13021	-0.00001	0.00133				-0.00203		8	2866.6	174.8	0.000
1.110	-0.12989		0.00108	0.00019			-0.00204		8	2866.6	174.8	0.000
1.140	-0.14717	0.00003			+	-0.00007			9	2866.7	175.0	0.000
1.136	-0.17319	-0.00001		0.00020					7	2866.8	175.0	0.000
1.140	-0.17323	-0.00001	0.00026						7	2867.1	175.3	0.000
1.132	-0.17059			0.00021				-0.00005	7	2867.1	175.3	0.000
1.133	-0.17316		0.00002	0.00018					7	2867.1	175.3	0.000
1.101	-0.10706	0.00003	0.00102	0.00021		-0.00007	-0.00195		10	2867.2	175.5	0.000
1.124	-0.12974		0.00141		+		-0.00203		9	2867.5	175.7	0.000
1.123	-0.14947	0.00003		0.00018		-0.00007		0.00004	9	2867.5	175.8	0.000
1.122	-0.14761	0.00003	0.00001	0.00020		-0.00007			9	2867.5	175.8	0.000

1.118	-0.14267		0.00156	-0.00018			-0.00296	0.00068	9	2867.6	175.8	0.000
1.108	-0.12066	0.00003	0.00159	-0.00022		-0.00007	-0.00302	0.00079	11	2867.9	176.1	0.000
1.154	-0.17285	-0.00001			+				8	2868.0	176.2	0.000
1.144	-0.17278			0.00016	+				8	2868.0	176.2	0.000
1.146	-0.17283		0.00035		+				8	2868.0	176.3	0.000
1.114	-0.10692	0.00003	0.00137		+	-0.00007	-0.00194		11	2868.2	176.4	0.000
1.113	-0.12984	-0.00001	0.00107	0.00021			-0.00205		9	2868.2	176.5	0.000
1.132	-0.14723	0.00003		0.00018	+	-0.00007			10	2868.4	176.7	0.000
1.135	-0.14726	0.00003	0.00035		+	-0.00007			10	2868.5	176.7	0.000
1.135	-0.17061	-0.00001		0.00023				-0.00005	8	2868.8	177.0	0.000
1.136	-0.17319	-0.00001	0.00001	0.00020					8	2868.8	177.0	0.000
1.132	-0.17059		0.00002	0.00021				-0.00005	8	2869.1	177.3	0.000
1.121	-0.14261	-0.00001	0.00156	-0.00016			-0.00297	0.00068	10	2869.2	177.5	0.000
1.126	-0.12969	-0.00001	0.00142		+		-0.00204		10	2869.2	177.5	0.000
1.120	-0.12951		0.00126	0.00011	+		-0.00204		10	2869.4	177.7	0.000
1.123	-0.14941	0.00003	0.00001	0.00018		-0.00007		0.00004	10	2869.5	177.8	0.000
1.146	-0.17277	-0.00001		0.00018	+				9	2869.7	177.9	0.000

1.149	-0.17284	-0.00001	0.00036		+				9	2869.7	178.0	0.000
1.143	-0.17279		0.00021	0.00010	+				9	2870.0	178.2	0.000
1.142	-0.17005			0.00019	+			-0.00006	9	2870.0	178.2	0.000
1.110	-0.10668	0.00003	0.00118	0.00014	+	-0.00007	-0.00196		12	2870.1	178.3	0.000
1.131	-0.14725	0.00003	0.00017	0.00013	+	-0.00007			11	2870.4	178.6	0.000
1.128	-0.14218		0.00176	-0.00026	+		-0.00297	0.00068	11	2870.4	178.7	0.000
1.133	-0.14894	0.00003		0.00015	+	-0.00007		0.00004	11	2870.4	178.7	0.000
1.118	-0.12017	0.00003	0.00175	-0.00030	+	-0.00007	-0.00302	0.00080	13	2870.7	178.9	0.000
1.135	-0.17063	-0.00001	0.00001	0.00023				-0.00005	9	2870.8	179.0	0.000
1.122	-0.12945	-0.00001	0.00122	0.00015	+		-0.00205		11	2871.1	179.3	0.000
1.145	-0.17278	-0.00001	0.00017	0.00013	+				10	2871.6	179.9	0.000
1.144	-0.17003	-0.00001		0.00021	+			-0.00006	10	2871.6	179.9	0.000
1.142	-0.17019		0.00021	0.00013	+			-0.00006	10	2872.0	180.2	0.000
1.130	-0.14203	-0.00001	0.00172	-0.00023	+		-0.00297	0.00068	12	2872.1	180.3	0.000
1.132	-0.14906	0.00003	0.00017	0.00010	+	-0.00007		0.00004	12	2872.4	180.6	0.000
1.144	-0.17019	-0.00001	0.00017	0.00016	+			-0.00006	11	2873.6	181.8	0.000
1.053									4	3120.9	429.1	0.000

