Tales of adaptation: predatory and anti-predatory strategies of spiders on the surface of tree trunks

Alfonso Esteban Aceves Aparicio (BSc, MSc)

School of Natural Sciences, Faculty of Science and Engineering, Macquarie University
and
Department of Biology, Universität Hamburg

Thesis presented for the requirements for the degree of
Doctor of Philosophy

September 2022

Statement of Originality

This thesis is being submitted to Macquarie University and Hamburg Universität in accordance with the Cotutelle agreement dated 29th June, 2017.

To the best of my knowledge and belief, the thesis contains no material previously published or written by another person except where due reference is made in the thesis itself.

Eidesstattliche Versicherung

Declaration on oath

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

I hereby declare, on oath, that I have written the present dissertation by my own and have not used other than the acknowledged resources and aids.

(Signed) ______________________________ Date: 30th September 2022

Alfonso Esteban Aceves Aparicio

Thesis evaluators
Dieter Hochuli, Professor - The University of Sydney
Michael Kasumovic, Dr - The University of New South Wales
Joerg Ganzhorn, Professor - University of Hamburg
Kathrin Dausmann, Professor - University of Hamburg
I-Min Tso Professor, - Tunghai University

Date of defense: 14th July 2023

Acknowledgements

I acknowledge the traditional custodians of the Macquarie University land, the Wattamattagal clan of the Darug nation, whose cultures and customs have nurtured and continue to nurture this land, since the Dreamtime. I pay my respects to Elders past, present and future.

My research and a lot of my personal growth over the last 4.5 years would not be the same without the help, time and patience that an amazing team of supervisors had me. Mariella, you are indeed a fearless leader, and one of the kindest persons ever. Thank you for always giving me the freedom to think out of the box but not too much that I would get lost in my thoughts. Jutta, one of the best things any student could ask for is having a good supervisor, but for me having you was way beyond any expectations. And I was even luckier because you were there when I ended up lost in my thoughts, you listened to me and brought me back. But the significant supervision did not stop there. Lizzie, I also had you on my corner. An example of a strong and warm human being, you offer me support, friendship and lots of laughs.
One of my dearest memories is having you three front and centre of the audience for my talk at the arachnology conference in New Zealand. I felt like my most confident self-knowing you were there knowing there would be a good story.

As often happens, people cross paths and end up unexpectedly becoming mentors. And I had the luck of having Ajay Narendra and Matt Bulbert share their expertise and knowledge to add value to my research. Dinesh, you keep a record of the longest time supporting my academic and scientific growth. Of course, you were there for me during my PhD work, even if at a distance and unofficially I could always go back to you to brainstorm and seek advice and friendship.

Lili, we have been classroom partners, friends, family, travel and life companions and more. And through all of those stages we have had together, I have always known I can count on your love and support. During the difficult times that came in the last years, you did not leave me alone. Another great memory came from having you help me with fieldwork in Australia and seeing you enjoy the spider work.

I am really grateful for having a family that has always shown me their support despite the distance or time differences. Mom and dad, you have always made your best effort to make sure I can follow my dreams no matter what the way looks like. Eva, what a sister to have, many late nights writing would have not been the same without your crazy funny spontaneous gifs and pictures on my phone. Angeles, you probably have no idea how valuable you are to me. You always take care of us and the important things we care about, thanks a lot!

And of course, I am also thankful to every friend that has been there when sharing a laugh, a conversation or a calming hug was needed.

In Australia, thank you all in the great behavioural ecology lab and everyone around us at Macquarie uni, what a blast of fun and productivity. Some of the greatest days of my life came from spontaneous moments with you, Mick, Zoe, George, Brax, Kawsar, Payal, Darsh, Sam, Bruno, Margarita, Sara, Ivan, Catarina, and Laura. Sue, Jim, Zoe, I think about you every day and miss you all a ton and a half, you guys turn Aussieland into a home for me. I can't wait to meet again soon.

In Germany, everyone in and around the Spinnen Labor, especially Marie, Marcelo, Bharat, Geli and Jasmin. Also, the last year has been a great time thanks to Shri, Paola, Cee, Chesca, Oliver, Elisa, Kati, Hannah, Linda, Ana, Pauline and Sensei.

In Mexico Avril, Cornelio and Juli, you guys made the more challenging days of the crazy pandemic much more tolerable and yes some of those we even had lots of fun.

And to you Katrina for having been my loyal and patient companion for almost 15 years. You sat next to me while working many hours day or night, and those included drafts for each of my theses, I will miss you.

Table of Content

Thesis summary

Spiders are the most diverse group of predators with a worldwide distribution (except the poles) having conquered terrestrial, aerial and even aquatic habitats. However, despite the great success of spiders as predators, spiders also fall prey to other predators in virtually every habitat. Accordingly, spiders not only display outstanding predatory strategies but also anti-predatory strategies specific to the habitat they occupy and the prevalent prey and predators.

While most readers associate spiders to occupy dense vegetation and even flowers, in this thesis I focused on a different type of habitat that is often regarded as ‘simple’ and even inhospitable - the surface of tree trunks. Compared to the rest of the tree (i.e., the root system and the canopy), the trunk surface is relatively poor in resources and highly exposed to adverse weather conditions (wind, rain, sun radiation). A crucial feature of tree trunks is that they offer limited cover for residents living and itinerants moving on them. Thus, occupying the surface of tree trunks would increase the chances of being visually spotted by potential predators and prey.

Despite the potential challenges to inhabiting the surface of tree trunks, in my thesis, I have studied three phylogenetically independent cases of spiders that are permanent residents of this habitat. Considerable previous work on tree trunks has focused on the diversity of the inhabiting species while ecological strategies, specifically the predatory and anti-predatory strategies of tree-trunk spiders have seen much less attention. The particular questions that drove my research for this thesis were 1) how do spiders that permanently occupy tree trunks access sufficient prey? And 2) how do they avoid visually guided predators in this highly exposed environment?

My detailed study of these three spider species revealed distinct specialised ways to reduce their visual conspicuousness to potential prey and predators, either via shifting to nocturnality, body colouration or the construction and decoration of silk retreats. Furthermore, highly specialised attack behaviour that is adapted to a vertical environment (ie the surface of tree trunks) seems to provide some spiders with access to abundant prey.

The first chapter in this thesis details the hunting strategy of the Australian ant-slayer *Euryopis umbilicata*. A rapid (milliseconds) set of movements allows this spider to capture large defended prey (*Camponotus* ants) with an unusually high success rate. By hunting after sunset, the spiders not only access abundant prey and are also likely to avoid most visually guided predators.

Unlike the Australian ant-slayer, diurnal spiders that reside in the tree trunk would be significantly exposed to visual detection by predators and prey. In Chapters 2 and 3, I described the building and decorating behaviour of the jumping spider *Arasia mullion*, which results in an, for jumping spiders, unusual sedentary life and sit-and-wait capture strategy. Visual modelling of the

decorated silk retreats of *A. mullion* suggests a cryptic appearance of the retreats to ecologically relevant observers.

Despite the absence of a retreat, Hersiliidae spiders remain immobile on the surface of tree trunks where their body colouration matches the appearance of the tree bark, at least to the human eye. In Chapter 4, I used novel multi-spectral colour pattern modelling from digital images to compare the colour patterns of two sympatric species of hersiliid spiders (*Tamopsis fickertii* and *Tamopsis brisbanensis*) occupying distinct types of tree trunk backgrounds (Eucalyptus trees with either smooth or rough bark surfaces). My results suggest that each species is best matched against its home tree, and are equally inconspicuous across most sites on the home tree. In this system, the extent of background matching depends on pattern complexity and viewing distance.

This thesis, not only describes the unusual natural history traits of spider residents of tree trunks but highlights novel strategies that seemingly provide great benefits in this challenging habitat. The relationship between the tree trunk habitat and the species inhabiting them is intricate and intriguing. These spiders have been shown as highly specialised in reducing detection and in capturing prey effectively. Clearly, spider camouflage is likely to aid both their predatory and anti-predatory strategies but seems more complex than assumed and deserves closer attention expanding previously well-studied systems whilst also discovering novel strategies.

Contributions

Thesis chapter	Contributors	Contributions
Introduction	Alfonso Aceves-Aparicio	Research, writing
	Marie E. Herberstein	Discussion, feedback
	Jutta Schneider	Discussion, feedback
Chapter 1	Alfonso Aceves-Aparicio	Design & perform research, data analysis, writing
	Ajay Narendra	Design & perform research, data analysis, writing
	Donal James McLean	Data analysis, writing
	Elizabeth C Lowe	Design, writing
	Marcelo Christian	Design & perform research, data analysis
	Jonas O. Wolff	Writing
	Jutta Schneider	Design, writing
	Marie E. Herberstein	Design, data analysis, writing
Chapter 2	Alfonso Aceves-Aparicio	Design & perform research, data analysis, writing
	Donal James McLean	Design & perform research, data analysis, writing
	Zoe Wild	Perform research, data analysis
	Jutta Schneider	Design, writing
	Marie E. Herberstein	Design, writing
Chapter 3	Alfonso Aceves-Aparicio	Design & perform research, data analysis, writing
	Jutta Schneider	Design, writing
	Marie E. Herberstein	Design, writing
Chapter 4	Alfonso Aceves-Aparicio	Design & perform research, data analysis, writing
	Cedric van den Berg	Data analysis
	Jutta Schneider	Design, writing
	Marie E. Herberstein	Design, writing

Introduction

Personal beginnings

My PhD journey began before I had even completed my master's degree, specifically when I was looking at the surface of a tree trunk and found a two-tailed spider (Hersiliidae). Before I knew what type of spider I was looking at, I was already mesmerised by its camouflage and how difficult it was to find and, if I lost it, to find it again (Figure 1).

Figure 1. Different colour morphs of the camouflaged Two-tailed spider *Neotama mexicana* (Hersiliidae). Photo credit: Alfonso Aceves.

Not long after that, I realised I had found an astounding system, filling my mind with interesting questions about the combination of camouflage, spiders and tree trunks. This system was personally very intriguing - a tree trunk seemed such an inhospitable place to inhabit. Tree trunks are particularly inhospitable in my place of residence at the time, Xalapa Veracruz, Mexico, where a tree trunk would be exposed to hours of intense sunlight, sudden rain, strong wind and rapid temperature change, all during a single day. Despite all of this, the two-tailed spiders remained on the trunk, not only withstanding these conditions but also remaining hidden in plain sight.

When the opportunity arose to work on a PhD project, I put together my collection of ideas and questions about this system and presented them to potential supervisors and was accepted to work on this project at Macquarie University. Several years later, after many hours of staring at tree trunks, I have come a long way and feel that I have 1) consolidated several different approaches to assess the camouflage of spiders against simple and complex tree trunk backgrounds, 2) discovered multiple predatory strategies used by spiders on tree trunks and 3) refined our understanding of tree trunks as ecosystems.

Camouflage

Camouflage refers to the mechanism by which animals can reduce their conspicuousness. The effectiveness of camouflage strategies relies on the ability of an animal to blend into its surroundings relative to the visual capabilities of an observer (either predator or prey; (Stevens and Merilaita 2009a). Although camouflage is mostly evoked in an anti-predator context (preventing detection of prey by predators), camouflage can also increase the foraging success of predators by reducing detection by potential prey (Pembury Smith and Ruxton 2020).

Camouflage itself is a metaconcept that can include crypsis (via background matching or disruptive colouration), masquerade and mimicry (Stevens and Merilaita 2009a; Merilaita, Scott-Samuel, and Cuthill 2017). Crypsis prevents the detection of the subject by decreasing its contrast against the background (background matching) or by eliminating the recognizable shape and colour patterning of an animal (disruptive colouration). Background matching reduces differences in colour patterning between that of the animal’s body and the background (Figure 2 A and D), while disruptive colouration relies on highly contrasted markings at the edge of the animal's body (Figure 2 C and F). These markings create false edges that disrupt the outline of the body and hinder detection or recognition (Stevens and Merilaita 2009b). Peppered moths are the iconic example of crypsis and demonstrate the power of natural selection in selecting novel cryptic morphs under changing environments (Cook and Saccheri 2013; Walton and Stevens 2018).

