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ESTRUTURA DA TEIA E ESTRATÉGIAS DE DEFESA DE *WIXIA ABDOMINALIS* O. PICKARD-CAMBRIDGE, 1882 (ARANEAE, ARANEIDAE)

Gabriel Máximo Xavier

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

Orientador

Prof. Dr. Marcelo de Oliveira Gonzaga

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APROVADO em 26 de fevereiro de 2016

Prof. Dra. Solange Cristina Augusto- UFU

Prof. Dr. Adalberto José dos Santos - UFMG

Orientador

Prof. Dr. Marcelo de Oliveira Gonzaga

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RESUMO

Xavier, Gabriel Máximo. 2016. Estrutura da teia e estratégias de defesa de *Wixia abdominalis* O. Pickard-Cambridge, 1882 (Araneae, Araneidae). Dissertação de Mestrado em Ecologia e Conservação de Recursos Naturais. Universidade Federal de Uberlândia. Uberlândia-MG. 52 p.

O forrageio e a defesa são os dois aspectos mais fundamentais da sobrevivência. Assim, a morfologia, fisiologia e comportamento de um animal devem refletir como demandas conflitantes entre forrageio e defesa são resolvidas ao longo de sua evolução, por meio da influência dos tipos de presas e predadores envolvidos em suas interações. Aranhas construtoras de teias orbiculares constituem um bom modelo para o estudo de ambos os aspectos. São predadoras e comumente presas de outros animais. A teia orbicular possibilita o estudo sobre a solução de demandas durante o forrageio. Seus componentes exercem funções distintas e sua disposição influencia os tipos de presas capturadas. Entretanto, a funcionalidade arquitetural destas teias não é completamente compreendida. Assim, diversas hipóteses, muitas conflitantes, foram propostas para explicar a distribuição diferencial de investimento em diferentes partes da teia e outros aspectos de sua estrutura. No capítulo 1, utilizando as teias orbiculares de *Wixia abdominalis* (Araneae, Araneidae) como modelo, nós avaliamos quais das hipóteses já apresentadas na literatura melhor explicam o padrão encontrado e até que ponto mecanismos incidentais interferem neste padrão. Nossas análises indicam que uma abordagem com múltiplas hipóteses é necessária para explicar a arquitetura destas teias. Algumas hipóteses, entretanto, não foram corroboradas pelos dados obtidos. Aranhas construtoras de teias são comumente presas de predadores visualmente orientados, tal como vespas e aves. Diferentes tipos de defesas passivas, tal como a cripsia e o disfarce, tem sido propostos como sendo um resultado da pressão seletiva por parte destes predadores. Entretanto, estas atribuições ainda são subjetivas, uma vez que os sistemas visuais de predadores, como himenópteros e aves, são diferentes do humano e diferem entre si. Portanto, a funcionalidade do disfarce é direcionada a determinados tipos de observadores, sendo estes as potenciais fontes de pressão seletiva. No capítulo 2, por meio de modelos visuais, nós analisamos se de fato a coloração de *W. abdominalis* e de seu micro-habitat proporcionam o disfarce para seus potenciais principais predadores, vespas e aves. Nossos testes corroboram que o disfarce de fato ocorre quando *W. abdominalis* é vista em seu micro-habitat por ambos os sistemas visuais, himenópteros e aves. Nós discutimos também a potencial influência dos dois tipos de predadores sobre a evolução deste tipo de defesa.

ABSTRACT

Xavier, Gabriel Máximo. 2016. Web structure and defensive strategies of *Wixia abdominalis* O. Pickard-Cambridge, 1882 (Araneae, Araneidae). Master Degree Dissertation of Ecology and Conservation of Natural Resources. Universidade Federal de Uberlândia. Uberlândia-MG. 52 p.

Foraging activities and defense are the most fundamental aspects involved with survivorship. Thus, morphology, physiology and behavior of an animal reflect how trade-offs between foraging and defense are solved in its evolution, through the influence prey types and predators involved in its interactions. Orb-web weaver spiders are good models to assess both aspects. They are predators and usually are included in diet of other animals. The orb-web allow the evaluation on the solution of trade-offs during foraging. Its components exert different functions and their arrangement influences the size and kinds of prey captured. However, the architectural functionality of orb-webs is not completely understood. Thus, several hypotheses, some of them conflicting with each other, were proposed to explain the differential investment in distict parts of the web and other aspects of its design. In chapter 1, using orb-webs of *Wixia abdominalis* (Araneae, Araneidae) as a model, we assessed which of the hypotheses previously presented in literature better explain the observed pattern and how incidental mechanisms interfere in this pattern. Our analyzes indicate that multiple hypotheses are necessary to explain the orb-web architecture. Some, however, were not corroborated by our data on *W. abdominalis*. Orb-web weaver spiders are usually prey of visually oriented predators, such as wasps and birds. Different kinds of passive defenses, such as crypsis and masquerade, have been proposed to be the result of selective pressures by these predators. However, these assumptions are still subjective, since visual systems of predators, such as wasps and birds, are different from that of human and are different between them. Therefore, the function of masquerade is directed to specific kinds of observers, which are the sources of selective pressure. In chapter 2, by means of visual models, we assessed whether indeed the color of *W. abdominalis* and its microhabitat provides the masquerade against its potential main predators, wasps and birds. Our tests corroborate that indeed there is masquerade when *W. abdominalis*is seen in its microhabitat by visual systems of hymenopterans and birds. We also discussed the potential influence of both kinds of predators over the evolution of this kind of defense.

INTRODUÇÃO GERAL

A seleção natural atua sobre taxas de sobrevivência e, em última instância, sobre a reprodução. A sobrevivência está intimamente relacionada à capacidade de obtenção de alimento e à defesa contra predadores. Entretanto, frequentemente existe uma demanda conflitante entre estas duas necessidades (Huey & Pianka 1981, Rayor & Uetz 1990) e, ao forragear, um animal pode se tornar mais vulnerável à predação. De forma similar, ao evitar predadores o forrageio pode ficar restrito a um espaço ou tempo limitados (Smith 2009, Pekár 2014). Portanto, as características morfológicas, fisiológicas e comportamentais de um animal devem refletir como estas demandas conflitantes são resolvidas ao longo de sua evolução, sendo influenciadas pelos tipos de predadores e presas envolvidos em suas interações (Huey & Pianka 1981, Pekár 2014).

Aranhas são essencialmente predadoras e comumente presas de diversos outros animais (Foelix 2011). Essa posição intermediária em muitas teias tróficas as torna um modelo adequado para o estudo de como estes dois segmentos mais fundamentais da história natural animal, forrageio e defesa, podem ser moldados a partir de interações específicas.

As aranhas, em grande parte, são detentoras da peculiar capacidade de construir armadilhas de seda para a captura de presas (Foelix 2011). As espécies que fazem uso dessas armadilhas utilizam uma estratégia de forrageamento do tipo senta e espera, o que tem implicações importantes tanto em sua susceptibilidade à predação (Huey & Pianka 1981, Blackledge *et al.* 2003), quanto aos impactos promovidos sobre populações de suas presas (Liu *et al.* 2015). As vantagens desta estratégia de caça estão relacionadas à redução de riscos associados com a busca ativa por presas (Huey & Pianka 1981). Entretanto, são as presas que devem vir até a teia e a seda é um material proteico dispendioso (Blackledge *et al.* 2011). Assim, um evento de intercepção falho deve implicar alto custo.

Diversos grupos de aranhas são capazes de ajustar a arquitetura de suas teias para maximizar a captura de diferentes tipos de presas. Um bom exemplo são as variações nas teias orbiculares (Sandoval 1994, Blackledge *et al.* 2011). A forma, o tamanho e cada componente de uma teia orbicular, por exemplo, exercem uma função distinta durante o processo de captura (Herbestein & Heiling 1999, Blackledge & Zevenbergen 2006, Sensenig *et al.* 2012). Este tipo de teia tem sido o objeto de estudo de diversos trabalhos que investigam se suas arquiteturas são ajustadas para maximizar o sucesso de captura de presas ou até que ponto são influenciadas por fatores incidentais (Heiling & Herberstein 1998, Herbestein & Heiling 1999, Eberhard 2014, Zschokke & Nakata 2015). Dessa forma, diversas hipóteses, tanto da vertente funcional quanto incidental, tem sido propostas para explicar a arquitetura de teias orbiculares. Entretanto, as atuais análises de tais hipóteses ainda são provisórias e a avaliação de mais espécies é necessária para se conhecer regras gerais. No capítulo 1 deste estudo, avaliamos a arquitetura da teia orbicular de *Wixia abdominalis* (Araneae, Araneidae) e discutimos, a partir desta, quais das atuais hipóteses sobre a distribuição de raios e espiras são corroboradas pelos dados obtidos.

Além de capturarem uma grande diversidade de presas, aranhas construtoras de teias são também comumente presas de diversos grupos de predadores, sendo vespas (Blackledge *et al.* 2003, Gonzaga & Vasconcellos-Neto 2005) e aves (Gunnarsson 2008) os principais. Himenópteros e aves são orientados pela visão (Peitsch *et al.* 1992, Hart 2001). Diversos tipos de defesas passivas são direcionados à ação de predadores visualmente orientados, tal como a cripsia e o disfarce (*masquerade*) (Skelhorn *et al.* 2010, Pekár 2014). Teoricamente estas duas defesas diferem em sua funcionalidade (Skelhorn *et al.* 2010). A cripsia atua por meio da dificuldade de detecção por predadores. Isto é alcançado por meio de padrões disruptivos de coloração (Cuthill *et al.* 2005) ou por meio do ajuste por coloração a um determinado plano de fundo (Théry *et al.* 2005). O disfarce atua por meio da classificação incorreta pelo observador (Skelhorn *et al.* 2010, Pekár 2014). Isto é alcançado por meio da semelhança de um organismo com um objeto não comestível comum no ambiente circundante. As duas defesas podem agir de maneira associada ou não, dependendo de objeto imitado (Skelhorn *et al.* 2010). Ambas as defesas têm sido sugeridas como as principais apresentadas por aranhas contra predadores visualmente orientados (Pekár 2014). Entretanto, estas atribuições ainda são subjetivas, uma vez que os sistemas visuais de predadores, como himenópteros e aves, são diferentes do humano e diferem entre si (Giurfa *et al.* 1997, Hart 2001). Portanto, se os sistemas visuais são diferentes, a funcionalidade das defesas é direcionada a determinados tipos de observadores, sendo estes as potenciais fontes de pressão seletiva. No capítulo 2, por meio de modelos visuais nós analisamos se de fato a coloração de *W. abdominalis* e de seu micro-habitat proporciona tais defesas contra seus potenciais principais predadores, vespas e aves.