1.063				+	6	3122.3	430.6	0.000
1.044			0.00021		5	3122.5	430.7	0.000
1.056	-0.00001				5	3122.7	430.9	0.000
1.048		0.00024			5	3122.8	431.1	0.000
1.051			0.00023	+	7	3123.7	432.0	0.000
1.057		0.00041		+	7	3123.9	432.2	0.000
1.066	-0.00001			+	7	3124.1	432.3	0.000
1.047	-0.00001		0.00023		6	3124.2	432.4	0.000
1.044		-0.00003	0.00022		6	3124.5	432.7	0.000
1.051	-0.00001	0.00025			6	3124.6	432.8	0.000
1.053	-0.00001		0.00026	+	8	3125.4	433.6	0.000
1.059	-0.00001	0.00041		+	8	3125.7	433.9	0.000
1.051		0.00016	0.00019	+	8	3125.7	433.9	0.000
1.047	-0.00001	-0.00004	0.00024		7	3126.2	434.4	0.000
1.053	-0.00001	0.00011	0.00022	+	9	3127.3	435.6	0.000

CONSIDERAÇÕES FINAIS

Neste estudo investigamos dois grandes aspectos da ecologia de aranhas construtoras de teias orbiculares: a captura de presas e o comportamento de construção. Além disso, como as teias mediam estas questões, dedicamos também um capítulo a aprimorar estimadores do comprimento total de fios pegajosos em teias orbiculares, uma vez que esta variável é importante para esta linha de pesquisa. Assim, por meio de um raciocínio matemático simples, que envolve o somatório de elementos em progressões aritméticas em que os termos são arcos, chegamos a duas novas fórmulas. Estas fórmulas produziram estimativas acuradas e, assim, poderão ser usadas em conjunto em trabalhos que envolvam teias circulares e não-circulares, mantendo a simplicidade de aplicação. Embora os métodos tradicionais também resultem em boas estimativas, pensamos que o ganho em eficiência do novo método pode ser de especial importância para questões mais sensíveis a desvios de estimativas ou amostragens carregadas com teias assimétricas, uma vez que nossos cálculos se mostraram um pouco mais resilientes a isso.

Quando nós investigamos, no segundo capítulo, a influência de diferentes comportamentos e características arquiteturais das teias sobre a captura de presas, vimos que a área de captura da teia e o período das interações possuem poder preditivo sobre o tamanho dos insetos capturados. Aranhas com teias maiores e de atividade noturna foram mais propensas a capturar insetos maiores, enquanto presas pequenas eram de comum interceptação em todos os tipos de teias. Assim, é provável que as teias maiores contenham em seus fios propriedades mecânicas mais aptas ao amortecimento de mais alta energia cinética. As aranhas que possuem estas teias mais aptas em parar grandes insetos em voo, por sua vez, devem ajustar o período de construção de teia quando estes insetos são mais ativos. Estas variáveis, então, podem ser discutidas como características funcionais que determinam as interações entre aranhas e suas presas. Contudo, a aplicação de redes bipartidas a estes eventos de capturas naturais, demonstraram que todas as aranhas envolvidas no trabalho capturavam majoritariamente as mesmas famílias de presas. Isso reforça o pressuposto de que as diferentes espécies de aranhas possuem um amplo tamanho de nicho, sobrepondo-se, mesmo que alguns tipos de insetos sejam mais frequentemente capturados por um dado conjunto de aranhas. A inovação desta abordagem é que colocamos à prova das observações naturais um conjunto de pressupostos que têm sido investigados isoladamente por meio de métodos laboratoriais e de um conjunto restrito de espécies-modelo.

Finalmente, no terceiro capítulo, investigamos o poder explicativo de tradicionais hipóteses para as decisões comportamentais das aranhas ao construir teias orbiculares. Estas hipóteses propõem explicações alternativas ou complementares para o fato de que há grande variação na forma de distribuição de fios nas teias entre espécies e até mesmo entre indivíduos quando a função básica de todas as teias seja a mesma. Cada uma destas hipóteses tem recebido suporte por meio de estudos prévios, conduzindo a explicações multifuncionais. Entretanto, constata-se que pelo menos três erros analíticos estão presentes nestes estudos, inviabilizando uma avaliação independente para cada uma das hipóteses. Dessa forma, as relações de causa e efeito são confundidas e o mesmo peso explicativo é dado a cada hipótese. Então, aqui conduzimos uma investigação em busca de uma explicação simplificada e generalizável para os comportamentos de construção de teias de modo a corrigir estes erros analíticos. Ao final vimos que, embora plausíveis, as explicações tradicionais possuem poder explicativo limitado. A necessidade de compensar o maior tempo de chegada até a presa interceptada, por sua vez, demonstra ser importante o suficiente para determinar amplamente qual é a maneira ótima de distribuir fios pegajosos ao longo da teia.

Em suma, aqui investigamos diferentes aspectos da ecologia de aranhas de teias orbiculares partindo da aquisição de variáveis, passando pelo comportamento e suas interações no meio natural. Se uma das finalidades da ciência é identificar padrões e encontrar explicações plausíveis para os fenômenos da natureza reduzindo o viés analítico, pensamos que esta tese assim ajuda a esclarecer algumas das questões relacionados a esse grupo taxonômico.