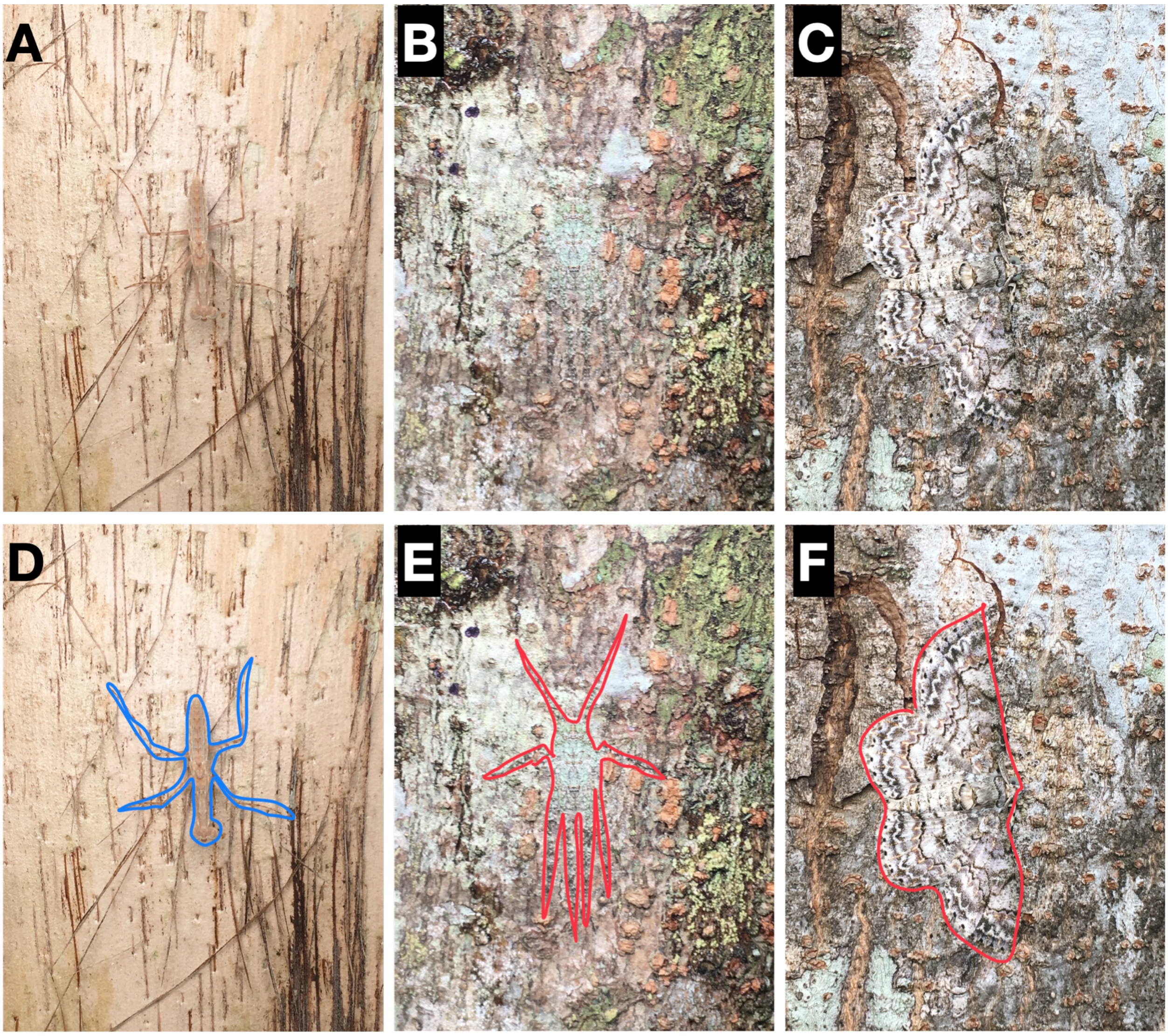


Figure 2. Cryptic arthropods in the surface of tree trunks were found on a single day during fieldwork in May 2019 in east Queensland, Australia. Top row (A-C) shows the cryptic animals as found using a LED panel light of 7x11 cm. It is worth noting that the light panel helps make the outline of the animals more noticeable than it is under natural ambient light. Bottom row (D-F) shows the same photographs with the outlines of the animals delimited with coloured lines for easier identification. The left column (A and D) shows a praying mantis on a relatively smooth surface in which its body colouration closely matches the colour of the trunk. In the center column (B and E) is a lichen spider on a rougher tree trunk. The colouration and the patterning of the spider also seem to match the rough appearance of the lichen around it. The right column (C and F) shows a resting moth on a high-contrast tree trunk surface. Here, together with the colouration patterns of the moth's body, more salient features like black lines that cross from the distal to the proximate part of the wings are likely to disrupt the outline of the body. Photo credit: Alfonso Aceves.

In nature, background matching and disruptive colouration often act together, exemplified by moths that rest on trees (e.g. Figure 2 C and F), including the peppered moth. But in other instances, these mechanisms might act separately, even among individuals of the same species.

Price et al. (2019), found that juvenile shore crabs expressed either background matching or disruptive colouration depending on the background of the habitat they occupied. Crabs in rock pools showed high contrast disruptive patterns and low colour matching while crabs in mudflats showed high colour matching and no disruptive patterns (Price et al. 2019).

Masquerade and mimicry, on the other hand, do not hide the animal, but reduce the recognition of it, despite being detected. Mimics gain protection against predators by resembling the appearance of a defended model species. Clearwing moths are non-toxic insects that resemble the appearance of more aggressive and defended bees and wasps to gain protection from predators. Furthermore, these moths might increase the protective functionality of their morphological similarity to hymenopterans by mimicking their flight patterns (Skowron Volponi et al. 2018). Masqueraders, on the other hand, resemble inanimate and inedible objects (Skelhorn et al. 2010). For example, the orchid mantis (Figure 3) can be highly conspicuous and share the colour and shape features of local flowers. However, they are not recognised as predators by pollinators who approach the mantid at high frequencies (O'Hanlon, Holwell, and Herberstein 2013; O'Hanlon, Holwell, and Herberstein 2014).

Figure 3. From (O'Hanlon, Holwell & Herberstein, 2014). *A sub-adult female H. coronatus feeding on a bee.*

Methodological biases and limitations of camouflage studies

While the above examples are intuitively convincing, the objective and empirical assessment of camouflage phenomena are not without challenges. An early problem in the field was that judgements about the detectability of a creature were based on human perception. For many years, when trying to assess whether animals could be detected or recognised, researchers relied solely on human perception. In short, if a human could see the animal, it was considered conspicuous, if not, cryptic. Yet, animals can have vastly different colour perceptions from humans. For example, human colour receptors are sensitive to blue, green and red light, while insects and birds have colour receptors that can detect UV light (Hempel de Ibarra, Vorobyev, and Menzel 2014; Lunau 2014; Kelber 2019). This makes inferences about conspicuousness based on human perception problematic.

Advances in technology (e.g. spectrometry, multispectral digital imaging, and computational image processing) and modelling methodology (e.g. Receptor Noise Limited model and colour spaces) have allowed us to better approximate what animals can or can't see. Not surprisingly this has led to a surge of camouflage studies (a web of science search for the terms "camouflage" and "evolution" reveals an order of magnitude increase in the number of publications since 2000). Despite these advances, we are still limited to model species, whose visual physiology has been established in great detail. These model species are frequently used in the absence of adequate knowledge of the species of interest. Considering the diversity of animal visual systems, researchers should be cautious when assuming surrogate parameters to assess perception in non-model species. Rather, each novel system should be assessed independently (Kemp et al. 2015). For instance, it might be reasonable to utilise surrogate visual parameters among well-known visual systems like those of hymenopterans or primates (Osorio et al. 2004; Dyer, Paulk, and Reser 2011). For other systems, such as birds and some insect groups, it may be necessary to identify close relatives or highly conserved visual systems (Hart and Vorobyev 2005; Hart and Hunt 2007). Nevertheless, cross-species assumptions are always problematic.

At this stage, it would be remiss not to highlight the experimental difficulty in unambiguously demonstrating masquerade: the difficult part is to show that the viewer has indeed misidentified the object. For instance, a bird might not attack a caterpillar that looks like a twig because it did not detect the caterpillar, which would not classify as masquerade, or because it did indeed see the caterpillar but took it as something inedible such as a twig. This subtle difference is difficult to demonstrate empirically, but Skelhorn et al. (2010) performed a clever experiment that allowed them to differentiate between these two explanations using chicks and hawthorn-twig-caterpillars. Naïve chicks were divided into two groups and were first presented with either a normal hawthorn-twig or a hawthorn-twig bound with purple thread. Then all chicks were confronted with the caterpillar against highly contrasting backgrounds and without any other distractions, where the two groups responded differently. Chicks that previously learned that normal twigs were inedible avoided the caterpillars, leading the researchers to conclude that the chicks misclassified them. The clever control group was the chicks that had learned about twigs with purple threads. As these did not resemble the caterpillars, the chicks treated the caterpillars as novel objects, readily attacking them (Skelhorn et al. 2010).

Spiders

Spiders are the most diverse group of predators (Coddington and Levi 1991), have a cosmopolitan distribution, with the exception of the poles (Foelix 1996) and are no strangers to camouflage. Camouflage can provide a selective advantage for prey capture. For example, some ambush hunters, like some crab spiders, target pollinators visiting flowers. They remain undetected as their body matches the colour of the flower they perch on. This is especially common among European and North American species. Some are even able to change their colour to match the colour of the flower (Chittka 2001; Anderson and Dodson 2015; Gawryszewski et al. 2017). Crab spiders are an excellent example of how methodological advances in colour metrics have improved our understanding of animal perception. For instance, the Australian crab spiders (*Thomisus spectabilis*) seem perfectly cryptic to the human eye: a white spider sitting on a white flower. However, from an insect's perspective, they are conspicuous against the flower because they are highly UV reflective relative to the flower background (Heiling, Herberstein, and Chittka 2003). Unlike the previously described crab spiders, *T. spectabilis* spiders do not hide from pollinators, but instead, exploit the sensory bias of their prey towards conspicuous UV patterns to capture them. Even active hunting spiders like the jumping spiders of the genus *Portia* can benefit from camouflage. The unusual appearance of *Portia* resembles detritus more than a spider's body. Its appearance, in combination with elegant slow movement and stopping patterns, enhances its stealthy approach to prey with great vision like other jumping spiders (Jackson and Wilcox 1998).

Despite the great success of spiders as predators (Nyffeler and Birkhofer 2017), spiders also fall prey to other predators and are thus mesopredators in virtually every habitat. Camouflage as an anti-predatory strategy for spiders is often overlooked, despite some intriguing examples such as spiders that masquerade as inanimate objects such as bird droppings (Yeargan 1994) or parts of plants (Kuntner et al. 2016). Clearly, spider camouflage is likely to aid both their predatory and anti-predatory strategies.

The infamous tree trunk

Tree trunks receive little attention in research studies, perhaps because of their apparent simplicity. However, they carry distinct and highly variable attributes, such as structural complexity and micro-climatic conditions (Nicolai 1986; Prinzing 2003; German A. Villanueva-Bonilla et al. 2021), that can lead to the evolution of ecological adaptations. The apparent simplicity of tree trunks is superficial as this habitat consists of attributes that set them apart from the rest of the tree (surface structure and colour, light exposure, temperature, humidity, available space, etc.; (Nicolai 1986; Prinzing 2003; German A. Villanueva-Bonilla et al. 2021)). A crucial feature of tree trunks is that they offer limited cover for residents and itinerants. Thus, we expect that tree trunk inhabitants are under selection to minimise conspicuous appearances.

These attributes of the tree trunk as a habitat, together with the ecological importance of spiders as both predators and prey, were key to the development of the aims in this thesis. For instance, given that tree trunk attributes are widely variable (e.g., bark texture, colour, and microclimate; (Nicolai 1986; German Antonio Villanueva-Bonilla, Salomão, and Vasconcellos-Neto 2017)), they can lead to specialisation within the broad concept of camouflage. As I had seen in my field observations, two-tailed spiders closely matched the appearance of the tree or the part of the tree trunk they occupied. Thus, variation among individuals was similar to the variation among the tree trunks (Figure 1). Furthermore, these spiders display a wide range of adaptations to this habitat beyond just colouration patterning. For instance, behavioural and morphological traits, such as remaining immobile and having flattened bodies, help them to remain concealed on tree trunks (Baehr and Baehr 1987; German Antonio Villanueva-Bonilla, Salomão, and Vasconcellos-Neto 2017).

Thesis aims

This thesis aims to bring a new perspective to tree trunk habitats. I do this by shifting the focus from quantifying the diversity of tree trunk arthropods (Nicolai 1986; Proctor et al. 2002; Szinetár and Horváth 2005; Croft, Reid, and Hunter 2012; German A. Villanueva-Bonilla et al. 2021) to analysing how ecological strategies, specifically the predatory and anti-predatory strategies of tree-trunk spiders, are uniquely linked to this peculiar habitat.

Chapter 1

Here, I discovered a tree trunk spider with a highly unusual predatory strategy - the Australian ant slayer *Euryopis umbilicata*. This spider is a permanent resident of the tree trunks, it remains hidden behind bark during the daytime. As the sun sets, the ant slayer utilises an unusual acrobatic strategy taking less than half a second to attack and subdue large and dangerous ants. The ant slayer spiders achieve a capture rate outstanding among predatory animals, which is particularly notable as it deals with dangerous prey.

Chapter 2

In this chapter, I describe the unique decorative behaviour of the arboreal jumping spider, *Arasia mullion*, for the first time. Unusually, *A. mullion* builds silk retreats against the exposed surface of tree trunks and proceeds to decorate the retreat with pieces of bark debris it collects from the trunk. Not only is this decorating behaviour unusual, but its entire life history is also dependent on this retreat, which is very unusual for a jumping spider. As the ecology of this species is unknown, I established its phenology with monthly surveys and detailed descriptions of its retreat building behaviour, including the decorating behaviour.

Chapter 3

Based on the results of Chapter 2, I test the hypothesis that decorating the silk retreat reduces its visibility against the tree trunk. I use spectrometry methods and physiological modelling to assess the visual effect that the decorations have on the visibility of their silk retreats to potential prey and predators. The reduction in the UV reflectance of the silk due to the decorations is likely to provide the *A. mullion* spiders with selective advantages in an anti-predatory rather than a foraging context. These findings are of importance as empirical evidence of decorative camouflage is scarce for animal retreats. Additionally, these results can add value to our understanding of spider web ecology and to a body of studies that is commonly focused on aerial capture webs, such as the orb web.

Chapter 4

Despite its wide distribution and a large number of species, the family of the two-tailed spiders (Hersiliidae) remains understudied in most aspects of its biology. Their wide distribution might be in part due to the highly cryptic appearance across all species and in every habitat they occupy. In this chapter, I investigate the relationship between the cryptic appearance of Hersiliidae spiders and their selected habitats. I use multispectral digital imaging to model the cryptic appearance of two sympatric species of Hersiliidae spiders to evaluate the efficacy of camouflage against different tree species with contrasting trunk surfaces.

Thesis conclusion

Finally, I reflect on the contributions of my work, and the value of my experiences throughout the development of this thesis from both an academic and a personal perspective. These involved wonderful collaborations with a wide range of scientists but also the mentally draining circumstance of the COVID-19 pandemic.

References

Anderson AG, and Gary ND. 2015. Colour change ability and its effect on prey capture success in female *Misumenoides formosipes* crab spiders. *Ecological Entomology* 40 (2): 106–13.

Baehr B and Baehr M. 1987. The australian Hersiliidae (Arachnida : Araneae): taxonomy, phylogeny, zoogeography.” *Invertebrate Systematics* 1 (4): 351.