O modelo deste estudo, *W. abdominalis*, segrega estes dois segmentos de história natural entre o dia (defesa contra predadores visualmente orientados) e a noite (forrageio). O estudo de forrageio por meio de teias orbiculares se concentra em grande parte em um grupo restrito de espécies modelo. Assim, a partir da teia de *W. abdominalis* podemos analisar a generalidade de tais hipóteses. Além disso, nós identificamos variações intraespecíficas nestas teias, possibilitando a discussão sobre as implicações destas sobre a aplicabilidade das atuais hipóteses. *Wixia abdominalis* constitui também um bom modelo para o estudo de estratégias de defesa uma vez que aparenta exibir defesas passivas associadas à sua peculiar morfologia.

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CHAPTER 1

Orb web architecture of *Wixia abdominalis* O. Pickard-Cambridge, 1882 (Araneae, Araneidae): intra-orb variation of web components

Abstract

The distribution of sticky spirals and radii within orb webs is usually not uniform. Distinct patterns of silk investment in inner and outer portions of the orb may influence the web's capacity of stopping and retaining specific prey types. Several incidental and functional hypotheses have been previously proposed to explain the variation in web patterns. Herein, we described the webs built by spiders of the monospecific genus *Wixia* O. Pickard-Cambridge, 1882 (Araneidae) and evaluated web-building hypotheses, considering the presence of a free-sector, vertical symmetry, sticky spiral distribution and radii spacing. Because all information available on the ecology of *Wixia* is restricted to the species that were subsequently transferred to other araneid genera, there is no information about the webs of the last species remaining in this genus, *Wixia abdominalis.* We observed that this spider builds complete orbs, but some individuals add a free-sector, remaining resting on a twig above the orb and holding a signaling thread. Spiral distribution follows the pattern of increasing densities from the edge to the hub on the upper part of the orb. However, in the lower part of orbs, this pattern is present just in complete webs. While, the pattern of spiral distribution observed in lower part of webs presenting a free-sector is homogeneous from the edge to the hub. We discussed possible implications of the web structure of *W. abdominalis* for prey capture and how the incidental and functional hypotheses may explain the patterns of spiral spacing observed in this species.

Keywords: Free-sectors, orb-webs, sticky spiral spacing, prey capture

Introduction

Webs spun by araneoid ecribellate orbicularians are composed of distinct types of silk, each one with particular mechanical properties and functions (Blackledge *et al.* 2011). The non-adhesive radii, for example, are responsible for stopping prey by absorbing its kinetic energy upon impact with the web (Sensenig *et al.* 2012). Sticky spirals, on the other hand, retain prey in the web long enough to the spider to move to the interception site and subdue the prey (Blackledge & Zevenbergen 2006). In addition, spiders may regulate vertical displacement of the hub from the web's geometric center to increase the probability of prey capture (Nakata & Zschokke 2010, Zschokke & Nakata 2010, Blackledge *et al.* 2011). Therefore, measurements of the spacing of sticky spirals and radii, and vertical asymmetry of the web provide important information regarding the spider's foraging behavior.

Despite their apparent geometrical uniformity, there is significant inter- and intraspecific variation in orb web design (e.g., presence and types of shelters; free sectors; patterns of symmetry; presence, shape, and composition of stabilimenta) (Manicom *et al.* 2008; Blackledge *et al.* 2011; Gonzaga & Vasconcellos-Neto 2012; Eberhard 2014). For example, sticky spiral distribution is usually not uniform from the edge to the hub within orb webs (Herberstein & Heiling 1999; Zschokke 2002; Eberhard 2014). Moreover, the distribution of sticky spirals typically varies between the upper and lower parts of the web, as it does radii distribution (Zschokke & Nakata 2015). These features are, in some way, linked with web dimensions. For example, the more extensive the web part (upper or lower) is, the greater the spacing between the spirals and the more parallel the radii will be (Zschokke & Nakata 2015). However, the upper part typically has a lower density of sticky spirals, and the radii are less parallel than are those in the lower part. This difference can persist even in symmetric webs (Zschokke & Nakata 2015).

Several incidental and functional hypotheses have been proposed to explain intra-orb variation in sticky spiral and radii distribution (see Eberhard 2014), as well as differences in investment between the upper and lower parts of the web. Incidental hypotheses are explanations associated with physical or physiological constraints during web building (Eberhard 2014). The first incidental hypothesis, hereafter "Peters' segment rule," states that the gradual decrease in sticky spiral spacing from the edge to the hub is a consequence of the geometric spacing between adjacent radii, which decreases in the same direction. Therefore, spiders would adjust sticky spiral spacing based on the distance between adjacent radii (Peters 1954). According to Peters' segment rule, it is expected that sticky spiral spacing always increases from the hub to the edge, and this increase should be greatest where adjacent radii are less parallel. The second incidental hypothesis is referred to as the "energetic constraint hypothesis" (Herberstein & Heiling 1999). Because spiders usually have to lift their abdomens to make attachments above the hub, the greater spiral spacing in the upper part of the web is a result of the larger energetic cost imposed during the web building in that part. As the spider fixes the spirals higher up, the greater is the energy expenditure, because the turns are larger than web part bellow the hub. According to this hypothesis, therefore, a larger increase from the hub to the edge in sticky spiral spacing and greater distances between spirals in the upper part compared to the lower part of the web is expected. Additionally, asymmetric webs with smaller upper parts are expected to be common, because building the upper part is energetically more expensive.

Functional hypotheses consider that edge-to-hub differences in sticky spiral spacing improve the foraging efficiency (Eberhard 2014). The first functional hypothesis, hereafter the "attack-time hypothesis," is based on the assumption that spiders would invest more silk in web areas where they are more likely to capture prey successfully (Heiling & Herberstein 1998). Therefore, larger investment in sticky threads near the hub is expected because these locations can be reached faster by spiders. A higher investment in the lower part of the web is also expected because orb weavers usually rest facing downward and run faster in this direction (Heiling & Herberstein 1998). This hypothesis is supported by the vertical asymmetry of several orb webs, which typically has a longer bottom part (below the hub) than top part (Heiling & Herberstein 1998; Herberstein & Heiling 1999; Zschokke 2002; Hesselberg 2010; Nakata 2012). The "radii-density hypothesis," on the other hand, suggests that spiders invest more silk in sticky spirals in segments with a greater capacity to stop prey. Therefore, the high investment in sticky spirals follows the density of radii (Zschokke 2002). Thus, a higher investment in sticky spirals near the hub and in the web part where radii are more parallel is expected. Finally, there are two additional hypotheses, the "sticky spiral entanglement" (Eberhard 2014) and the "prey tumbling" hypotheses (de Crespigny *et al.* 2001). The first is concerned with the idea that larger distances between sticky spirals near the edge may assure a lower chance of contact between adjacent loops because of the disturbance caused by the wind. The latter hypothesis states that smaller spaces between loops at the innermost area above the hub and outermost area below the hub of some spider species' webs could increase capture success when prey tend to escape by tumbling in vertical orb webs.

Tests of these hypotheses are restricted to a few common model species (Eberhard 2014). Therefore, the extension of evaluation to other orb-web weavers must provide information on each hypothesis. In this study, we describe the orb web of *Wixia abdominalis*, and discuss the implications of web architecture in the scope of the functionality of its components. Stowe (1978) first described the unusual "asterisk" web of a *Wixia* species. According to him, the webs of *W. ectypa* (Walckenaer, 1841) presented a simple hub and typically only eight radii. Adhesive spirals were absent and spiders preyed exclusively on pedestrian arthropods. This adaptation to prey-specific capture is often mentioned in the literature on orb webs (Blackledge *et al.* 2011) and is attributed in general to *Wixia*. However, all 49 species, except *W. abdominalis*, previously included in *Wixia* were transferred to other genera, mostly to *Ocrepeira*, and also to *Acacesia*, *Alpaida*, *Wagneriana*, or considered as *nomen dubium* (*Wixia proxima* Mello-Leitão, 1940) (WSC 2015). Data available in the literature on *W. abdominalis* is restricted to its morphology (Pickard-Cambridge 1882; Levi 1993) and to a few records of distribution in Guyana, Brazil (Pirenópolis, State of Goiás) and Bolivia (Levi 1993). Herein, we present the first record of the web pattern of the last species remaining within the genus *Wixia* showing that there is no impressive modification from the conventional orb-web structure, such as those described in asterisk webs.

Methods

Webs of *W. abdominalis* were located in a *Eucalyptus* plantation in Fazenda Nova Monte Carmelo (18°45′11″S, 47°51′28″W), Estrela do Sul, MG, Brazil. Areas covered by *Eucalyptus* were interspersed by fragments of Cerrado vegetation, but our surveys were restricted to regions within the monoculture. All webs were located at night during monthly expeditions and photographed after being lightly coated with cornstarch (see Eberhard 1976). Expeditions were conducted from August to December 2014 and surveys were restricted to the period from 19:00 to 0:00. All web measurements were performed from the photographs using the software ImageJ (National Institutes of Health, USA).

Web asymmetry (departure of shape of the web from a circle) and hub asymmetry (displacement of the hub from the web's geometric center) indices were evaluated according to Blackledge and Gillespie (2002). For the first index, positive values indicated vertically elongated webs. For the second index, positive values indicated upwardly eccentric webs. In both indices, values close to zero indicated symmetric webs.

Procedures to evaluate spacing of sticky spirals and radii were established following Eberhard (2014). We calculated the distance ratio between adjacent radii for each part of the webs, upper and lower. This ratio was obtained by dividing the distance between two adjacent radii at the outer edge by that of adjacent radii at the inner edge of the capture zone. We selected three pairs of adjacent radii for each part of the web (three pairs nearest to 0° and three pairs nearest to 180°), and used these to measure distance ratios. Then, we averaged the values for each part of the web. Ratios close to one indicate parallel radii. The distance ratios between adjacent radii in the upper and lower part of the webs were compared using a paired *t*-test.

We measured the distances between all the spiral loops on the most vertical radius for each part of the webs, upper and lower. These distances were standardized by dividing each measurement by the median space on that radius. The standardized 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. We conducted a linear regression analysis of standardized spaces between loops of sticky spirals and the relative distance from edge-to-hub. In this regression, we excluded 20% of these standardized spaces in the inner and outer portions of the capture zone and used the 60% in the middle portions. We used this approach, because these innermost and outermost portions have spaces between spiral loops especially smaller or greater in many species, generating non-linear data (Eberhard 2014). We compared the spaces of these portions with the middle portion, using Friedman paired tests and Nemenyi *post-hoc* tests (see Pereira *et al.* 2015) by means of the 'PMCMR' R package (Pohlert 2014). We performed data analysis in R software, version 3.3.2 (R Development Core Team 2016).

Previously, we observed that some individuals constructed webs with a free-sector. These spiders remaining out of the hub, holding a signal line connected to the hub from a position on a branch of *Eucalyptus* (Fig. 1D). The presence of free-sectors may implicate behavioral changes during prey capture and may impose constraints on other web components. Hence, we evaluated webs with and without free-sectors separately. We performed analyses of covariance (ANCOVA) in order to assess if: (1) the linear regressions differ between webs with and without free-sector, (2) the linear regressions differ between upper and lower part of all webs. To use parametric tests, we assessed the assumptions of normality and homoscedasticity by means of graphical analysis of residual distribution.

Results

Individuals of *W. abdominalis* are active nocturnally, ingesting their webs at dawn. During the day, the spiders remained motionless in a cryptic position on the branches of *Eucalyptus* trees (Fig. 1A). In this position, they resembled a piece of broken wood.

We recorded webs of 28 juvenile individuals (all at antepenultimate or penultimate instars, weighing 0.024 ± 0.007g, mean ± se, min. 0.0059g and max. 0.1819g) and two adult females (weighing 0.047 and 0.074g). All webs appear to be more or less vertically oriented (Fig. 1B-D). Some webs spun by juveniles included a free-sector (n = 16). The angle of signal lines in the free sectors deviated slightly from vertical orientation (16.69° ± 4.02, mean ± se) . In these webs, spiders remained on a branch located immediately above the orb at night, holding a thread connected to the web hub. In webs without a free-sector (n = 14), spiders waited for prey interception at the hub, facing downward. However, the frequency of these behaviors was not quantified herein. Webs with and without free-sectors were analyzed separately, because there was no information on how or whether this variation in orb design would influence other web parameters.

Juvenile individuals built slightly vertically asymmetric webs (web asymmetry index = 0.119 ± 0.03) and webs with hubs were displaced upward (hub asymmetry index = 0.325 ± 0.03). The two webs built by adults were more vertically asymmetric (web asymmetry index = 0.328 and 0.273), and their hubs were displaced upward (hub asymmetry index = 0.494 and 0.129).

From the analysis of the webs of immature and adults pooled, the average distance ratio between adjacent radii was 7.15 ± 0.404 in the upper part and 5.96 ± 0.45 in the lower part of the webs (n = 29). The upper part had greater ratios than the lower part of the webs (paired *t*-test: t = 2.818, P = 0.009). Therefore, in the upper part, the radii were less parallel and the difference in radii density between inner and outer portions was more pronounced than in the lower part of the webs. Webs with and without free-sectors were not different in distance ratios between adjacent radii in the upper (*t*-test: t = -1.569, P = 0.128) or lower part of the webs (*t*-test: t = -1.753, P = 0.091).

The tendency of increasing sticky spiral spacing from the hub to the edge of the capture zone was confirmed (Table 1, 2, Fig. 2). However, when only webs with free-sectors were analyzed, a uniform pattern of sticky spiral spacing in the lower part was detected (Table 2, Fig. 2). In the upper part of the webs, the increase of sticky spiral from the hub to the edge was more accentuated in webs with than webs without free-sectors (ANCOVA: $F_{1,835} = 6.882$, $P < 0.01$). In the lower part of webs, the increase of sticky spiral from the hub to the edge was more accentuated in webs without than webs with free-sectors (ANCOVA: $F_{1,360} = 7.108$, $P < 0.01$). In general, the increase in sticky spiral spacing from the hub to the edge was more accentuated in the upper part than in lower part of the webs (ANCOVA: $F_{1,119} = 30.601$, $P < 0.001$), but the 20% outermost distances between sticky spirals in the upper and lower web parts were similar ($t = 0.410$, df = 26, $P = 0.685$).

Discussion

Wixia abdominalis webs were vertically elongated with upwardly displaced hubs. The radii were always less parallel in the upper part and there was increasing sticky spiral spacing from the hub to the edge of the capture zone. The increase was larger in the upper part. However, webs presenting a free-sector exhibited an uniform spiral spacing. Despite that, we observed a similar enlargement in the 20% outermost spacing in both parts of the webs. These results did not fit well in any single hypothesis proposed to explain differential investment in distinct web segments. Based on our results, more than one hypothesis could be used to explain web architecture of *W. abdominalis*.

According to Peters' segment rule, we would expect sticky spiral spacing to increase from the hub to the edge. In addition, this increase would be greater for segments adjacent to less parallel radii (at the upper part). However, we observed that the 20% innermost spirals of webs were not less spaced than the 60% spirals of the middle part. Another pattern that contradicts Peters' segment rule is the uniform pattern of sticky spiral spacing in the lower part of the web of *W. abdominalis*. Similarly, spiral spacing of other species, including *Nephila clavipes* (Linnaeus, 1767), *Metepeira* sp. F. O. Pickard-Cambridge, 1903, (Eberhard 2014), *Argiope keyserlingi* Karsch, 1878, (de Crespigny *et al.* 2001), and some *Cyclosa* species Menge, 1866, (Zschokke & Nakata 2015), cannot be explained by this incidental hypothesis.

The “energetic constraint” incidental hypothesis, on the other hand, was partially corroborated by the greater increase in sticky spiral spacing from the hub to the edge in the upper part. However, at the higher distances at the outer segment of the upper part this would be expected. Instead, the webs of *W. abdominalis* showed similar distances between sticky spirals at outer edges of upper and lower web parts. Despite this contradiction, the asymmetric webs observed in *W. abdominalis* and in other species (Herberstein & Heiling 1999) suggest some degree of energetic constraint during web building. Indeed, it was found that spiders spent more energy building the upper part of vertical orb webs than the lower part (Coslovsky & Zschokke 2009). However, it is difficult to accept that variation in stick spirals could be determined solely by energetic constraints during web building, especially when accounting for the functional value of the uneven distribution of silk (Masters & Moffat 1983).

The greater investment in sticky spirals near the hub and in the lower part of the web is in accordance with the “attack-time hypothesis” (Heiling & Herberstein 1998). *Araneus diadematus* Clerck, 1757 , for example, presents a similar web pattern, with spirals evenly spaced below the hub and it can indeed run faster downward (ap Rhisiart & Vollrath 1994). However, *W. abdominalis* has a special condition regarding spider movements during prey capture events. Individuals with a free-sector in their webs remain on the branch located above the orb, holding a signal line, whereas individuals with complete orbs wait at the hub. In the first case, after the detection of movements of an entangled prey, the spider moves first from the resting position at the twig to the hub and then goes to the location of the prey on the web. Therefore, the spider moves for a longer distance to reach the prey. We observed that webs with free-sectors presented a pattern of spacing in the lower part that was more homogeneous than the pattern of the webs without free-sectors. This architecture is not congruous with the scope of “attack-time hypothesis”, because spiders are investing in retention further away from themselves. It may be a compensatory mechanism for spiders that rest out of web. Thus, it occurs just in lower part because it is the web part where spiders reach faster. This “compensation hypothesis” provides a theoretic understanding of the function of the uniform distribution of spirals at the lower part of webs with free-sectors; however, behavioral observations during prey capture events are still needed.

The “radii-density hypothesis” was also corroborated by our data, because there was a higher increase in sticky spiral spacing from the hub to the edge in the upper part of the webs, where radii were less parallel. However, according to this hypothesis, we would expect heterogeneity in the pattern of spiral distribution in the lower part of the webs with free-sectors. Similarly, the spiral spacing of other species is also not in complete accordance with this hypothesis, for example, *Nephila clavipes* and *Metepeira* sp., have a higher density of spirals at the edge of their orbs and adopt other strategies to increase the absorption of their prey’s kinetic energy, such as the maintenance of auxiliary spirals and division of radii, increasing radii density toward the middle and outer edges of the web (Eberhard 2014). However, these auxiliary structures to absorb kinetic energy are absent in webs of *W. abdominalis*. Therefore, the uniform pattern of spiral distribution in the lower part of the webs with a free-sector may be a result of an interaction between absorbing kinetic energy (Zschokke 2002) and compensating for the longer distance to the interception site (Heiling & Herberstein 1998).