Chittka L. 2001. Camouflage of predatory crab spiders on flowers and the colour perception of bees (Arachnida: Thomisidae / Hymenoptera: Apidae). *Entomologia Generalis* 25 (3): 181–87.

Coddington JA and Levi HW. 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* 22 (1): 565–92.

Cook LM and Saccheri IJ. 2013. The peppered moth and industrial melanism: evolution of a natural selection case study. *Heredity* 110 (3): 207–12.

Croft P, Reid N, and Hunter JT. 2012. The bark of eucalypt trees: habitat quality for arthropods and impact of fire. *Pacific Conservation Biology: A Journal Devoted to Conservation and Land Management in the Pacific Region* 18 (3): 186.

Dyer AG, Paulk AC and Reser DH. 2011. Colour processing in complex environments: insights from the visual system of bees.” *Proceedings. Biological Sciences / The Royal Society* 278 (1707): 952–59.

Foelix R. 1996. *Biology of spiders*. 3rd ed. New York, NY: Oxford University Press.

Gawryszewski FM, Calero-Torralbo MA, Gillespie RG, Rodríguez-Gironés MA, and Herberstein ME. 2017. Correlated evolution between coloration and ambush site in predators with visual prey lures. *Evolution; International Journal of Organic Evolution* 71 (8): 2010–21.

Hart NS and Hunt DM. 2007. Avian visual pigments: characteristics, spectral tuning, and evolution. *The American Naturalist* 169 Suppl 1 (January): S7–26.

Hart NS and Vorobyev M. 2005. Modelling oil droplet absorption spectra and spectral sensitivities of bird cone photoreceptors. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 191 (4): 381–92.

Heiling AM, Herberstein ME and Chittka L. 2003. Crab-spiders manipulate flower signals. *Nature* 421 (6921): 334–334.

Hempel de Ibarra N, Vorobyev M and Menzel R. 2014. Mechanisms, functions and ecology of colour vision in the honeybee. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 200 (6): 411–33.

Jackson RR and Stimson Wilcox R. 1998. Spider-eating spiders: despite the small size of their brain, jumping spiders in the genus Portia outwit other spiders with hunting techniques that include trial and error.” *American Scientist* 86 (4): 350–57.

Kelber A. 2019. Bird colour vision – from cones to perception. *Current Opinion in Behavioral Sciences* 30 (December): 34–40.

Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall J and Whiting. 2015. An integrative framework for the appraisal of coloration in nature. *The American Naturalist* 185 (6): 705–24.

Kuntner M, Gregorič M, Cheng RC and Li D. 2016. Leaf masquerade in an orb web spider. *Arachnologische Mitteilungen* 44 (3): 397–400.

Lunau K. 2014. Visual ecology of flies with particular reference to colour vision and colour preferences. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology* 200 (6): 497–512.

Merilaita S, Scott-Samuel NE and Cuthill IC. 2017. How camouflage works. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 372 (1724). https://doi.org/10.1098/rstb.2016.0341.

Nicolai V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69 (1): 148–60.

Nyffeler M and Birkhofer K. 2017. An estimated 400–800 million tons of prey are annually killed by the global spider community. *The Science of Nature* 104 (3): 30.

O’Hanlo JC, Holwell GI and Herberstein ME. 2013. Pollinator deception in the orchid mantis. Dryad. https://doi.org/10.5061/dryad.g665r.

O’Hanlon JC, Holwell GI and Herberstein ME. 2014. Predatory pollinator deception: does the orchid mantis resemble a model species? *Current Zoology* 60 (1): 90–103.

Osorio D, Smith AC, Vorobyev M and Buchanan-Smith HM. 2004. Detection of fruit and the selection of primate visual pigments for color vision. *The American Naturalist* 164 (6): 696–708.

Pembury-S MQR and Ruxton GD. 2020. Camouflage in predators. *Biological Reviews of the Cambridge Philosophical Society* 95 (5): 1325–40.

Price N, Green S, Troscianko J, Tregenza T and Stevens M. 2019. Background matching and disruptive coloration as habitat-specific strategies for camouflage. *Scientific Reports* 9 (1): 7840.

Prinzing A. 2003. Accessibility of high temperature and high humidity for the mesofauna of a harsh habitat—the case of exposed tree trunks. *Journal of Thermal Biology* 28 (5): 403–12.

Proctor HC, Montgomery KM, Rosen KE and Kitching RL. 2002. Are tree trunks habitats or highways? a comparison of oribatid mite assemblages from hoop-pine bark and litter. *Australian Journal of Entomology* 41 (4): 294–99.

Skelhorn J, Rowland HM, Speed MP and Ruxton GD. 2010. Masquerade: camouflage without crypsis. *Science* 327 (5961): 51.

Skowron-Volponi MA, McLean DJ, Volponi P and Dudley R. 2018. Moving like a model: mimicry of hymenopteran flight trajectories by clearwing moths of southeast asian rainforests. *Biology Letters* 14 (5): 20180152.

Stevens M and Merilaita S. 2009a. Animal camouflage: current issues and new perspectives. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364 (1516): 423–27.

———. 2009b. Defining disruptive coloration and distinguishing its functions. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364 (1516): 481–88.

Szinetár C and Horváth R. 2005. A review of spiders on tree trunks in Europe (Araneae). *European Arachnology* 1: 221–57.

Villanueva-Bonilla GA, Messas YF, Souza HS, Gonzaga MO, Brescovit AD and Vasconcellos-Neto J. 2021. Trunk structural complexity determines the diversity of bark-dwelling spiders in a tropical forest. *Ethology Ecology & Evolution* 33 (2): 108–24.

Villanueva-Bonilla GA, Trevizoli Salomão A and Vasconcellos-Neto J. 2017. Trunk structural traits explain habitat use of a tree-dwelling spider (Selenopidae) in a tropical forest. *Acta Oecologica* 85 (November): 108–15.

Walton OC and Stevens M. 2018. Avian vision models and field experiments determine the survival value of peppered moth camouflage. *Communications Biology* 1 (August): 118.

Yeargan K. 1994. Biology of bolas spiders. *Annual Review of Entomology* 39 (1): 81–99.

PNAS BRIEF REPORT | ECOLOGY OPEN ACCESS

Fast acrobatic maneuvers enable arboreal spiders to hunt dangerous prey

Alfonso Aceves-Aparicio[a,b,c,1], Ajay Narendra[a], Donald James McLean[a], Elizabeth C. Lowe[a], Marcelo Christian[b], Jonas O. Wolff[a,d], Jutta M. Schneider[b], and Marie E. Herberstein[a]

Edited by Raghavendra Gadagkar, Indian Institute of Science, Bangalore, India; received April 5, 2022; accepted August 2, 2022

Spiders, the most specious taxon of predators, have evolved an astounding range of predatory strategies, including group hunting, specialized silk traps, pheromone-loaded bolas, and aggressive mimicry. Spiders that hunt prey defended with behavioral, mechanical, or chemical means are under additional selection pressure to avoid injury and death. Ants are considered dangerous because they can harm or kill their predators, but some groups of spiders, such as the Theridiidae, have a very high diversification of ant-hunting species and strategies [J. Liu et al., *Mol. Phylogenet. Evol.* 94, 658–675 (2016)]. Here, we provide detailed behavioral analyses of the highly acrobatic Australian ant-slayer spider, *Euryopis umbilicata* (Theridiidae), that captures much larger and defended *Camponotus* ants on vertical tree trunks. The hunting sequence consists of ritualized steps performed within split seconds, resulting in an exceptionally high prey capture success rate.

diet | coevolution | silk | Australia

Euryopis umbilicata hide under the bark of *Eucalyptus* trees during the day and emerge at evening twilight. With no capture web, they adopt a downward-facing position, flush against the trunk surface waiting for prey (Fig. 1*C*). The hunting sequence starts with a sit-and-wait period, followed by an acrobatic strike to the prey and successful capture by immobilizing the prey. As they settle, the spiders attach a silk line (dragline) to the tree trunk surface. Then, they use a continuous line of adhesive viscid silk (Fig. 1 *G*–*I* and Movies S1 and S2) to strike and immobilize their prey, the crepuscular banded sugar ants, *Camponotus consobrinus*, that also forage on *Eucalyptus* trees (1). We surveyed multiple trees and found up to nine spiders actively hunting on a single tree. We collected all prey items captured by spiders and found that the spiders almost exclusively captured ants (99.45%, $n = 181/182$), predominantly a single species, *C. consobrinus* (90.60%, $n = 164/181$). Such extreme prey specialization is unusual, since predators typically feed on diverse prey types (2). Moreover, most predators feed on relatively smaller prey. However, the ants measured approximately twice the body length of the spiders, but with similar mass (*SI Appendix*). Ants are considered dangerous, and only ~0.3% of known spider species feed on ants (3). Myrmecophagy is rare among most other taxa too, likely because ants have strong mandibles, the ability to spray formic acid, and strength in numbers (4). However, the spider family Theridiidae likely diversified together with ants during the Cretaceous (5), resulting in relatively numerous myrmecophagous species and hunting strategies as seen in the genus *Euryopis* (6, 7).

The analysis of the spider's capture strategy started when the spider first moved from the sit-and-wait position. A successful capture event involved two distinct phases. The first phase was an acrobatic strike during which the spider tumbled from its resting hunting position over the ant, irrespective of which direction the ant was approaching the spider from ($ø = 306.17° \pm 11.76$, $r = 0.101$, $n = 38$, Rayleigh test, $Z = 0.385$, $P = 0.68$; Fig. 1*D*). The sudden initiation of attack was triggered either by contact ($n = 55$) or when prey was at close range ($n = 5$), possibly triggered by ants contacting silk lines. During these tumbles, the spider used its hind legs to pull viscid silk (Fig. 1*G*) from its spinnerets and attached it to the ant, preventing its escape (Fig. 1 *A* and *B*, *1*–*3*). The spider then dropped off the tree trunk and was secured by the viscid silk line attached to both the ant and the trunk. During this acrobatic choreography, the spider reached a maximum speed of 25.47 ± 2.29 cm/s (mean ± SEM) within milliseconds (74 ± 4 ms, $n = 22$; Fig. 1 *E* and *F*). Maximum speed was independent of spider size (generalized linear model, $P = 0.07$, explained deviance 16.78%) and the direction of the attack ($R^2_{x\theta} = 0.12$, $P = 0.27$). The acrobatic strike ended when the spider reestablished contact with the tree trunk, still holding the viscid line (Fig. 1 *A* and *B*, *4* and *5* and Movies S1 and S2).

Author affiliations: [a]School of Natural Sciences, Macquarie University, Sydney, NSW 2109, Australia; [b]Department of Biology, Universität Hamburg, 20146 Hamburg, Germany; [c]Max-Planck-Institut für Chemische Ökologie, Research Group Predators and Toxic Prey Jena, 07745 Germany; and [d]Zoological Institute and Museum, University of Greifswald, 17489 Greifswald, Germany

---

Author contributions: A.A.-A., A.N., E.C.L., M.C., J.M.S., and M.E.H. designed research; A.A.-A., A.N., and M.C. performed research; A.A.-A., A.N., D.J.M., M.C., and M.E.H. analyzed data; and A.A.-A., A.N., D.J.M., E.C.L., M.C., J.O.W., J.M.S., and M.E.H. wrote the paper.

The authors declare no competing interest.

See online for related content such as Commentaries.

[1]To whom correspondence may be addressed. Email: bioarach@gmail.com.

This article contains supporting information online at http://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2205942119/-/DCSupplemental.