The “sticky spiral entanglement” hypothesis is contradicted by the observation that spiral spacing was not significantly greater at the edge above the hub than at the edge below the hub. Some spiders may use alternative strategies to reduce web damage from the wind, softening the constraints imposed on its web architecture, such as the reduction of sagging of threads making them stiffer under windy conditions (Vollrath *et al.* 1997) and changing orb web orientation according to wind direction (Hieber 1984). The “prey tumbling” hypothesis also was not supported by our data, because there was an enlargement in spiral spacing on the outer edge of the lower part of the webs. However, prey tumbling is highly variable depending on web adhesiveness and prey identity (Zschokke *et al.* 2006).

In the present study, we recorded the web structure of *W. abdominalis* and observed that it differed dramatically from the patterns previously attributed to the genus *Wixia*. The architecture of the *W. abdominalis* web allowed us to discuss several hypotheses based on differential investment in distinct parts of the web as it applied to the observed characteristics.

The web architecture of *Wixia abdominalis* was better explained by the “energetic constraint” incidental hypothesis (Herberstein & Heiling 1999), and “attack time” and “radii density” functional hypotheses (Heiling & Herberstein 1998, Zschokke 2002). Our results are in accordance with the findings of Eberhard (2014) and Zschokke and Nakata (2015) in that different parts of the orb web present different properties and functions. The analysis of interspecific variation in orb-web designs and the association of these designs with aspects of the natural history of each species are important to understand the conditions determining each pattern. In addition, our study showed there was relevant intraspecific variation in certain web traits (such as inclusion of a free-sector) that might also influence web design.

Acknowledgments

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Table 1. Analyses of differences in the sticky spiral standardized spaces between the portions of orbs: the outer (0–20% of spirals from the edge to the hub), the middle (20–80%) and the inner (80–100%). We assessed the difference between the means of standardized spaces of each web portion using Friedman paired tests. The letters indicate differences between orb portions in the Nemenyi *post-hoc* tests with $P < 0.05$, and n corresponds to the number of webs.

			Means ± SD			Friedman test	
Web		*n*	Outer	Middle	Inner	χ^2	*P*
Upper	With free-sector	16	1.55 ± 0.70 a	1.05 ± 0.45 b	0.85 ± 0.37 b	22.87	< 0.05
	Without free-sector	11	1.30 ± 0.66	1.03 ± 0.32	1.02 ± 0.55	3.81	0.14
	All	27	1.45 ± 0.70 a	1.04 ± 0.40 b	0.92 ± 0.46 b	24.22	< 0.01
Lower	With free-sector	16	1.28 ± 0.70 a	1.01± 0.38 b	1.15 ± 0.49 ab	7.87	< 0.05
	Without free-sector	11	1.43 ± 0.71 a	1.03 ± 0.35 b	1.03 ± 0.45 b	13.16	< 0.01
	All	27	1.34 ± 0.71 a	1.01 ± 0.37 b	1.11 ± 0.47 ab	18.28	< 0.01

Table 2. Linear regression analyses of standardized sticky spiral spacing and the relative distance from the edge to the hub in the middle portion of the capture zone (between 0.2 and 0.8).

Web part		R^2	F	DF	Equation	*P*
Upper	With free sector	0.216	54.921	1, 199	y = -1.223x + 1.668	<0.001
	Without free sector	0.167	29.383	1, 147	y = -0.755x + 1.406	<0.001
	All	0.192	82.915	1, 348	y = -0.02x + 1.554	<0.001
Lower	With free sector	0.010	2.864	1, 298	y = -0.217x + 1.114	0.092
	Without free sector	0.065	14.554	1, 211	y = -0.478x + 1.25	<0.001
	All	0.025	13.149	1, 511	y = -0.33x + 1.174	<0.001

Figure captions

Fig. 1. *Wixia abdominalis*. (A) Resting position on an Eucalyptus branch; (B) Subadult male capturing a termite; (C) Web without free sector; (D) Web with a free-sector. The arrow indicates the spider position. Scales: A, B: 5mm; C, D: 1cm.

Fig. 2. Edge-to-hub patterns of relative standardized sticky spiral spacing in orb-webs of *Wixia abdominalis*. 'Relative distance to the hub' was calculated following Eberhard (2014) and is defined as the ratio between the 'number of sticky loops between the site in the orb and the outer edge of the capture zone' and 'total number of sticky spiral loops from the outer edge to the hub'. The value 1 is the closest to the hub.

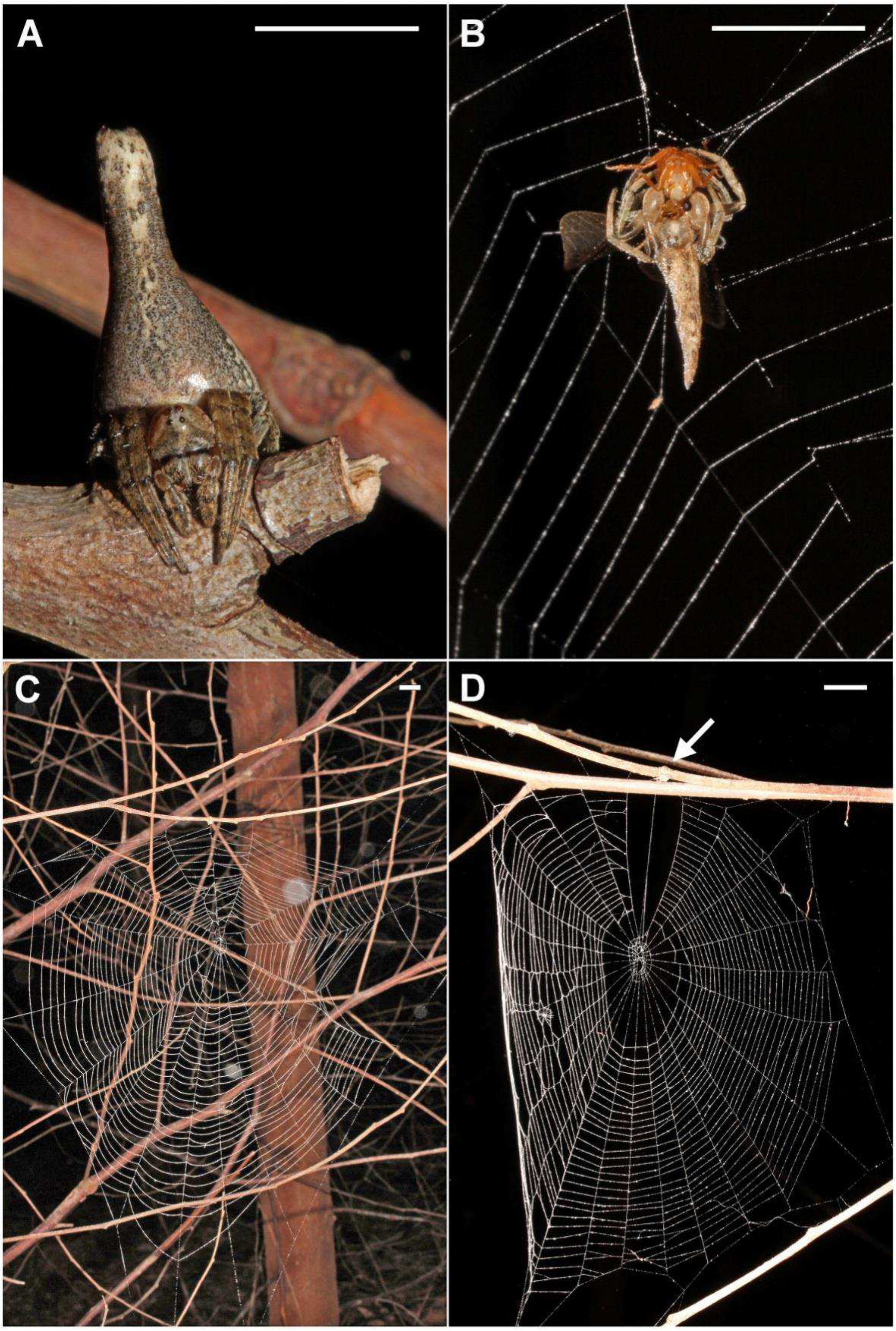

Fig. 1

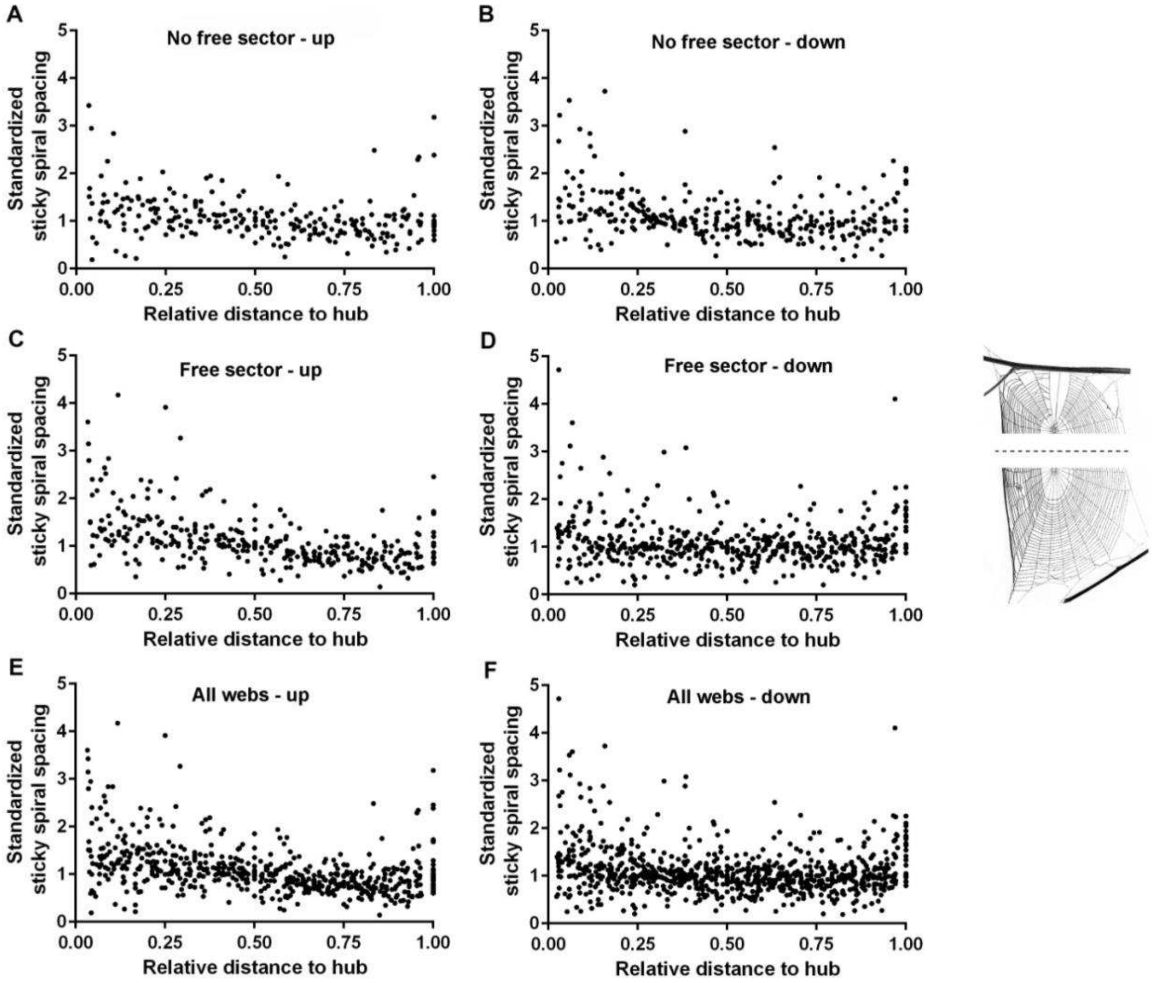
A
No free sector - up
B
No free sector - down
C
Free sector - up
D
Free sector - down
E
All webs - up
F
All webs - down
Standardized sticky spiral spacing
Relative distance to hub
0
1
2
3
4
5
0.00
0.25
0.50
0.75
1.00