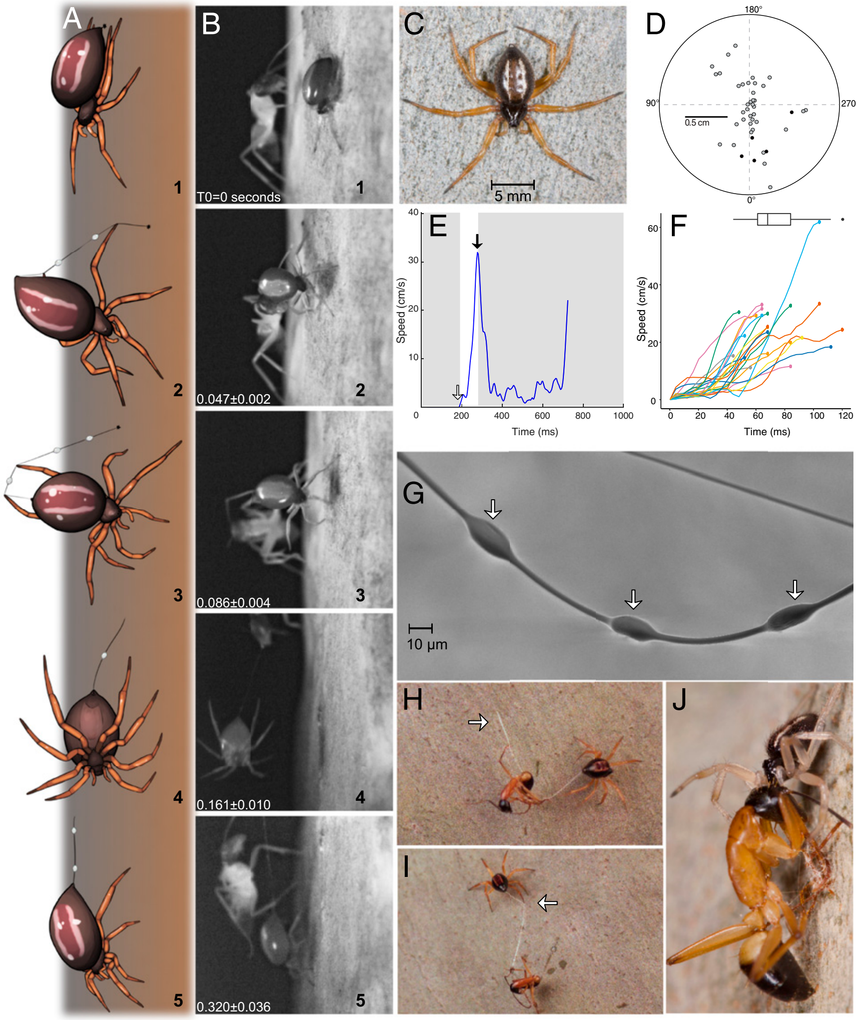


Fig. 1. Hunting choreography of the Australian ant-slayer spider, *E. umbilicata*. (*A*) Images *1*–*5* illustrate spider poses (prey not shown) at the five critical steps during the ant-slayers' strike (illustrations: Zoe Wild). (*B*) Images *1*–5 show corresponding frames from high-speed videos: (*1*) waiting flat position, (*2*) deploying viscid silk using hind legs, (*3*) directing silk toward the potential prey, (*4*) drop-off from trunk surface, and (*5*) resettling on the trunk. Each frame displays the average elapsed time and SEM in seconds between stages (n = 22). (*C*) *E. umbilicata*—dorsal view of the Australian ant-slayer spider in a hunting position (photo credit: A.A.-A.). (*D*) Circular plot showing the direction and distance at which spiders attack the ants, with the center representing the spider position (0 = downward in the plane of the trunk). Successful attacks are shown in gray circles (n = 38), and unsuccessful attacks are shown in black circles (n = 5). (*E*) An example speed profile of a spider during the capture sequence (unshaded area, strike phase; white arrow, last resting position; black arrow, maximum speed reached during strike). (*F*) Individual strike profiles (normalized t starts at 0 s) of different spiders during the tumble. (*Inset*) Boxplot (5th to 95th percentile and median) of time taken from resting phase to top speed. (*G*) SEM of the adhesive droplets on the viscid silk used during captures. Arrows point to glue droplets. (*H* and *I*) Two stills from high-speed video recordings of the ant-slayer circling (clockwise) the ant (*C. consobrinus*). A line of viscid silk keeps the ant attached to the tree trunk (white arrow in *H*). The spider holds the silk line with its right hind leg (white arrow in *I*) while the other end of the silk is attached to the ant. (*J*) Image of the ant-slayer feeding on *C. consobrinus* ant.

In the second phase, the spider circled the ant, entangling it in viscid silk before biting it. It is possible the spider switched to dry silk during at this stage, as proposed by Carico (6) for *Euryopis funebris.* However, the resolution of our high-speed video does not allow us to determine this with confidence. Finally, the ant was detached from the trunk and carried away to be fed upon, often while dangling from a strand of silk (see also ref. 6). While the acrobatic strikes took less than a second, spiders spent significant time immobilizing and killing the prey during the second phase (637 ± 371 s, n = 22). The success of each attack was determined within the first few hundred milliseconds of the strike phase (323 ± 38 ms) when the spider tagged (i.e., contacted with sticky silk) and restrained the ant with the viscid silk. All ants that were successfully tagged during the initial acrobatic tumble (85% of all encounters, n = 51/60) were captured (100%, n = 51/51). Upon contact, the viscid silk effectively held the ant, and the spider continued the capture into phase 2 of the attack (Fig. 1 *H*–*J*). The silk itself did hold the ant for a considerable amount of time, but not indefinitely—when we prevented the spider from biting the ant after tagging, the ant eventually escaped from the viscid silk (time from being tagged to dropping free, n = 15, mean ± SEM = 280.8 ± 31 s). Only in five instances were spider attacks unsuccessful (black circles in Fig. 1*D* and Movie S2). These typically occurred when ants fell from the trees before the viscid silk contacted their body. In one instance, the attack was unsuccessful because the ant changed its heading direction immediately after the spider initiated the attack.

Among theridiid spiders, the evolution of gum-footed silk lines and wrapping of prey with adhesive silk has likely enhanced the access to abundant but dangerous prey such as ants (3, 5, 6, 8). Selection on traits that improve capture rates and avoid harm is predicted to be strong (9), as failure when hunting dangerous prey can potentially incur the greatest fitness cost (death). However, we never observed the ant-slayer being harmed or killed during prey capture ($n = 60$), despite the lack of a web. Most ant-eating spiders either use a web that immobilizes the ants from a safe distance (2, 3), which has evolved multiple times among spiders (10), or they cautiously approach ants from behind with substantial attack distance before attacking (e.g., the jump attack of a jumping spider). Instead, the behavioral precision of the ant-slayer's attack within hundreds of milliseconds combined with adhesive viscid silk appear to be essential for the successful retention of the ants.

Generally, ants are very abundant, with few predators, and, therefore, neutralizing the risk from hunting ants gives access to virtually unlimited prey with little competition (3). The ant-slayer is remarkable, as it almost exclusively captures a single species of ant—*C. consobrinus* at our study site. This extreme degree of prey specialization may reflect local *C. consobrinus* abundance, and/or it may be common to the genus (6). The precise evolution of this complex behavioral sequence could have resulted from the synergistic effects of ant abundance and basal predatory traits in theridiids such as sticky silk (5, 6, 8). The ant-slayer attaches its adhesive silk with a strike speed comparable to that of other non-web-building spiders such as wolf (0.05m/s to 0.3m/s) and jumping (1.5m/s) spiders that rely on moving the entire body toward prey, although not as fast as the slingshot spider (4.2 m/s) that catapults itself and its web toward approaching prey (11, 12).

Compared to other Australian ant predator specialists, the ant-slayer has an extraordinarily high prey capture success rate. For example, the feather-legged assassin bug also hunts large venomous jumper ants (*Myrmecia pilosula*) on tree trunks, but only 2.5% of their ant encounters result in successful captures (13). The ant-slayer's capture success is also high on a per encounter basis, far surpassing apex predators, such as solitary cheetahs and group hunting lions and wolves that usually succeed in less than 50% of their encounters with prey (14–16). Ant-slayers are even more impressive, as they forage solitarily and attack larger and dangerous prey (4, 9).

The evolution of specialized diets is uncommon among predators, and even less common when it involves large and dangerous prey (9). However, due to technological advances allowing for infrared high-speed videography, we have been able to describe what appears to be an almost flawless strategy to capture dangerous prey. While relatively fast and easy access to unlimited prey is the likely main benefit, the potential costs of this strategy remain elusive. Further research is needed to understand the physiological components that enable 1) the spiders to recognize particular prey types (e.g., chemosensory structures) or avoid recognition (e.g., chemical camouflage), 2) the mechanics of executing and modulating each movement within hundreds of milliseconds, and 3) the achievement of rapid and efficient viscid silk adhesion to the ant cuticle. For example, how and when does the spider adjust the position of its body or leg joints to precisely target prey, and is its silk adapted to adhere to the cuticle of ants? A detailed comparison of hunting strategies among congenerics (6) might reveal convergent strategies as well as species-specific solutions to a similar foraging niche.

Methods

Using field observations and experiments, we determine how these small arboreal spiders capture such large and defended prey. We used high-speed videography and scanning electron microscopy to characterize the spider attack and silk use during staged attack sequences in their natural habitat. We collected their preferred prey, *C. consobrinus* ants, and released them individually a few centimeters from the spiders. We filmed the acrobatic strikes at 250 frames per s (fps; $n = 38$ for assessment of strategy steps; from these, we analyzed the attack speed from sequences where the spider remained within the field of view throughout the whole strike, $n = 22$) and the entire capture sequence at 25 fps ($n = 22$) and carried out a frame-by-frame analysis of the spider movement in two dimensions (*SI Appendix*). Each ant and spider was only included once in staged encounters.

Data Availability. All original data and code for analyses have been deposited in the publicly accessible GitHub repository (https://github.com/PonchoAceves/Ant_slayer) (17).

ACKNOWLEDGMENTS. We thank Helen Smith for her assistance with species identification and Zoe Wild for her illustration work. A.A.-A. was supported by a Cotutelle International Macquarie University Research Excellence Scholarship. A.A.-A. thanks Liliana Cadavid Florez for all her support. We acknowledge the lands of the Wallumattagal people of the Darug nation on which this study was conducted.

1. P. Schultheiss, C. A. Raderschall, A. Narendra, Follower ants in a tandem pair are not always naïve. *Sci. Rep.* **5**, 10747 (2015).
2. S. Pekár, S. Toft, Trophic specialisation in a predatory group: The case of prey-specialised spiders (Araneae). *Biol. Rev. Camb. Philos. Soc.* **90**, 744–761 (2015).
3. P. E. Cushing, Spider-ant associations: An updated review of myrmecomorphy, myrmecophily, and myrmecophagy in spiders. *Psyche (Stuttg.)* **2012**, 151989 (2012).
4. T. Eisner, I. T. Baldwin, J. Conner, Circumvention of prey defense by a predator: Ant lion vs. ant. *Proc. Natl. Acad. Sci. U.S.A.* **90**, 6716–6720 (1993).
5. J. Liu, L. J. May-Collado, S. Pekár, I. Agnarsson, A revised and dated phylogeny of cobweb spiders (Araneae, Araneoidea, Theridiidae): A predatory Cretaceous lineage diversifying in the era of the ants (Hymenoptera, Formicidae). *Mol. Phylogenet. Evol.* **94**, 658–675 (2016).
6. J. E. Carico, Predatory behavior in *Euryopis funebris* (HENTZ) (Araneae: Theridiidae) and the evolutionary significance of web reduction. *Symp. Zool. Soc. Lond.* **42**, 51–58 (1978).
7. E. Líznarová, S. Pekár, Trophic niche and capture efficacy of an ant-eating spider, *Euryopis episinoides* (Araneae: Theridiidae). *J. Arachnol.* **47**, 45–51 (2019).
8. W. Eberhard, *Spider Webs: Behavior, Function, and Evolution* (University of Chicago Press, 2020).
9. S. Mukherjee, M. R. Heithaus, Dangerous prey and daring predators: A review. *Biol. Rev. Camb. Philos. Soc.* **88**, 550–563 (2013).
10. J. O. Wolff, M. Řezáč, T. Krejčí, S. N. Gorb, Hunting with sticky tape: Functional shift in silk glands of araneophagous ground spiders (Gnaphosidae). *J. Exp. Biol.* **220**, 2250–2259 (2017).
11. O. Dangles, N. Ory, T. Steinmann, J.-P. Christides, J. Casas, Spider's attack versus cricket's escape: Velocity modes determine success. *Anim. Behav.* **72**, 603–610 (2006).
12. S. L. M. Alexander, M. S. Bhamla, Ultrafast launch of slingshot spiders using conical silk webs. *Curr. Biol.* **30**, R928–R929 (2020).
13. M. W. Bulbert, M. E. Herberstein, G. Cassis, Assassin bug requires dangerous ant prey to bite first. *Curr. Biol.* **24**, R220–R221 (2014).
14. G. B. Schaller, Hunting behaviour of the cheetah in the Serengeti National Park, Tanzania. *Afr. J. Ecol.* **6**, 95–100 (1968).
15. G. J. Vermeij, Unsuccessful predation and evolution. *Am. Nat.* **120**, 701–720 (1982).
16. R. K. Humphreys, G. D. Ruxton, The dicey dinner dilemma: Asymmetry in predator-prey risk-taking, a broadly applicable alternative to the life-dinner principle. *J. Evol. Biol.* **33**, 377–383 (2020).
17. A. Aceves-Aparicio, Data and code for "Fast acrobatic maneuvers enable arboreal spiders to hunt dangerous prey," PonchoAceves/Ant_slayer. GitHub. https://github.com/PonchoAceves/Ant_slayer. Deposited 25 May 2021.

Supplemental information

Fast acrobatic manoeuvres enable arboreal spiders to hunt dangerous prey

Alfonso Aceves-Aparicio[1, 2, 3], Ajay Narendra[1], Donald James McLean[1], Elizabeth C. Lowe[1], Marcelo Christian[2], Jonas O. Wolff[1, 4], Jutta M. Schneider[2] and Marie E. Herberstein[1]

[1] School of Natural Sciences, Macquarie University, Sydney, NSW, 2109, Australia

[2]Department of Biology, Universität Hamburg, Hamburg, Germany

[3]Max-Planck-Institut für Chemische Ökologie, Jena, Thüringen, Germany

[4]Zoological Institute and Museum, University of Greifswald, Germany

Corresponding author: Alfonso Aceves-Aparicio

Correspondence: bioarach@gmail.com

Supplemental experimental procedures

Study site

Euryopis umbillicata (Australian ant-slayer) were abundantly found on the Macquarie University campus, the Wallamatagal campus (North Ryde, NSW, Australia). Observations regarding this publication were conducted between April 2018 and June 2019. A patch of vegetation consisting of 107 *Eucalyptus* trees was selected for collection of prey carcasses (as described below) and for the recording of attack sequences. We measured a subset of the trees where the spiders were observed, mean (± SD) diameter = 35.47 ± 10.11 cm (n = 11).

Spider diet

The prey captured by *Euryopis umbilicata* was recorded from, 1) direct observation of naturally occurring feeding events and 2) collection of carcasses of prey attached to the surface of trunks. For two days during the first week of each month between April and November 2018, we inspected the trunks of our study site to collect the carcases of the ant slayers' prey. Collections were conducted between 10 am and 1 pm with a total of 25 hours of collection time. Additionally, all naturally occurring captures observed during video recording dates were collected (video recording details below). Amongst the 17 non-*Camponotus consobrinus* ants, we found individuals belonging to three other different species (13 *Crematogaster* sp., 1 *Polyrhachis* sp., 3 *Camponotus* sp.). Despite *Crematogaster* sp. being the second most common ant prey, they comprised only 7.1 % of all prey items. From our video recordings we observed 12 naturally occurring encounters between the ant-slayer and *Crematogaster* ants. In 11 of these encounters, the spiders moved away without attempting the capture strike. In only one instance the spider directed a strike against the *Crematogaster* ant. However, after silk tagging, the spider did not initiate entangling the ant with silk further, but instead it transported the ant with the viscid silk line used for capture to a different location where it started feeding on the ant.