Fig. 2

CHAPTER 2

Colour matching in an orb-web spider: A twig-masquerading species as seen by colour visual systems of potential predators

Abstract

Defensive strategies in animals have been hypothesised to be an evolutionary result of the interaction with predators with different colour vision abilities. In this sense, distinct predator groups perceive prey colour and brightness differently because they harbour distinct visual systems. Therefore, the evaluation of visual-based defensive strategies must be assessed from the perspective of the visual abilities of potential predators. *Wixia abdominalis* O.P. Cambridge, 1882 (Araneae, Araneidae) is a masquerader species that imitates its substrate, the twigs of *Eucalyptus* spp. Using reflectance spectrophotometry and colour visual models, we tested and subsequently corroborated the hypothesis that colour matching occurs in this species based on how it is perceived by the visual system of its primary predators, hymenopterans and birds. The results supported the assumption that both groups of predators play important roles selecting for this adaptive response in spiders. However, this type of passive defence also involves behavioural constraints, and it is unevenly distributed in spider families. Thus, we discussed the causes and implications of this defensive strategy in *W. abdominalis* and similar spider species.

Keywords: Masquerade, defensive strategy, visual models

Introduction

Predation exerts strong selective pressure and results in adaptive responses in prey (Bond & Kamil 2002). In this sense, numerous passive and active defensive strategies have evolved because predators are diverse and use many cues to detect their prey (Ruxton *et al.* 2004, Pekár 2014). A common and taxonomically widespread kind of passive defence is crypsis (Ruxton *et al.* 2004). In some species, it is the primary type of passive defences against visually oriented predators (Johnsen 2014, Pekár 2014). A cryptic organism can present a disruptive colouration pattern, such as bands or other markings that break up the outline of its body when seen by a predator (Tso, Lin & Yang 2004, Cuthill *et al.* 2005). It can also involve matching the colour of a background of the environment to avoid being visually perceived by predators (Eterovick *et al.* 2010, Théry *et al.* 2005, Théry & Casas 2002). Thus, the function of crypsis is to avoid detection (Skelhorn *et al.* 2010).

Another kind of passive defence, masquerade, is a process that is considered different from crypsis (Pekár 2014, Skelhorn *et al.* 2010). In this defence strategy, species have evolved morphologies that allow them to be mistaken for inedible objects that are common in their environment. They masquerade as twigs, leaves, stones, bird droppings, and other things (Skelhorn *et al.* 2011, Pékar 2014). Therefore, the function of masquerade is to lead the predator to misclassify the visual recognition of the prey and not to preclude detection as in crypsis (Skelhorn *et al.* 2010). Although masquerade has been addressed by recent papers (Skelhorn *et al.* 2011, Pékar 2014, Zhang *et al.* 2015), its principle of action still need to be clarified regarding the role of colour in such misclassification (Skelhorn *et al.* 2010).

Some species employ masquerade without using colour matching with some specific surface to avoid predation or to capture prey (Endler 1981). Some spiders, for example the bird-dropping masquerade *Cyclosa ginnaga* Yaginuma, 1959 , even present a high contrast with the background (Hickman 1971, Liu *et al.* 2014). Other spiders, such as *Ariamnes cylindrogaster* Simon, 1889 (Theridiidae), achieve defensive success mainly by means of appropriate postures associated with their unusual body shape (Zhang *et al.* 2015). Species presenting this colour matching-independent masquerade are referred to as ‘object imitators’, and can be misclassified by predators in a wide range of backgrounds (Skelhorn *et al.* 2010). Conversely, animals can employ masquerade using colour matching with some specific object simultaneously. This happens primarily when species resemble an unattractive element that is abundant in the environment, such as the leaves and twigs used for resting. Animals presenting this strategy are referred to as ‘element imitators’, and are more dependent on appropriate surfaces, in terms of colour (Skelhorn *et al.* 2010). The cost imposed by these ‘element imitators’ are likely associated mostly with behavioural constraints. For example, a cryptic defence is more efficient when the animal is not moving, which may constrain its search for food or mates (Skelhorn *et al.* 2010). In spiders, cryptic and masquerader species usually restricts their activities to night time because must stay static to conduct their defensive strategies efficiently during the daytime, when visually oriented predators are active (Pekár 2014).

There are also examples of very elaborate forms of masquerade spider species, such as spiders in the genus *Poltys* C.L. Koch, 1843 (Araneidae) (Smith 2003, 2009; Kuntner *et al.* 2016). Some *Poltys* species have abdominal morphologies that resemble little broken twigs (Smith 2003, 2009). The South American orb-weaver species *Wixia abdominalis* O. Pickard-Cambridge, 1882 (Araneidae) also presents unusually shaped abdomens, similar to those of some *Poltys* species; however, there is apparently little morphological variation (pers. obs.). These kinds of morphologies are, probably, a result of the strong selective pressure by visually oriented diurnal predators, since both *Poltys* as *Wixia abdominalis* present foraging activities restricted to night-time (pers. obs., Smith 2009). Indeed, web-building spiders can suffer greater predatory pressure during the daytime (Rypstra 1984).

A wide range of wasps, such as sphecids, pompilids, crabronids (Rayor 1996, Blackledge & Pickett 2000, Blackledge & Wenzel 2001, Blackledge, Coddington & Gilliespie 2003, Gonzaga & Vasconcellos-Neto 2005, Araújo & Gonzaga 2007), and vespids (Chou *et al.* 2005), are known to be some of the main diurnal predators of spiders. Other wasps, such as ichneumonids, are known to be koinobiont ectoparasitoids of spiders (Eberhard 2000, Gonzaga & Sobczak 2007, Gonzaga *et al.* 2010). Avian predators also exert strong predation pressure on spiders during the daytime (Gajdoš & Krištín 1997, Gunnarsson 2008). However, hymenopterans and avian have very different visual systems e does not distinguish the colours in the same way (Peitsch *et al.* 1992, Giurfa *et al.* 1997, Hart 2001). Therefore, if the colour matching is employed in a masquerade depending on specific observers, the visual system responsible for the selective pressure over the prey should have difficulties to visually discriminate it from its substrate. Thus, if wasps and birds were responsible for strong selective pressure on a spider, a successful strategy based on colour matching would have to conceal the spiders from both predator groups. Therefore, assessing the hymenopteran and avian ability to colour discriminate the same masquerade spiders against their substrate should provide information regarding the directionality of the defence. Thus, in this study, because of the apparently strong selective pressure from these predators, we tested the hypothesis that the colour matching is present in the masquerade defence of *W. abdominalis* when hymenopteran and avian predators see it. Therefore, we expected the colouration of *W. abdominalis* to present fine colour matching as seen by the visual system of these two groups of predators.

Methods

Study site and species

The study was conducted in a *Eucalyptus* plantation on Fazenda Nova Monte Carmelo, property of Duratex S.A. (18°45′11′′S, 47°51′28′′W), Estrela do Sul, Minas Gerais, Brazil. *Wixia abdominalis* is a widespread South American species previously recorded from Guyana, Bolivia, and Brazil (Levi 1993). In our study site, the individuals rest cryptically during the daytime on *Eucalyptus* twigs (Fig. 1). At night they build their orb-webs (pers. obs.), and are easily located by searching for their webs with flashlights. We located spiders between August and December 2014 by nocturnal visual inspections on the branches of *Eucalyptus* trees at heights between 0 and 2 m from the ground.

Visual models analysis

Our intention with using visual models analysis was to assess how the main potential predators of *W. abdominalis* perceive and discriminate the colours of the spiders and its substrates, taking into account the influence of the background and illumination condition. Basic sensory information in this kind of analysis is the observers' photoreceptors sensitivity (Kemp *et al.* 2015). However, this kind of data is available just for a limited number of hymenopterans and birds. Thus, our main concerns in analysis was to choose those sensitivities the best represent the potential predators in question and to build a conservative approach. Therefore, we used two approaches in a complementary manner: Chromaticity diagrams and Receptor-noise-limited model (*see* Kemp *et al.* 2015).

Chromaticity diagrams represent color stimuli according to the relative stimulation of photoreceptor classes (Kemp *et al.* 2015, Stoddard & Prum 2008, Chittka 1992) and follow calculations analogous to neural processing (Kemp *et al.* 2015). Therefore, they provide information about how stimulus differences are perceived by a given viewer. This approach does not require any detailed information about a specific visual system, such as the influence of the size and relative abundance of each kind of photoreceptor in a species.

The receptor-noise-limited model (Vorobyev & Osorio 1998) considers the random variations of photon capture by photoreceptors during the same stimulus. This noise can be estimated from many factors, like the intensity of light, photoreceptor size, and the density of photopigment in the photoreceptors (Kemp *et al.* 2015). Briefly, the receptor-noise-limited model considers that two color stimuli can be discriminated only if they are different enough in relation to the degree of noise (Kemp *et al.* 2015, Vorobyev & Osorio 1998). This approach is considered generalizable and suitable for discrimination questions (Kemp *et al.* 2015). Therefore, this analysis can mitigate our lack of information about specific thresholds in chromaticity diagrams approaches.

Reflectance measurement

We measured the spectral reflectance (wavelengths from 300 to 700 nm) of juvenile *W. abdominalis* (N = 18), *Eucalyptus* twigs (where the spiders rest during the daytime) (N = 68) and fallen leaves (the background where spiders and twigs are sough against) (N =205) by using a spectrometer (Jaz, Ocean Optics Inc., Dunedin, FL, U.S.A.). We recorded the spectral reflectance of a circular spot (diameter 1 mm) on each sample, by positioning the probe perpendicular and 2 mm from the sample.

Spectral reflectance was used to model the visual systems of hymenopteran and avian predators and to calculate the colour contrast perceived by them. The illumination D65 (Commission internationale de l'éclairage - CIE) was used in all calculations because it best represents the lit condition where the spiders were found. All reflectance curves used in the following analysis were corrected for noise using the smooth 0.2 function of the R package 'pavo' (Maia *et al.* 2013, R Development Core Team 2016).

Colour contrast in visual models

We calculated photoreceptor excitation values (E) following the method described in Chittka and Kevan (2005). In the hymenopteran colour vision model, we used the photoreceptor sensitivity of the bee *Apis mellifera* Linnaeus, 1758 (Peitsch *et al.* 1992). It has a trichromatic vision, and consequently we calculated E_{UV}, E_{BLUE}, and E_{GREEN} values. In the avian colour vision model, we used the photoreceptor sensitivity of the blue tit, *Cyanistes caeruleus* Linnaeus, 1758 (Maia *et al.* 2013, Hart *et al.* 2000). It has tetrachromatic vision, and thus, we calculated E_{UV}, E_{BLUE}, E_{GREEN}, and E_{RED} values. We chose *A. mellifera* because its spectral sensitivities are similar with wasp species belonging to *taxa* that hunts spiders (Peitsch *et al.* 1992). Furthermore, some information about discrimination thresholds in chromaticity diagrams (Théry & Casas 2002) and receptor-noise-limited model (Vorobyev & Osorio 1998) are not known for wasps. We chose *C. caeruleus* (synonym *Parus caeruleus*) sensitivities (Hart *et al.*

2000) because it is a spider predator (Gajdoš & Krištín 1997). Moreover, it has spectral sensitivities of short wavelengths in the ultra-violet range stead in violet that is similar to other Passeriformes and other groups (Hart 2001), composed by birds that predate spiders frequently (Gajdoš & Krištín 1997).

To determine whether the modelled observers could distinguish between spiders and twigs, we used the E values in the hexagonal chromaticity diagram for hymenopteran colour vision (Chittka 1992), and in the tetrahedral chromaticity diagram for avian colour vision (Stoddard & Prum 2008).

In the hexagonal diagram, we considered spiders and twigs indistinguishable by hymenoptera chromatic vision if the Euclidian distances between them were less than 0.05 (Théry & Casas 2002). This threshold value was calculated for *A. mellifera*, considering that they can distinguish two objects spectra differing by a minimal colour distance of 5 nm (von Helversen 1972). In the tetrahedral diagram, we considered spiders and twigs indistinguishable by avian chromatic vision if the Euclidian distances between them were less than 0.06 (Théry *et al.* 2004). This threshold value was calculated for the pigeon *Columbia livia* Gmelin, 1789, considering that they can distinguish two objects spectra differing by a minimal colour distance of 5 nm (Théry *et al.* 2004). We hypothesize that this surrogate threshold is acceptable since *C. livia* photoreceptors sensitivities peaks are close to those of *C. caeruleus* (Hart 2001). These thresholds for both diagrams are very conservative because they are calculated without discount effects of the lack of conditioning that can reduce the total discrimination capacity in some animals (Dyer & Chittka 2004). In both chromaticity diagrams, we calculated the Euclidian distances between colour *loci* generated for each spider and the mean *loci* generated for twigs.

Hymenopterans and birds also use achromatic contrast to detect small objects or objects at long distances (Osorio, Jones & Vorobyev 1999; Spaethe, Tautz & Chittka 2001). To do this, hymenopterans use only green photoreceptors (Giurfa *et al.* 1997, Giurfa & Vorobyev 1998, Spaethe *et al.* 2001), whereas birds use double-cones, which combine the spectra of medium and long wavelength photoreceptors (Hart 2001). Thus, to calculate hymenopteran achromatic discrimination, we divided the E_{GREEN} values generated by spider reflectance by the mean of the

E_{GREEN} values generated by twig reflectance. If the value was not significantly different from one, the spider and twigs were indistinguishable. To calculate bird achromatic discrimination, we followed the same process, but used double-cone E values for blue tits.

Colour overlap in chromaticity diagrams

When inferring colour similarity between two objects, it is also important to determine whether the two groups occupy the same colour visual space of the observer. If they do so, they must have considerable colour overlap inside the hexagon and tetrahedron space. Therefore, we calculated the percentage of polygonal overlap of the *loci* generated for spiders and twigs in the hexagonal space. To do this, we generated polygons using the x and y coordinates and analysed overlap using the R packages 'raster' (Hijmans 2016) and 'rgeos' (Bivand & Rundel 2017). In tetrahedron space, we determined the percentage of volume overlapping the points generated for spiders and twigs using the R package 'pavo' (Maia *et al.* 2013).

Receptor-noise-limited model

In the receptor-noise-limited model, the differences in perception between color stimuli are assessed in terms of just noticeable differences (JND) (Vorobyev & Osorio 1998). One JND was used as a threshold to identify the minimum stimulus difference between stimuli required to produce detectable variation by a given viewer (Kemp *et al.* 2015, Vorobyev & Osorio 1998). Thus, following the calculations of Vorobyev & Osorio (1998) for quantum catches, we assessed the discrimination capability of *A. mellifera* and *C. caeruleus* when viewing the spiders and twigs. For *A. mellifera* we considered its known photoreceptors noises (UV 0.13, Blue 0.06, Green 0.12) (Vorobyev & Osorio 1998). For *C. caeruleus* we applied the Weber fraction (*i.e.* only neural noise mechanisms) considering its relative number of photoreceptors cells (UV 1, Blue 2, Green 2, Red 4) (Maia *et al.* 2013). We performed the analysis using the R package 'pavo' (Maia *et al.* 2013).

Results

There was a high degree of overlap in reflectance curves for *W. abdominalis* and *Eucalyptus* twigs (Fig. 2). The colour *loci* inside the hexagonal (hymenopteran colour vision – Fig. 3) and tetrahedral (avian colour vision – Fig. 4) chromaticity diagrams also indicated a high degree of colour overlap between spiders and their daytime resting substrate. According to chromaticity diagrams analysis, *W. abdominalis* was indistinguishable from twigs when seen by chromatic (values not greater than the threshold 0.05) and achromatic hymenopteran vision (values were not different from one). However, for avian vision, they were indistinguishable only when seen by chromatic vision (values not greater than the threshold 0.06) (Table 1). According to receptor-noise-limited model, W. abdominalis was also indistinguishable from twigs when seen by chromatic of both hymenopteran and avian vision (JNDs were not greater than the threshold 1) (Table 1).

Based on spatial colour overlap analysis, the *W. abdominalis* polygon shared 99.43% of its area with twig polygons in hexagonal space. In tetrahedral space, 96.03% of the volume of *W. abdominalis* volume overlapped twig volume.

Discussion

In this study, because of the potential selective pressure exerted by hymenopterans and birds on spiders, we tested the hypothesis that the colour matching is present in the masquerade defence of *W. abdominalis* when it is seen by both predators groups. Our results corroborated our expectation: the colour of *W. abdominalis* presents fine colour matching as seen by the visual system of these two groups.

Hymenopterans use their chromatic vision to detect nearby objects, whereas achromatic vision (only green photoreceptors) is used to detect distant ones (Giurfa *et al.* 1997, Giurfa & Vorobyev 1998, Spaethe *et al.* 2001). We found that *W. abdominalis* was indistinguishable both chromatically and achromatically from the substrate where it rested during the day, *Eucalyptus'* twigs, when seen by hymenopterans. Thus, hymenopterans are unable to discriminate this spider from the twigs at long distances using only colour information, and may still be unable to detect it using colour vision at close range (Giurfa *et al.* 1997, Giurfa & Vorobyev 1998, Spaethe *et al.* 2001). Moreover, this effect should be more pronounced, because the spatial resolution of compound eyes of insects is very poor (Vorobyev *et al.* 1997). However, hymenopterans may use other cues beyond colour to detect *W. abdominalis* on their substrate during the daytime. Chemical cues, for example, play an important role when wasps are searching for spiders. Wasps can perceive spiders by means of detection of hydrocarbons in the cuticles of spiders (Uma & Weiss 2010). *Sceliphron caementarium* (Drury, 1770) (Sphecidae) detected recently dead spiders using vision, but the subsequent attack depended on whether the spider was or was not washed with hexane (it is used to wash hydrocarbons) (Uma & Weiss 2010). This suggests that visual and chemical cues may be used at different moments in the capture process. Therefore, determining whether visually cryptic spiders are also more cryptic to other senses, such as chemical perception, in future studies should provide accurate information regarding the selective pressure of wasps.