Tree trunk diameter and ant density

We have no data on how tree diameter relates to ant density on these trees and their particular habitat. However, we predict with a model described below, that it is most likely that the ant density is higher on thicker tree trunks, as thicker trunks usually carry larger crowns and hence harbour proportionally more resources for ants than small trees. If we assume the number of ants climbing the tree is determined by the available resources, and resources are proportional to the area of the crown, C_a (which is a conservative assumption, since it is more likely to be proportional to the volume of the crown), then we can estimate the average density of the ants distributed around the trunk. Crown area is proportional to the square of crown diameter, C_d. Trees exhibit a strong linear relationship between trunk diameter, t, and crown diameter [1] so:

$$C_a \propto C_d^2 \propto t^2 \qquad \text{Equation 1}$$

where the symbol $\propto$ indicates “proportional to”. Our assumption is that the number of ants climbing the trunk, n, is proportional to crown area, hence, from equation 1:

$$n \propto t^2 \qquad \text{Equation 2}$$

We divide number of ants by trunk circumference to get density of ants around the trunk, d:

$$d \propto {t^2}/{2t} \propto t \qquad \text{Equation 3}$$

Consequently, based on these reasonable assumptions, we deduce that the thicker the trunk, the greater the expected density of ants, and the greater the expected encounter rate for spiders.

Camponotus consobrinus navigation

Camponotus consobrinus engage in tandem runs, but we know that (a) tandem running is carried out by a small proportion of outbound foragers (~10% per day), and (b) tandem runs mostly occur before the start of evening twilight, thus in bright light conditions (see Fig 2, [2]). In Camponotus ants, tactile stimuli appear to be essential along with surface pheromone for tandem running [3]. *C. consobrinus* ants rely on vision and have a light-dependent pupillary mechanism that allows them to see in low light [4].

Silk inspection

Three ants were collected before the ant slayer spiders could remove them to feed. We prepared the ants and the viscid silk on them for SEM imaging. Samples were air-dried and then coated with gold. Samples were then scanned with a Phenom XL Scanning Electron Microscope (10kV, 4.114mm, 1Pa).

We inferred from our close inspection of the capture sequences (supplementary videos) and the collected silk samples where the ant slayer only used viscid silk to capture. This silk is likely to be the product of flagelliform and aggregate glands as for other Theridiidae spiders [5,6].

Body length and mass measurements

Spiders (n = 30) were photographed with a scale while in flat ambush position on the surface of trunks. Body size was measured from rear end of the opisthosoma (the visible tip of the spinnerets) to the front edge of the of the anterior median eyes (at approximately the edge of the prosoma). Ants (n = 30) were collected from the field and anaesthetised with CO_2 to be photographed similarly to the spiders. Body size was measured from the tip of the mandibles to the rear end of the abdomen. All measurements were conducted using ImageJ v 1.52k [7].

The mass of both spiders (n = 13) and ants (n = 13) was measured using a Mettler Toledo microbalance to the nearest 0.01 mg.

Camponotus consobrinus are approximately twice the body length of the ant-slayer spiders (ant (n = 30): 11.23 ± 0.28 mm (mean ± SD); range 8.18 - 14.51 mm; spider (n = 30): 5.04 ± 0.12 mm; range: 3.57 - 6.12 mm;) but of similar mass (ant (n = 13): 0.0243 ± 0.00339 g (mean ± SEM); range 0.0130 - 0.0549 g, spider (n = 13): 0.0217 ± 0.00216 g (mean ± SEM); range 0.0122 - 0.0374 g).

Video recordings

The staged encounters were filmed in two different modes. A standard frame rate of 25 frames per second and high-speed frame rate at 250 frames per second. In both cases, a measuring tape was placed after the capture events without changing focus point or framing on the surface of the trunk for calibration. A minimum of 50 trees was haphazardly inspected during each night for the presence of ant-slayer spiders.

For each recording, the camera was positioned perpendicularly to the plane of the tree trunk surface. We estimated the speed as a 2-dimensional movement as the surface of the tree is mostly flat. From exploratory recordings (not included in the analyses), we determined that most of the movement occurs on the x and y axes in the plane of the trunk. By measuring the 2-dimensional speed, we calculated a conservative estimate of the attack speed (i.e. lower than the real speed). The spider remained in the camera's field of view during the entire recording duration.

Standard videography

Capture sequences at 25fps were recorded using a DSLR camera (Canon T2i with 100mm macro lens) to record the full capture sequences from the ant's approach to its removal by the spiders to be fed upon. Recordings were made over 13 nights between May and August (2 in May, 8 in June, 1 in July and 2 in August), between the 18:00 and 21:00 hours.

High-speed videography and cartesian coordinates data

High-speed footage was recorded over four nights in 2018 (one night in May, two nights in June and one night in October) and two nights in April 2019, between the 18:00 and 21:00 hours. Five to seven videos were recorded per night.

To describe the attack choreography of the spiders, we filmed the staged encounters of spider-ant pairs using an infrared-sensitive Optronis camera (CR600 x 2, Kehl, Germany; at 250 fps, image size 1024 x 1024 pixels) or a Chronos camera (v1.4, Kron Technologies, Barnaby, Canada; at 250 fps, image size 1280 x 1024 pixels) mounted on a tripod. For illumination, we used custom-built infra-red LED light sources mounted on magic arms (Manfrotto, Vitec Imaging Distribution Australia) which were attached to the tripod. We carried out a frame-by-frame analysis at 4 ms inter-frame interval to determine body orientation of both the spider and the head position of the ant. For this, we converted videos to image sequences in Final Cut Pro (version 10.2.3, Apple Inc.). We extracted x, y coordinates of the cephalothorax and abdomen of the spider and the head position of the ant using a custom-written Matlab (Mathworks, Natick, Massachusetts, USA) based program (courtesy Jan Hemmi and Robert Parker). The tracking of each body part was done manually.

We used the R package Trajr [8] to convert the x, y coordinates to the trajectories followed over time, and to assess the speed changes during the strike phase of the ant slayer. The particular functions used are included with the supplied R script to reproduce our speed analyses (GitHub and Zenodo repositories accessible with this publication, https://github.com/PonchoAceves/Ant_slayer).

From the video footage (250 fps and 25 fps), we calculated the attack angles from the x, y coordinates of the spider on the last stationary position before attack and x, y coordinates of the spider at the first instance of contact with the ant. We used this to generate circular plots in Matlab and carried out circular analyses in Oriana (version 4.0, Kovach Computing Services, UK). We used a Rayleigh test to identify whether the attack angles were uniformly distributed.

Circular analyses were carried out only on successful attack dataset.

Capture strategy analysis from videos

The videos start when the ants approach the spiders and are at a distance of at least four ant body lengths. For the high-speed sequences, t = 0 is the last frame in which the spider remains immobile in sit-and-wait position. The following steps for each of the attack phases are described below:

Strike phase. The acrobatic strike begins with the spider detecting of the ant prey while in its flattened position (last immobile frame is considered T = 0). The first movement is considered, t = 1.

First step – Waiting flat position.

After wandering the tree trunk, the spider stops at a location and begins settling by repeatedly pressing its spinnerets against the trunk surface to draw a thread of silk. Then, the spider spreads and press all of its legs flat on the trunk. The spider remains in this position for the potential encounter with ant prey.

Second step – deploying viscid silk using hind legs.

During silk deployment, the spider begins lifting its hind legs making visible the extension of the viscid silk line. The silk line is anchored (likely to a dragline attachment point) to the surface the tree trunk at one end and to the spinnerets on the other. Deployment of the silk continues with the spider lifting and directing its opisthosoma (abdomen) from the trunk and towards the potential prey position.

Third step – directing silk towards the potential prey.

One of the hind legs is extended towards the position of the potential prey. This leg holds the viscid silk line with the terminal claws. At this moment, the body of the spider turns towards the prey item. The viscid silk line is extended between the end of the spiders' abdomen and the extended leg. This silk section is the one directed towards the prey and responsible for the first contact with it.

Fourth step – drop-off from trunk surface.

Upon contact with the potential prey, the spider releases its legs from the surface of the trunk and begins free-falling.

The spider is secured by the viscid line attached to the ant (if successfully tagged) and simultaneously by the dragline threads previously attached to the trunk surface. This step begins with the release of the last leg from the trunk surface.

Fifth step – re-settling on the trunk's surface.

Once the spider has come back into contact with the trunk and its legs are holding its position.

Capture phase. After re-settling on the trunk, the spider begins to entangle the ant with more viscid silk before biting and killing it.

First, the spider pulls and holds a new segment of viscid silk line with its hind leg. Then it touches the ant with the new adhesive silk segment and continues with a circular movement around the ant. This is repeated several times until the ant is almost immobile. The spider then bites the ant and retreats until the ant is completely immobile.

The effect of spider size and attack direction on maximum speed

We ran a generalised linear model (GLM) with a log-link and Gamma error structure to analyse the relationship between spider size and the maximum speeds reached during the strikes. The angles of each attack were standardised to zero with the axis of the spider body. When spiders capture prey that are directly in front of them = '0°'; spiders that capture prey that are directly behind them = 180°. For the successful attacks, we tested the association between linear (maximum speed) and circular (attack orientation) variables with the Johnson–Wehrly–Mardia correlation coefficient (see chapter 8 in [9]). Where $R^2_{x\theta}$ ranges between zero and one. Values closer to one refer to stronger associations. Spiders did not exhibit any preference for the direction in which they attacked the prey. All the analyses were done in R statistical software [10].

Data and code utilised for analysis available at:
https://ponchoaceves.github.io/Ant_slayer/ms.html#Assessing_attack_speed

SI 1 movie legend:
The acrobatic attack of the Australian ant slayer spider (*Euryopis umbilicata*).
Euryopis umbilicata - the Australian ant slayer spider predominantly captures *Camponotus consobrinus* ants on the surface of Eucalyptus trees in eastern Australia. They wait for their prey flushed down against the trunk surface after sunset. Upon contact, they perform a series of fast and accurate acrobatic steps to capture their prey.

SI 2 movie legend:
Example high-speed footage of unsuccessful attacks of the Australian ant slayer spider (*Euryopis umbilicata*).

Supplementary references:

[1] Hemery, G. E., Savill, P. S. & Pryor, S. N. Applications of the crown diameter–stem diameter relationship for different species of broadleaved trees. For. Ecol. Manage. 215, 285–294 (2005).

[2] Schultheiss, P., Raderschall, C. A. & Narendra, A. Follower ants in a tandem pair are not always naïve. Sci. Rep. 5, 10747 (2015).

[3] Hölldobler, B., Möglich, M. & Maschwitz, U. Communication by tandem running in the ant *Camponotus sericeus*. J. Comp. Physiol. 90, 105–127 (1974).

[4] Narendra, A., Ramirez-Esquivel, F. & Ribi, W. A. Compound eye and ocellar structure for walking and flying modes of locomotion in the Australian ant, *Camponotus consobrinus*. Sci. Rep. 6, 22331 (2016).

[5] Eberhard WG, Agnarsson I, Levi HW. Web forms and the phylogeny of theridiid spiders (Araneae : Theridiidae): chaos from order. System Biodivers 2008;6:415–75. doi:10.1017/s1477200008002855.

[6] Sahni V, Blackledge TA, Dhinojwala A. A Review on Spider Silk Adhesion. J Adhes 2011;87:595–614. doi:10.1080/00218464.2011.583588.

[7] Schneider CA, Rasband WS, Eliceiri KW. NIH Image to ImageJ: 25 years of image analysis. Nature Methods 2012;9:671–5. doi:10.1038/nmeth.2089.

[8] McLean DJ, Skowron Volponi MA. trajr: An R package for characterisation of animal trajectories. Ethology 2018;124:440–8. doi:10.1111/eth.12739.

[9] Pewsey A, Neuhäuser M, Ruxton GD. Circular statistics in R. Oxford University Press; 2013.

[10] R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R-project.org/.

Novel decorating behaviour of silk retreats in a challenging habitat

Alfonso Aceves-Aparicio[1,2,3], Donald James McLean[1], Zoe Wild[1],
Jutta M. Schneider[2] and Marie E. Herberstein[1]

[1] School of Natural Sciences, Macquarie University, Sydney, New South Wales, Australia
[2] Institute of Zoology, Universität Hamburg, Hamburg, Germany
[3] Max-Planck-Institut für Chemische Ökologie, Jena, Thüringen, Germany

ABSTRACT

Many ecological interactions of spiders with their potential prey and predators are affected by the visibility of their bodies and silk, especially in habitats with lower structural complexity that expose spiders. For instance, the surface of tree trunks harbours relatively limited structures to hide in and may expose residents to visual detection by prey and predators. Here we provide the first detailed description of the novel retreat building strategy of the tree trunk jumping spider *Arasia mullion*. Using fields surveys, we monitored and measured over 115 spiders and 554 silk retreats. These spiders build silk retreats on the exposed surface of tree trunks, where they remain as sedentary permanent residents. Furthermore, the spiders decorate the silk retreats with bark debris that they collect from the immediate surrounding.
We discuss the role of silk decoration in the unusual sedentary behaviour of these spiders and the potential mechanisms that allow *A. mullion* to engineer their niche in a challenging habitat.

Subjects Animal Behavior, Ecology, Entomology, Zoology
Keywords Building behaviour, Jumping spider, Tree trunks, *Arasia mullion*, Spectral reflectance, Natural history, Australia

Submitted 18 May 2021
Accepted 5 January 2022
Published 22 March 2022

Corresponding author
Alfonso Aceves-Aparicio,
bioarach@gmail.com

Academic editor
Clint Kelly

Additional Information and Declarations can be found on page 15

DOI **10.7717/peerj.12839**

INTRODUCTION

Habitat structural complexity (the quantity, composition, and spatial arrangement of biotic and abiotic elements) can be a major challenge for some animals. Consequently, the degree of complexity influences strategies that maximise fitness (*Gigliotti et al., 2020*). Habitats with relatively high complexity can concentrate resources and offer greater cover that reduces encounter rates with predators at higher trophic levels (*Langellotto & Denno, 2004*). In comparison, less complex habitats can be challenging for animals as both food and cover from predators are less abundant. Even in low complexity environments, some animals can overcome these habitat limitations through building behaviour, also known as 'extended phenotype'. This refers to traits expressed beyond the boundaries of the animal's body, such as building constructions to hide under, hunt with or breed in (*Dawkins, 1982*).