Avian chromatic vision is used to detect near objects, whereas achromatic vision (using double-cones that combine the sensitivity spectra of medium and long wavelength photoreceptors) is used to detect the farther ones (Hart 2001). We also found that *W. abdominalis* is chromatically indistinguishable from its substrate when seen by birds. In spite of that, spiders were detectable in avian achromatic vision because *W. abdominalis* was brighter than twigs. This suggests that the difficulty for birds is detecting the spider in the near field. Indeed, mean reflectance of *W. abdominalis* increases more than that of twigs near the long wavelengths, as seen in their spectral curves. However, we note that the difference in the mean of double-cone E values for spider and twigs appears only at the third decimal place (*W. abdominalis*: 0.247, twigs: 0.242). This generated a statistical significant effect, but we do not know if this minimum excitation difference is biologically relevant. Bird cones contain pigmented oil droplets that narrow their spectral sensitivity, causing better colour discriminability (Hart 2001). Nevertheless, *W. abdominalis* was chromatically indistinguishable from twigs. Therefore, we assume that, in general, there is fine colour matching in bird vision as well.

In spatial overlap analysis, we found that the colour of *W. abdominalis* and twigs overlapped. However, *W. abdominalis* triggered a more compact colour perception inside both visual models, so that it was submerged into the twig colour space. This suggests the existence of a small range of appropriated microhabitats that *W. abdominalis* can choose and still do not be distinguishable, and this should include other plants with similar reflectance. In this study, the substrate assessed was *Eucalyptus* (non native of Brazil) twigs because *W. abdominalis* select them to rest during daytime. Previously, we have recorded some individuals of *W. abdominalis* resting in twigs of native plants in forest areas of Brazilian Cerrado (pers. obs.). Then, the native substrates selected by *W. abdominalis* should have similar reflectance from that of *Eucalyptus*, however, an evaluation about microhabitats selection is still needed.

It is also important to observe that *W. abdominalis*' body colour does not change, otherwise their colour perception would not be so restrict rather it would be as wide as its substrate. Thus, future studies should address how colour variability between individuals in cryptic species allows the exploitation of different microhabitats.

In passive defences, the use of masquerade is thought to be a more derived strategy than crypsis (Skelhorn *et al.* 2010, Pekár 2014). It is suggested that masquerade evolved first from solely cryptic ancestors, and then, mutants with a superficial resemblance to a model began to gain benefits, being misclassified (Skelhorn *et al.* 2010). Indeed, an estimation of the ancestral state revealed that crypsis preceded masquerade as a defensive strategy in several spider families and genera (Pekár 2014). Masqueraders may have suffered a long evolutionary history of pressure from visually oriented predators, leading to fine colour matching with their habitat. However, to employ this strategy efficiently, potential preys assume behavioural constraints. They limit their activities to periods when visually oriented predators are not active, because movement increases the probability of detection (Skelhorn *et al.* 2010, Pekár 2014). For example, the spider *Poltys noblei* (Araneidae) resembles a small twig. It rests on twigs during the daytime and forages at night by constructing an orb-web. As such, this spider moves relatively little compared with other web-weaver spiders (Smith 2009). *Wixia abdominalis* also resembles a twig and has a similar defensive strategy; thus, this is likely a way to maximise the masquerade.

Masquerade appears to be more common in araneids than theridiids, and absent in other groups such as linyphiids (Pekár 2014). The vulnerability to predation appears to be more intense in orb web spiders, such as araneids, than in tridimensional-web spiders, such as theridiids and linyphiids (Blackledge *et al.* 2003). Mud-dauber wasps usually capture proportionally more orb spiders, even considering that tridimensional-web spiders are more abundant in their environment (Blackledge *et al.* 2003). Thus, there is strong evidence that the web is an important factor dissuading wasp attack and determining spider vulnerability to some predators. Therefore, in some ways, because of their higher exposition, orb spiders may be under greater pressure to develop alternative defensive strategies, such as masquerade.

We assumed that the main potential predators responsible for defensive strategies of *W. abdominalis* were hymenopterans and birds. Spiders are attacked by a wide range of families of predators or parasitoids wasps (Rayor 1996, Blackledge & Pickett 2000, Blackledge & Wenzel 2001, Blackledge *et al.* 2003, Gonzaga *et al.* 2010). Likewise, a wide range of avian predators also exerts pressure on spiders, being strong enough to trigger consequences both in communities and at specific levels (Gunnarsson 2008). Indeed, we found that the colour of *W. abdominalis* is indistinguishable from its substrate by both visual systems and *W. abdominalis* may benefit from this resemblance. Field observations and manipulative experiments, however, are still necessary to provide accurate information on the intensity of predation pressure by each predator groups, and others, on masquerader spiders.

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Table 1: One-sample *t* test. Chromatic and achromatic contrasts between *Wixia abdominalis* and twigs as seen by hymenopteran and avian vision. For chromaticity diagrams (c d), the constrast is represented in Euclidian distances, the discrimination thresholds for chromatic vision are 0.05 for hymenoptera and 0.06 for birds, and 1 for achromatic vision of both. For receptor-noise-limited model the (r-n), the contrast is represented in JND and the discrimination threshold is 1.*Both objects can be distinguished by this vision.

		Mean ± SD	T	Df	p-value
	Hymenoptera vision				
	Apis mellifera				
cd	Chromatic contrast	0.037 ± 0.029	-1.903	17	0.074
	Achromatic contrast	1.009 ± 0.185	0.218	17	0.830
r-n	Chromatic contrast	1.518 ± 1.217	1.805	17	0.089
	Bird vision				
	Cyanistes caeruleus				
cd	Chromatic contrast	0.02 ± 0.007	-25.324	17	< 0.001
	*Achromatic contrast	1.018 ± 0.008	9.082	17	0.000
r-n	Chromatic constrast	0.977 ± 0.475	-0.207	17	0.838

Figure captions

Fig. 1 A. Details of a female *Wixia abdominalis* resting on a *Eucalyptus* branch, B. Immature individual in resting position seen at a long distance

Fig. 2 Spectral reflectance (mean ± standard deviation) of wavelengths covering the range from 300 to 700 nm for *W. abdominalis* and *Eucalyptus* twigs

Fig. 3 Colour coordinates inside the hexagonal space combining green, blue, and ultra-violet photoreceptor excitation values for the bee *Apis mellifera*. The black points represent maximum excitation values for the photoreceptors

Fig. 4 Colour coordinates inside the tetrahedral space combining red, green, blue, and ultra-violet photoreceptor excitation values for the blue tit (*Cyanistes caeruleus*). They are represented from all angles of view: A, B, C, and D

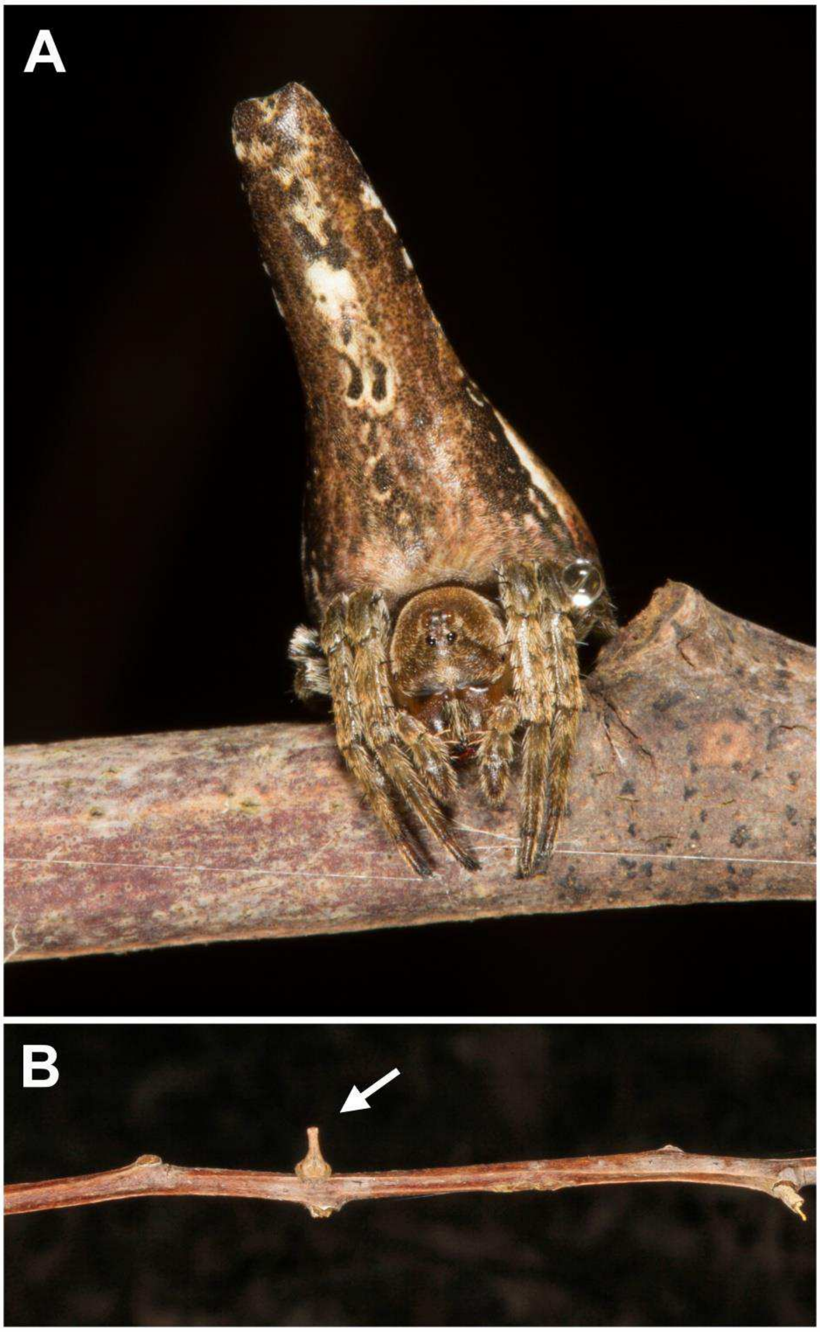

Fig. 1

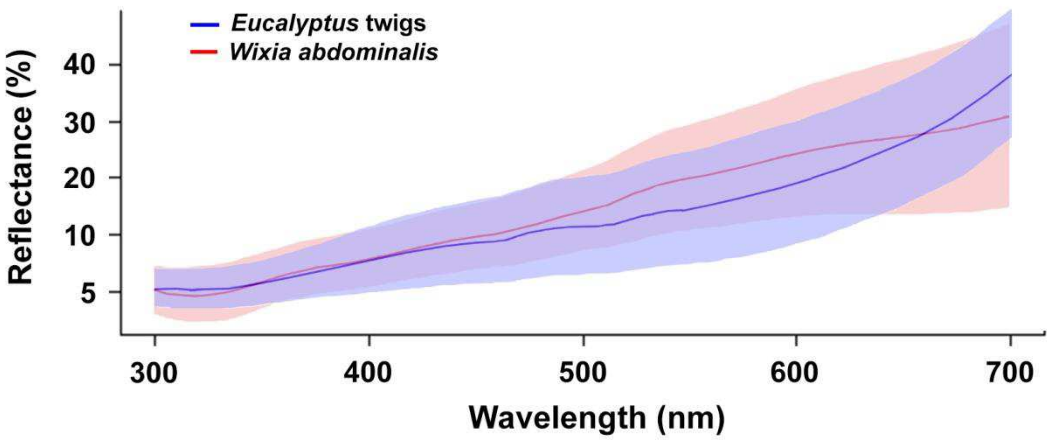
Eucalyptus twigs
Wixia abdominalis
Reflectance (%)
40
30
20
10
5
300
400
500
600
700
Wavelength (nm)

Fig. 2

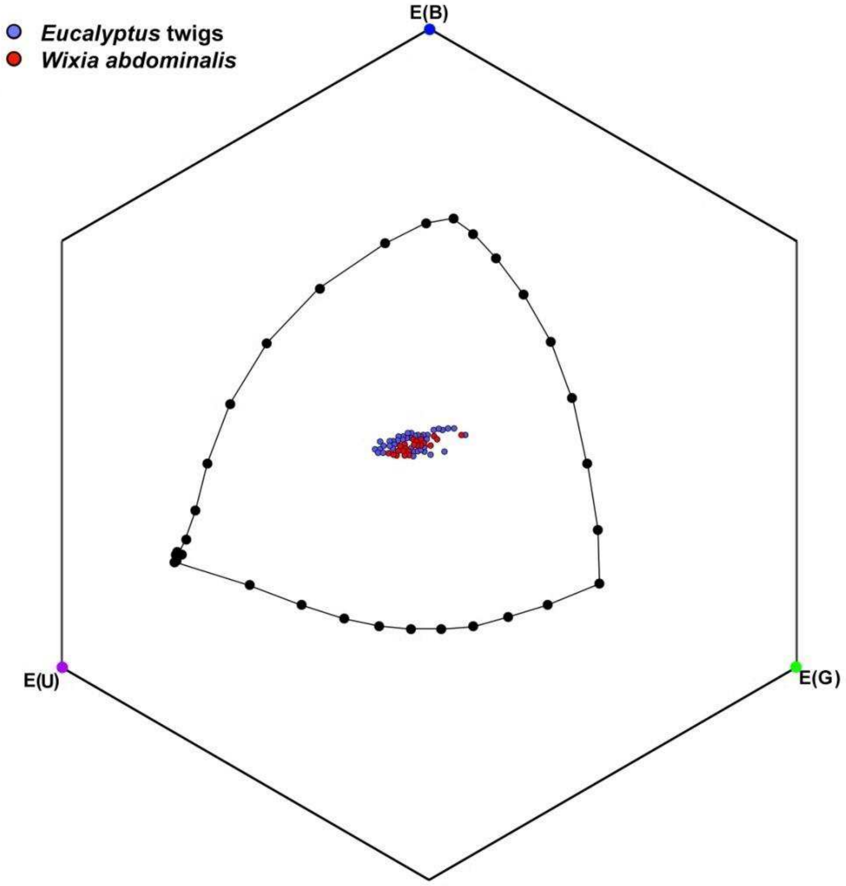

Fig. 3

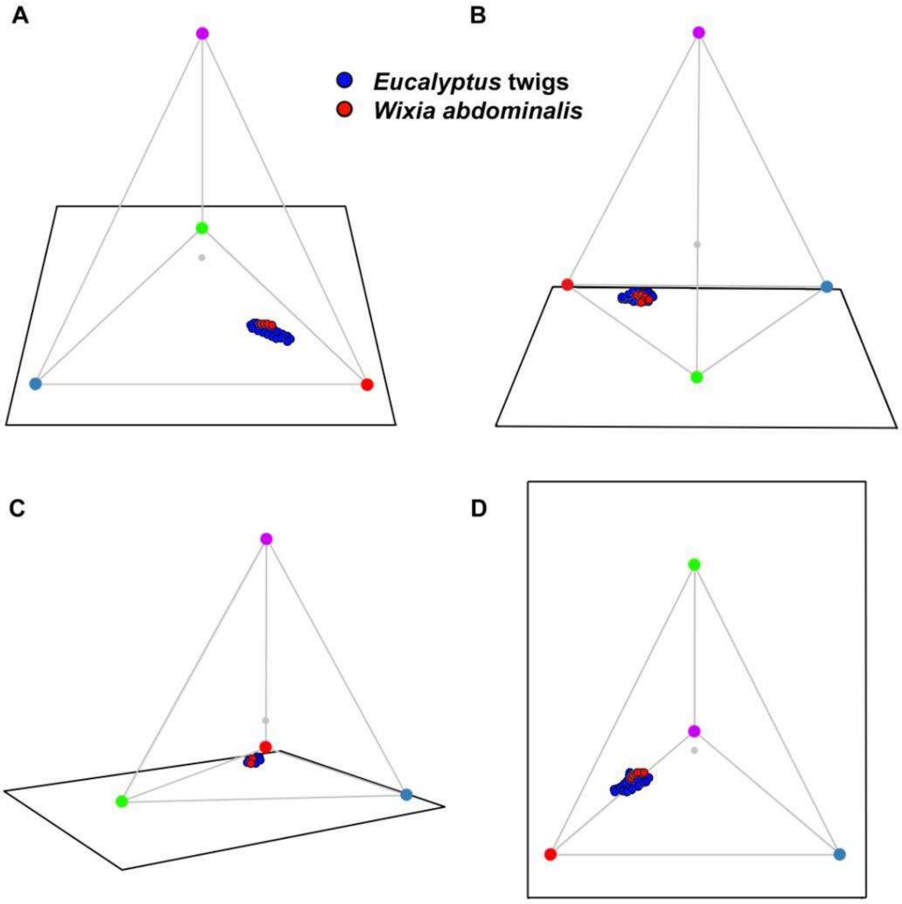

Fig. 4

CONSIDERAÇÕES FINAIS

Neste estudo, tomando *Wixia abdominalis* como nossa espécie modelo, avaliamos importantes aspectos das estratégias de forrageio e defesa em aranhas orbitelas. No capítulo 1, por meio da análise arquitetural das teias orbiculares de *W. abdominalis,* concluímos que nenhuma das hipóteses previamente propostas para explicar o investimento diferencial em distintas partes da teia é totalmente satisfatória para explicar como são estruturadas. Diversas características das teias possivelmente refletem pressões moldadas por sua funcionalidade, podendo haver também algumas restrições incidentais durante o processo de construção. Fomos capazes também de identificar hipóteses que não são explicativas ao menos para esta espécie. As hipóteses, tanto incidentais quanto funcionais, abordadas neste estudo estão dispersas entre diferentes trabalhos que utilizaram as poucas espécies tradicionalmente usadas como modelo para este tipo de estudo. A tentativa de se avaliar como estas hipóteses interagem para explicar a arquitetura de teias orbiculares de maneira mais geral ainda é provisória. Por isso, achamos que este estudo contribui para que seja possível avaliar o quanto estas hipóteses são generalizáveis para outras espécies.

Wixia abdominalis exibe, pelo menos em nossa visão, um tipo importante de defesa passivas, o disfarce. Que tem sido atribuída como uma das principais apresentadas por aranhas contra predadores visualmente orientados. Entretanto, o sistema visual do observador envolvido define se a coloração de dois objetos é distinguível ou não. Portanto a associação entre ajuste de cores entre indivíduos e substrato no disfarce pode não ser a mesma para diferentes tipos de predadores. Isso nos motivou a avaliar no capítulo 2 se a presença do ajuste de cores no disfarce em *W. abdominalis* é consistente na visão dos principais predadores de aranhas. Nós concluímos que de fato o ajuste de cores ocorre quando *W. abdominalis* é vista em seu substrato pela visão de himenópteros e aves, e que isto deve ser um reflexo da pressão seletiva por parte de ambos.

Procedimentos observacionais e experimentais deverão esclarecer melhor como de fato *W. abdominalis* interage com suas presas e seus predadores. Entretanto, este estudo fornece o embasamento teórico necessário para avaliar como o forrageio por meio de teias orbiculares e as estratégias de defesa refletem as interações e pressões seletivas por parte de presas e predadores. Devemos destacar também que o gênero *Wixia* sofreu diversas mudanças, com a exclusão de praticamente todas as espécies antes nele incluídas. Desta forma, *W. abdominalis* é agora a única dentro do gênero. Portanto, este trabalho fornece as primeiras informações ecológicas que de fato pertencem ao gênero.