Spiders are well known for their conspicuous expression of extended phenotypes through their web building behaviour. These silk constructions overcome vegetation gaps up to 10 m (*e.g.* across water bodies: *Gregorič et al., 2011*). Similarly, the large and complex

How to cite this article Aceves-Aparicio A, McLean DJ, Wild Z, Schneider JM, Herberstein ME. 2022. Novel decorating behaviour of silk retreats in a challenging habitat. **PeerJ 10:e12839 DOI 10.7717/peerj.12839**

three-dimensional colony webs cover large portions of trees and create a foraging, mating and communication platform for the entire colony of spiders (*Nentwig, 1985*; *Eberhard, Agnarsson & Levi, 2008*). In highly exposed habitats, spiders deploy silk to reduce the risk of predation. For example, some aerial webs include silk scaffolding to detect or deter approaching predators, such as wasps or birds (*Cloudsley-Thompson, 1995*). Leaf curling spiders wrap a leaf into the centre of the web into which they retreat instead of sitting at the exposed web hub (*Thirunavukarasu, Nicolson & Elgar, 1996*). Silk constructions can also be used to facilitate the exploitation of otherwise challenging environments. For instance, buckspoor spiders of the genus *Seothyra* shelter from the extreme thermal conditions in the Namib desert dunes (up to 73 °C on the sand surface) in underground burrows lined and covered with silk (*Lubin & Henschel, 1990*). Spiders of the genus *Wendilgarda* attach sticky silk lines to the surface of water streams to capture insects that move on the water surface (*Coddington & Valerio, 1980*). Finally, the unique diving bell spider (*Argyroneta aquatica*) takes the occupation of inhospitable environments even further by building a silk nest underwater, where it lives its entire life (*Seymour & Hetz, 2011*).

Considering the functionality, flexibility, and broad benefits of web building, it is surprising that some groups have abandoned capture webs and instead hunt by vision and ambush (*e.g.*, jumping spiders) (*Richman & Jackson, 1992*; *Hill & Richman, 2011*; see also *Wolff, Wierucka & Uhl G.Herberstein, 2021*). Yet, they may still utilise silk for overcoming some habitat constraints, in the form of building retreats or abseiling with a dragline (*Herberstein, 2011*). Jumping spiders (Salticidae) are the most speciose family of spiders with 6,344 known species (*World Spider Catalog, 2021*), of which most are cursorial predators inhabiting virtually all terrestrial ecosystems (except for the poles). Given the astoundingly acute vision of jumping spiders, they visually assess the complexity of their surrounding environment (*Jackson & Blest, 1982*; *Aguilar-Argüello, Gerhard & Nelson, 2019*) and navigate complex habitats when searching for prey or mates. Some jumping spiders build and occupy hidden silk retreats (*e.g.*, underneath leaves or behind bark or rocks) when inactive or when reproducing (*Richman & Jackson, 1992*; *Hoefler & Jakob, 2006*).

When exploring less complex and more exposed environments like tree trunks, most species of jumping spiders rely on rough, highly contrasting surfaces for concealment (*Cumming & Wesołowska, 2004*; *Robledo-Ospina et al., 2017*). Thus, we would not expect jumping spiders to be generally active on, nor to inhabit, highly exposed habitats such as smooth and bright bark. Based on preliminary surveys of spiders occupying tree trunks, we became interested in the tree trunk jumping spider *Arasia mullion* (*Zabka, 2002*) for several reasons. First, these spiders occurred in unexpected high abundances on tree trunks. Second, unlike other spiders that inhabit tree trunks, *A. mullion* was mostly found occupying a silk retreat during the day, which is uncommon for jumping spiders. This species exhibits a prolonged reliance on using a multi-purpose silk retreat on the exposed surface of trunks of a small range of tree species. The trees occupied by these spiders seem unlikely permanent niches for animals as their smooth and bright surfaces are likely to render residents highly conspicuous.

These observations generated a number of research question that we wished to address: (1) how do these spiders build their silk retreats; (2) what is the overall phenology of this species and how consistently are silk retreats occupied; (3) how do they decorate their retreats and how does decoration affect the visual quality of the silk? Here, we provide the first detailed descriptions of *A. mullion's* retreat building behaviour and discuss the natural history of the retreats in this challenging environment.

METHODS

Study species

Arasia mullion Zabka, 2002 are recently discovered small jumping spiders (Salticidae) that are locally abundant on trees in eastern Australia. Currently, they are thought to be endemic to New South Wales (*Zabka, 2002*) and very little is known about their behaviour, life history, or the characteristics of the habitats they occupy.

Study site

Observations were performed in approximately 6,500 m^2 on the Macquarie University campus (Macquarie Park, NSW, Australia). Within our study site, 57 trees were inspected for the presence of spiders. Every tree was identified to species and individually labelled. A total of 19 trees were periodically monitored for 16 months to observe the spiders' natural history, including activity patterns, retreat construction and occupancy, and inter-and intra-specific interactions (detailed below).

Retreat building

Arasia mullion spiders are commonly found in their silk retreats; close observation of the silk retreats revealed the presence of fine debris attached to the silk. To understand the retreat-building behaviour and determine the origin of the debris on the silk, 20 spiders were captured, and their retreats were removed from the tree trunk surface. After 1 h, spiders were released back onto their original trees, then periodic observations were conducted four times a day for 5 days to observe the building of new retreats. Four instances of retreat building behaviour were filmed using a compact camera (Samsung TG-5, 12MP) on a tripod or with a hand-held mobile phone camera (Apple iPhone 6S).

Phenology and retreat occupancy

We conducted phenological surveys to determine habitat occupancy patterns (if any) throughout the seasons. Six surveys were conducted at approximately three-month intervals between July 2018 and November 2019. During each survey, all retreats detected on the surface of the tree trunks from the ground up to a height of 2 m were labelled with permanent marker; labels were placed 10 cm from the retreat to reduce the possible effect of increased visibility or conspicuousness. As the retreats appeared to be sessile structures, we considered all the retreats we found without a label code during subsequent surveys to be newly built. All newly built retreats were then labelled according to the chronological survey number. All retreats were photographed with their labels and a scale for reference (Fig. 1).

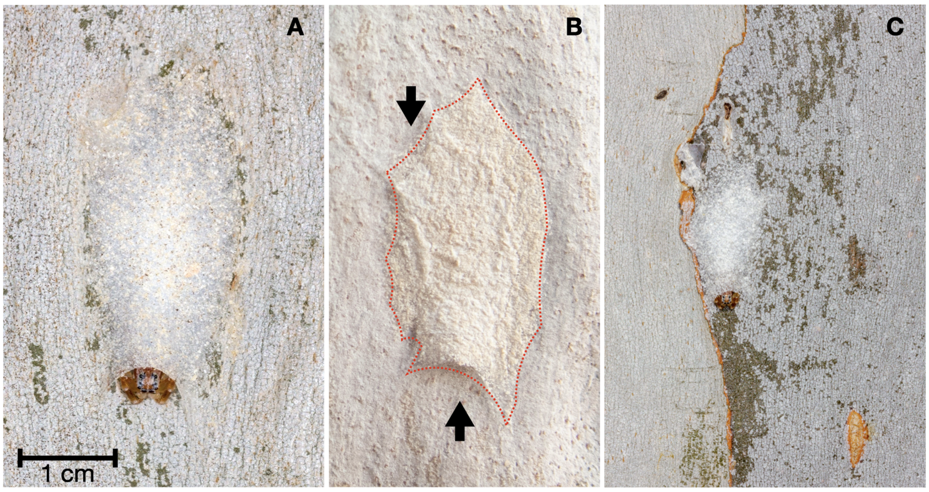


Figure 1 **Typical appearance of the silk retreat of *Arasia mullion* and its position on a tree trunk.** (A) The prosoma and legs of *A. mullion* are shown protruding from the bottom opening of the retreat. (B) Silk retreat of *A. mullion* which visually matches the appearance of the tree trunk surface of Sydney Blue Gum (*Corymbia maculata*). The dotted line outlines the edge of the silk retreat. The black arrows point to the top and bottom openings. (C) Frontal view of a silk retreat on the trunk's surface where scarring from debris collection is visible. Scars occurred in the immediate surroundings of the retreat and commonly stretched outwards from both openings. Photo credit: Alfonso Aceves-Aparicio.
Full-size DOI: 10.7717/peerj.12839/fig-1

All marked retreats were checked for spider presence by gently depressing the silk from the top edge down with a paintbrush which caused the resident spider to emerge at the lower opening. A subset of spiders were collected in vials or photographed *in situ* with a scale, and we measured the prosoma width and length from the photographs. Photographs of retreats were manually converted to monochrome retreat outlines using ImageJ version 1.52k (*Schneider, Rasband & Eliceiri, 2012*). Retreat dimensions were measured from these outlines. Outline images were smoothed by applying Gaussian blur (sigma = 10). Retreat width was calculated as the length of the longest row of pixels in the outline, and length was the longest column. Lastly, area was the number of pixels within the outline shape. Width, length and area were scaled to convert pixels into mm or mm^2. All statistical analyses, including log transformations to meet statistical assumptions, were conducted in R (*R Core Team, 2021*). Unlike silk retreats, individual spiders could not be marked without compromising its appearance and thus survival against predators. Therefore, for this study we considered that it was highly unlikely to measure the same individual although this cannot be excluded entirely.

Silk reflectance—comparison with unusual samples

A small group of *A. mullion* spiders was found living on a concrete water tank in a small area of public parkland (3,000 m^2, North Ryde, NSW, Australia, 33°48′02″S, 151°08′13″E). They were part of a small local population that mostly occurred on trees. The retreats built on concrete lacked the debris normally covering tree retreats, which provided us with an unusual opportunity to compare retreats with and without debris. All the retreats found on the concrete tank were collected, $n = 5$ (non-decorated samples), and six silk retreats were collected from nearby tree trunks for comparison (decorated samples). Samples were then placed flat over black cardboard to measure their reflectance spectra. We used spectrometry to assess potential visual differences between these samples resulting from the lack of debris decoration. The reflectance spectra measurements were obtained using a Jazz Ocean Optics spectrophotometer (Ocean Optics, Largo, FL, USA) with the following settings: integration time = 40 ms, boxcar width = 10, averaged scans = 10. We used a PX-2 pulse xenon light source and all measurements were relative to a white standard WS-1. The light source and probe were set at an angle of 45 degrees to the cardboard. Measurements were restricted to the UV and visible part of the spectrum of light (between 300 and 700 nm) as this range is relevant to most ecological observers of spiders (*Cronin et al., 2014*). Each measurement was taken five times, and the results averaged. All spectral processing and exploration were carried out using the R package Pavo in R, versions 2.2 and 3.5.2, respectively (*Maia et al., 2019*; *R Core Team, 2021*).

RESULTS

The unusual sedentary life of a jumping spider

We found that *Arasia mullion* led a sedentary life on the surface of tree trunks, where they build, decorate, and occupy their silk retreats (described in detail below). Of the 21 species of trees within our study area, *A. mullion* was restricted to the following four species: Spotted Gum (*Corymbia maculata*), Smooth-barked Apple Myrtle (*Angophora costata*), Flooded Gum (*Eucalyptus grandis*) and Scribbly Gum (*Eucalyptus racemosa*). The traits that these tree species have in common are smooth bark with small depressions ("dimples") on the surface, which the spiders used as the foundation of their retreats. The remaining 17 species have bark characterised by fissured, fibrous, stringy textures or shedding in irregular flakes, which creates rough surfaces with deep elongated crevices where we did not record any *A. mullion* retreats (Table S1).

The silk retreats

The retreats of *A. mullion* were exclusively built over a dimple on the exposed surface of tree trunks. The retreat consisted of a sheet of silk laid on the surface of the trunk (Figs. 1A, 1B). The retreats varied in colour and visual texture. However, each retreat matched the bark on which it was situated (at least to the human eye). Each silk retreat had two openings, one at the top and one at the bottom. When active, the spider sat with only the front part of the body and two pairs of legs protruding from the lower entrance (Figs. 1A, 1B).

Retreat building behaviour

The fact that the colour and texture of the silk retreats matched their backgrounds was immediately noticeable. However, whether this was achieved passively (debris caught in the silk) or actively (spiders decorating their retreat with debris) was unclear. Despite the construction of new retreats being relatively uncommon to observe (compared to the number of retreats and spiders present), we were able to film the construction behaviour of a number of retreats after a spider had been removed and replaced (Video S1).

The spiders commenced construction by laying fine silk lines over a suitable dimple on the surface of the tree trunk. Then, using their chelicerae, they scraped the tree surface and collected fine debris. We observed debris being collected from the immediate surroundings of the retreat and from further away. After collection, the debris was carried back to the dimple underneath the silk lines. The spiders then used the debris to decorate the silk by brushing it onto the underside of the silk using active movements of their pedipalps. Once the debris had been applied, they added several layers of silk to the underside of the retreat using oscillatory movements of the spinnerets. These layers attached the debris to the initial silk lines. This process was conducted repeatedly (Video S1). Although we were not able to document the building of these retreats from start to finished, our observations suggest that this can vary between 2 and 4 h.

The process of scraping debris left visible scars on the bark, which allowed us to confirm that the observed decoration behaviour occurred in all of the surveyed retreats, even when we had not directly observed retreat construction. The scarring from the debris collection also allowed us to confirm that the spiders use debris directly from the dimple and the immediate surroundings of the retreat (Fig. 1C).

Phenology

The jumping spiders *A. mullion* spent their entire life on the surface of tree trunks. Unlike other salticids *A. mullion* spiders stayed in their silk retreats and were rarely seen wandering the surface of the tree trunks. The retreats were occupied by all life stages, from recent hatchlings to mature males and females. Our surveys showed an annual life cycle with egg sacs laid inside the retreats in late Australian spring and early summer—November to December. Early instars were found in newly spun retreats during January and February. Our surveys covered two phenological cycles with two surveys conducted during 2018 and four during 2019. Size variation in both the spiders and their retreats was recorded during each survey (Fig. 2).

We assessed the effect of occupancy (vacant and occupied) and time (yearly season) on the recorded size of the available retreats (length) using a linear mixed effects model. We set occupancy, season and their interaction as fixed effects and the individual ID of each silk retreat as a random effect. The length of silk retreats was log-transformed for normality (Shapiro-Wilk test, $p = 0.44$) and to meet the homogeneity of variance assumption (Levene's F test, $p = 0.282$).

Overall occupied retreats were larger than vacant retreats. Retreat size significantly varied between the seasons, increasing in size from summer to spring. The interaction of occupancy and season indicates that in summer occupied and vacant were similar in size whereas in autumn, winter and spring occupied retreats were larger than vacant retreats (Table 1, Fig. 3). The size increment of the silk retreats was analysed separately for newly recorded retreats in 2019. The length of newly built silk retreats in 2019 was log-transformed for normality (Shapiro-Wilk test, $p = 0.40$) and to meet the homogeneity of variance assumption (Levene's F test, $p = 0.382$). As such, the Fisher's ANOVA was used

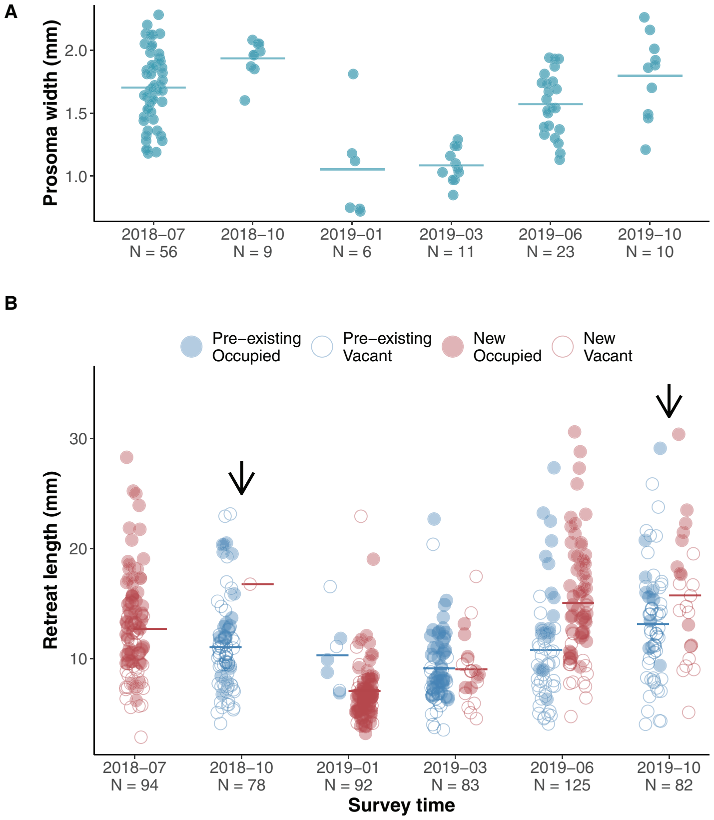


Figure 2 **Phenological size change in spiders and their silk retreats.** (A) Scatterplot of spider size during surveys, horizontal lines indicate means. The first two surveys captured size variation of subadult and adult stages at the end of the 2018 cycle, while 2019 surveys showed a clear increasing pattern as hatchlings developed. (B) Scatterplot of silk retreat size during surveys, horizontal lines indicate means. Within each survey, data points are grouped into pre-existing (blue left-hand clusters) or newly constructed (red right-hand clusters). For the first survey (July 2018), only the newly constructed cluster is shown as we account for no pre-existing retreats. Filled circles (red for newly built, blue for pre-existing) show occupied retreats while empty circles indicate that the retreat was vacant. Arrows indicate the presence of adult spiders during the survey. Full-size DOI: 10.7717/peerj.12839/fig-2

to determine statistically significant differences in retreat size between surveys, F (3, 55.9) = 65.8, $p < 0.001$. The mean size of newly built silk retreats increased continuously during 2019. We used the Tukey Post-hoc test to determine which survey transitions significantly differed in retreat size (Table S3). The size increments were significant between all transitions except for the transition between June and October (2019-06 and 2019-10).

Dynamics of retreat occupancy

Retreat persistence

We recorded a total of 306 silk retreats among the six surveys (two surveys in 2018 and four in 2019). During 2018, we recorded 94 retreats in 2018-07 and only one new retreat in the following survey 2018-10. The persistence of the retreats in between transitions varied

Table 1 **Results of a linear mixed-effects model for the effect of occupancy (vacant or occupied) and season on the size (log length) of the silk retreats of *A. mullion*.**

Mix model-fixed effect omnibus tests

	F	Num df	Den df	*p*
Occupancy	57.01	1	352	<0.001
Season	40.98	3	319	<0.001
Occupancy * Season	5.78	3	335	<0.001

Note:
Satterthwaite method for degrees of freedom.

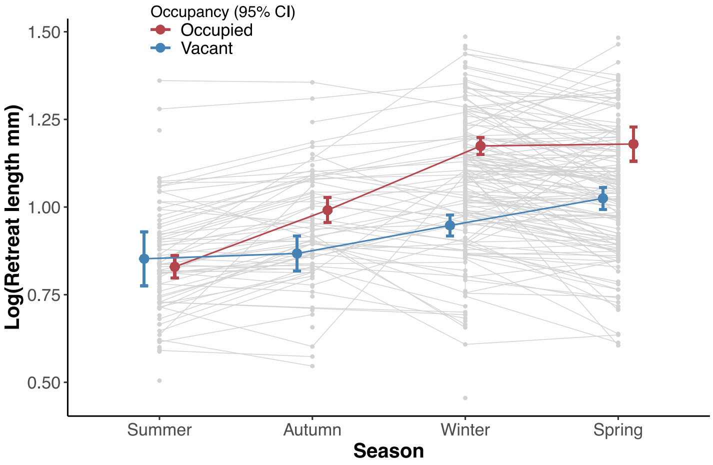


Figure 3 **Effect of the interaction between survey and occupancy status on the retreat size.** Circles denote the estimated mean retreat size (log length) for each factor and error bars are 95% confidence intervals (red colour for occupied and blue for vacant retreats). The light grey circles show the observed values for all retreats at a given season and lines are shown between circles that were recorded in more than one season. Full-size DOI: 10.7717/peerj.12839/fig-3

between 47–82% for all surveys except for the transition between 2018-10 and 2019-01 where persistence was reduced to 8.75%. The disappearance of the silk retreats during this transition coincided with bark shedding by the trees in our study area. During the first survey of the 2019 new phenological cycle (2019-01), we recorded 85 new retreats of which 74.11% persisted to the next survey (2019-03), and 18.18% persisted for the remaining span of the phenological cycle to the end of 2019.

Occupancy transitions

The persistence of an unoccupied silk retreat on the tree trunk allows other *A. mullion* spiders to find and occupy the vacant retreats. Accordingly, we recorded all the possible occupancy status transitions in retreats between surveys (*i.e.*, occupied-vacant, vacant-occupied, occupied-occupied and vacant-vacant). When spiders were pushed away from their retreats (*e.g.*, when inspecting retreats for occupants), some individuals were seen inspecting or entering a different retreat. Further, we found that persistent retreats between surveys were equally likely to increase or decrease in size independently of their occupancy status transition (*e.g.*, remain vacant or occupied and become vacant or occupied, Table S4).

Spectral reflectance

We used spectrometry methods to explore spectral differences between decorated and the highly uncommon undecorated silk retreats of *A. mullion* spiders (Figs. 4A, 4B). The reflectance spectrum of the silk (decorated or undecorated) showed no defined peaks between 300 and 700 nm. The undecorated silk spectra gradually decreased from 47.24% mean reflectance at 300 nm to 36.83% at 700 nm. The decorated silk gradually increased from 20.48% at 300 nm to 40.46% mean reflectance at 700 nm. The greatest difference between decorated and undecorated spectra occurs between 300 and 470 nm where there is no overlap between the reflectance values of the retreat types (decorated and non-decorated) nor the estimated SD (Fig. 4C). No meaningful statistics are included here given the small sample size of the unusual non-decorated silk retreats.

Additional natural history notes

Foraging. *A. mullion* ambushed prey from inside their silk retreats, launching attacks upon visual detection of prey moving nearby. Spiders either fed on their captured prey near their retreats or returned with captured prey to the ambush position inside the retreat when prey size allowed.

Retreat. Upon disturbance either by approaching humans, birds, ants or large bugs, spiders moved inside their silk retreats. *A. mullion* used their forelimbs to flatten and close the entrances of their retreats.

Agonistic interactions. Spiders were observed performing ritualised agonistic displays against conspecifics upon visual detection. Displays included the lateral extension of frontal legs and "twisting" of the opisthosoma. Instances of this behaviour were observed when a spider attempted to enter or approach an occupied retreat. The resident spider usually confronted the intruder by maintaining an aggressive posture near the entrance of the retreat.

Evictions. When a spider wandering the tree trunk encountered a silk retreat, it tapped repeatedly near the openings before attempting to enter. However, when the retreat was occupied, either the resident exited immediately, or the intruding spider entered the retreat before both exited the retreat. Once outside the retreat, both spiders faced each other off as described in "Agonistic interactions". When the intruding spider was substantially larger than the resident, the resident moved away and the intruder took up position in the silk retreat (n = 14).

Males' search for females. As males reached sexual maturity, they were increasingly found wandering the surface of the tree trunks. Males were seen inspecting retreats to ultimately enter and stay in the retreats occupied by females (see below). Both instances where males were accepted or rejected were observed.

Co-occupancy. During spring (the mating season), several retreats were occupied by both a female and a male together. In some instances, each spider occupied one of the entrances in their common hunting position.

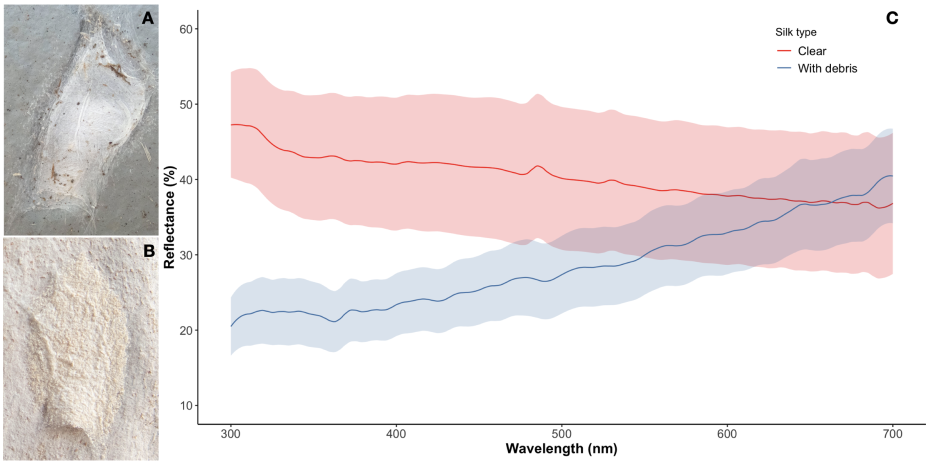


Figure 4 **Difference in appearance and reflectance spectra between decorated and non-decorated silk retreats.** (A) Silk retreat constructed on the side of a concrete water tank. The fine debris is missing while a few relatively large particles are present. (B) The usual decoration of the retreats covers the exposed silk with debris from the surrounding area of the tree trunk. (C) The reflectance curves of the silk retreat samples. The shaded areas denote standard deviations. The curves differ most at shorter wavelengths between 300 and 470 nm where there is no overlap between the mean values reflectance values and the standard deviations. Photo credit: Alfonso Aceves-Aparicio.

Full-size DOI: 10.7717/peerj.12839/fig-4

Egg-laying. Females laid their eggs within a minimal egg-sac inside the silk retreats.

Egg guarding. Occasionally, spiders residing in a retreat with their eggs were seen to detect small ants approaching. They ran to the ants and physically threw them off the tree trunk before returning to their retreats.

DISCUSSION

The aim of our study was to investigate an unusual semi-permanent retreat building behaviour in a jumping spider, a large family of spiders typically associated with a cursorial life style with only ephemeral retreats. By investigating the natural history of *Arasia mullion* we have made three major discoveries: (1) these spiders spent their entire lives on the exposed trunk's surface of a limited range of tree species; (2) they performed most aspects of their natural history in or around the silk retreats they built on the tree trunks' surfaces; and (3) during construction *A. mullion* followed a distinctive decorating behaviour using debris collected from the tree trunk that reduced the retreat's UV silk reflectance. These findings are the first description of silk decorating behaviour in jumping spiders, and highlight the unusual use of permanent silk retreats to exploit a low complexity and highly exposed environment. Our study puts a research lens on tree trunks as understudied but highly intriguing habitats.

Living in exposed environments

Our study shows that unlike most jumping spiders, *A. mullion* is predominantly a sedentary occupant of its silk retreats on tree trunks. Whether and how these spiders move between tree trunks is not yet known. Presumably, the relatively low structural complexity and thus, reduced availability of resources and cover on the trunks limits the prolonged presence of most animals (*Villanueva-Bonilla et al., 2020*). On the other hand, trunks could potentially provide abundant prey given the transit of insects moving between the ground and canopy. The trunks of the trees occupied by *A. mullion* offer little visual cover for the spiders. The surfaces are continuously smooth without contrasting colour patterns or crevices. Such traits pose challenging circumstances for invertebrate mesopredators such as spiders. The reduced complexity of the tree trunk surface makes the spiders vulnerable to visually oriented predators (*Gunnarsson, 1990*; *Villanueva-Bonilla et al., 2020*). Similarly, in this habitat, spiders are also more likely to be detected and avoided by their potential prey. Most animals, including jumping spiders, benefit from complex habitats and backgrounds that reduce conspicuousness (*Merilaita, Lyytinen & Mappes, 2001*). Dense foliage is used by many different spider families to physically hide their presence (*Gunnarsson, 1990*). Similarly, heterogeneous backgrounds can disrupt the visual cues used by potential prey and predators to detect jumping spiders (*Robledo-Ospina et al., 2017*).

Despite the challenges described above, other predators do reside on tree trunks. Some of these residents remain hidden behind bark or inside crevices during the day to emerge and hunt during the nights (*Cloudsley-Thompson, 1995*; *Villanueva-Bonilla et al., 2020*). Among other tree trunk residents, some astounding examples of highly cryptic appearance and posture can be found. The lichen huntsman spider (*Pandercetes gracilis*) and many species of two-tailed spiders (Hersiliidae) strikingly match the colouration patterns of the bark where they are settled. These camouflage attributes are more common in tropical forests where animals benefit from complex bark structures covered with lichen and moss (*Cloudsley-Thompson, 1995*). Unlike other tree trunk residents, *A. mullion* seems to rely on building and occupying a retreat on the surface of the trunks to allow extended trunk inhabitation.

The use of silk retreats

The retreats built by *A. mullion* are persistent structures, unlike the usual overnight silk retreats built by most jumping spiders (*Hallas & Jackson, 1986*; *Richman & Jackson, 1992*; *Jackson & Pollard, 1996*; *Hoefler & Jakob, 2006*). Also, unlike most jumping spiders which are very active hunters, *A. mullion* perform most aspects of their life as sedentary occupants of silk retreats. These spiders were present all year round and mostly found in their silk retreats, rarely seen wandering the surface of the tree trunks (except for adult males presumably searching for females during mating season). This unusual strategy was adopted by hatchlings and continued until maturity where females laid their egg sacs inside the retreats. As spiders grew over time, they not only built new, larger retreats but engaged in dynamic patterns of retreat occupancy, repair and defence. As retreats can potentially outlive any spider, abandoned silk retreats were re-occupied by spiders at any given time. Although these observations are limited in that we cannot estimate the number of spiders moving between silk retreats due to the lack of individual spider tracking, we inferred high dynamism of retreat occupancy from the observed natural history events.

Aceves-Aparicio et al. (2018) recorded similar patterns of silk structure reuse by spiders other than the builder during the dispersal stage of a subsocial spider, suggesting that the abandoned three-dimensional webs were used as stepping stones by males and females while new space was colonised. Additionally, the retreats of *A. mullion* were not only re-occupied at different times but were equally likely to increase or decrease in size. This indicates that spiders were actively repairing or expanding pre-existing silk structures on the tree trunks. This is similar to beavers, which constantly repair their dams to maintain the suitability of the safe space for protection and inhabitation (Andersen & Shafroth, 2010). At a much smaller scale, *A. mullion* dynamically occupied and repaired the available retreats in their landscape. It is likely that the construction of, and sedentary life in, the retreats counteract the lack of cover on these smooth tree trunks. Thus, each silk retreat would hold high value for the spiders as these seem more suitable spaces for them than any open space on the trunk's surface.

A novel method of retreat decoration

The construction behaviour of *A. mullion* is a key element to its unusual natural history. Although many jumping spider species build retreats similar in shape to those made by *A. mullion*, these are usually short-lived structures, hidden from sight on the underside of leaves, beneath rocks or behind bark (Hoefler & Jakob, 2006; Hill et al., 2019). These silk retreats serve as temporary resting sites or protective structures for egg sacs (Foelix, 2010). Due to the exposed nature of tree trunks, building a retreat that is hidden from view is not possible. We argue that decorating the retreat with the debris is a strategy to reduce the visibility of the bright silk. The debris is collected from close to the retreat position and serves to match the appearance of the retreat to that of its background, at least to a human observer. This scraping behaviour is reminiscent to other animals that utilise environmental material for camouflage. For example, grounds nesting birds also camouflage their eggs with soil they collect from immediate surroundings of the nest (Mayani-Parás et al., 2015).

Decorating behaviour among non-human animals has been primarily studied in aquatic species (Ruxton & Stevens, 2015). For example, decorator crabs collect elements from the environment to cover themselves, likely gaining physical protection and reducing detection by predators (Hultgren & Stachowicz, 2009; Ruxton & Stevens, 2015). Similar patterns have been documented for other aquatic fauna such as sea urchins, brachyuran, hermit crabs, and caddisfly larvae (Ross, 1971; Wicksten, 1986; Otto, 2000; Dumont et al., 2007). Comparable uses of external materials for decoration have been explored for terrestrial animals, mostly among larvae of several insect species (Nakahira & Arakawa, 2006; Jackson & Pollard, 2007; Khan, 2020). Spider species across several families have evolved setal microstructures that render them cryptic (Duncan, Autumn & Binford, 2007; Gawryszewski, 2014) by retaining debris in the case of *Stephanopis* (Thomisidae) and sand particles in *Sicarius* (Sicariidae) and *Homalonychus* (Homalonychidae) genera. In all these instances, the decorations are added to the animal's body. The use of decorations has also been recorded on the silk snares of some spider species (Herberstein et al., 2001). *Cyclosa* spiders decorate their webs with debris such as prey remains. By sitting within the decorations, the spiders successfully deflected attacks from avian predators in experimental laboratory trials (*Ma et al., 2020*). However, decorations among jumping spiders were previously unknown and remain generally unexplored among structures built by other animals (*Hansell, 2005*; *Stevens & Ruxton, 2019*).

The two main functions of constructions among animals are as protective retreats or as traps used by predatory species. Retreats protect against physical (temperature, humidity, rainfall) or biological hazards (predation or parasitism), while traps facilitate foraging by detecting, slowing or restraining potential prey (*Hansell, 2005*). Whether either of these constructions is actively decorated to reduce detection or recognition by unwanted observers has different implications. By definition, traps should not be detected or recognised by the intended target, thus these are commonly highly inconspicuous. On the other hand, the decoration of homes (retreats, nests or burrows) for protection has often been suggested but commonly lacks evidence (*Ruxton & Stevens, 2015*). Splitting these two functions is often problematic among spiders as their silk snares might act simultaneously as a retreat and as a trap. The retreat of *A. mullion* itself is not a trap, but it could contribute to the spider's hunting strategy by reducing its exposure to potential prey. Our study shows that the hunting strategy and virtually every behavioural trait is closely related to its decorated silk home, thus adding to the scarce evidence of the active hiding of animal-built structures.

As decorations were always present in the silk retreats, it is likely that these provide significant advantages over non-decorated silk in this habitat. The behaviour of *A. mullion* showed close dependence on its decorated retreat for both predator and defence strategies. The spiders waited for prey to approach them while remaining partially covered by the silk retreat. When the potential prey escaped these attacks, the spiders quickly returned to cover within the retreats and re-settled for further capture attempts. At the same time, when approached by potential threats, the spiders moved inside the silk retreats.

The comparison between non-decorated and decorated silk retreats gives us insights into how the debris cover might affect visibility. Spider silk visibility is a common constraint on silk structures in both foraging and anti-predator contexts. A web should be either attractive or not visible to the targeted prey, while to avoid predation it should be invisible or even act as a deterrent (*Zschokke, 2002*). How silk is perceived by predators and prey depends on their respective visual systems. Insects, lizards and birds are ecologically relevant observers of spider webs and can perceive light in the ultraviolet (UV) spectrum (*Blackledge & Wenzel, 2000*). Thus, if the debris reduced the overall reflectance of UV, it might also reduce the overall visibility of the silk retreats on the tree trunks. However, this remains to be explored as our study has not attempted to assess how *A. mullion* and their retreats are visually perceived. Further studies should especially consider visual systems with the capacity to detect UV light reflectance.

Alternative functions of external materials used in silk webs have been explored in multiple systems (*Herberstein et al., 2001*). A strengthening function has been suggested for the silk decorations added to orb webs to make these more stable (*Robinson & Robinson, 1970*). However, evidence is inconclusive and requires further study

(*Herberstein et al., 2001*). For *A. mullion*, strengthening might not be required for stabilisation but for direct deflection of attacks upon contact with intruders (other spiders) or predators. However, our observations have not identified potential predators of these spiders or their interaction with the silk retreats. The thermoregulation function of disc-shaped decorations in orb webs was tested in high-temperature environments and under direct exposure to sunlight. Juvenile *Neogea* spiders reduced their body temperature by moving behind the shadow produced by the silk disc (*Humphreys, 1992*). The silk retreats of *A. mullion* might be protected from direct sunlight for most of the day below the canopy. Exploratory measurements of the temperature inside and outside empty silk retreats under direct sunlight exposure did not reveal significant differences (unpublished data, Aceves-Aparicio). However, further exploration of temperature control might be pertinent considering the spiders and their manipulation of the silk retreat openings.

Researchers regularly discover novel and exceptional natural histories among jumping spiders, such as vegetarianism, blood-feeding, and sophisticated trial-and-error signalling behaviours (*Jackson & Wilcox, 1998*; *Jackson, Nelson & Sune, 2005*; *Meehan et al., 2009*). Our study of the natural history of *A. mullion* reveals a novel behavioural strategy on tree trunks. The construction of permanent retreats that are decorated with debris likely enables hunting of prey and hiding from predators in a highly exposed environment. Hence, these spiders engineer their own exclusive niche in a challenging habitat.
The strategy of *A. mullion* is unusual amongst jumping spiders, or indeed many animals that build retreats. Thus, this system provides a novel avenue to approach and bridge studies regarding the functions of animal constructions and concealment strategies.

CONCLUSIONS

In this study we have made fascinating observations that to our knowledge are unique among jumping spiders. Most other species of jumping spiders are itinerants on the surface of tree trunks, however the prolonged occupancy of *A. mullion* seems to provide benefits. The exploitation of tree trunks as a foraging arena is advantageous as tree trunks can concentrate insect traffic. We hypothesise that active search for prey on tree trunks is enhanced by hunting from a silk retreat, which would also protect the occupant from predators and unfavourable environmental conditions. *Arasia mullion* spends its entire life-cycle in these semi-permanent silk retreats. Thus, *A mullion* spiders behave like sit and wait predators, unlike most jumping spiders. We also discovered a novel decoration behaviour that may facilitate the exploitation of a highly exposed and challenging habitat–the tree trunk. The debris decorations applied to the silk retreats not only appear to match the tree trunk (at least to human observers) but also greatly reduce the UV reflectance of the silk.

Further studies are required to explore the effect of tree trunk variation on the appearance of the silk retreats and how this might affect detection by visually oriented prey and predators. Similarly, possible sources for trade-offs of this strategy are yet to be identified.

Diversity and inclusion statement

We unreservedly support equity, diversity and inclusion in science (*Rößler, Lotters & Da Fonte, 2020*). The authors come from different countries (Mexico, Germany, Austria and Australia) and represent different career stages (undergraduate student, PhD student, early career researcher to professor). One or more of the authors self-identifies as a member of the LGBTQI+ community. While citing references scientifically relevant for this work, we actively worked to promote gender balance in our reference list. We ensured sex balance in the selection of non-human subjects as we sampled both male and the female spiders.

ACKNOWLEDGEMENTS

We acknowledge the *Wallumattagal clan of the Dharug nation* as the traditional custodians of the Macquarie University land. We are grateful to Liliana Cadavid Florez for her assistance during spectral measurements and to Lizzy Lowe and Thomas White for their constructive and thoughtful comments. We thank two anonymous reviewers for their helpful and constructive comments.

ADDITIONAL INFORMATION AND DECLARATIONS

Funding

Alfonso Aceves-Aparicio was supported by a Cotutelle international Macquarie University Research Excellence Scholarship (CTiMQRES). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Grant Disclosures

The following grant information was disclosed by the authors:
Cotutelle international Macquarie University Research Excellence Scholarship.

Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Alfonso Aceves-Aparicio conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Donald James McLean conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Zoe Wild performed the experiments, analyzed the data, authored or reviewed drafts of the paper, and approved the final draft.
- Jutta M. Schneider conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

- Marie E. Herberstein conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The code and necessary data files to reproduce the results and figures are available on GitHub and Zenodo:

-https://github.com/PonchoAceves/Blankie-natural-history

-PonchoAceves. (2021). PonchoAceves/Blankie-natural-history: Submission (1.0). Zenodo. https://doi.org/10.5281/zenodo.4765276.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.12839#supplemental-information.

REFERENCES

Aceves-Aparicio A, Tapia-McClung H, Macías-Ordóñez R, Rao D. 2018. Subsocial spiders in space and time: a fine scale approach to the dynamics of dispersal. *Ethology* **124(7)**:458–467 DOI 10.1111/eth.12749.

Aguilar-Argüello S, Gerhard D, Nelson XJ. 2019. Risk assessment and the use of novel shortcuts in spatial detouring tasks in jumping spiders. *Behavioral Ecology* **30(5)**:1488–1498 DOI 10.1093/beheco/arz105.

Andersen DC, Shafroth PB. 2010. Beaver dams, hydrological thresholds, and controlled floods as a management tool in a desert riverine ecosystem, Bill Williams River, Arizona. *Ecohydrology* **3(3)**:325–338 DOI 10.1002/eco.113.

Blackledge TA, Wenzel JW. 2000. The evolution of cryptic spider silk: a behavioral test. *Behavioral Ecology* **11(2)**:142–145 DOI 10.1093/beheco/11.2.142.

Cloudsley-Thompson JL. 1995. A review of the anti-predator devices of spiders. *Bulletin of the British Arachnological Society* **10**:81–96.

Coddington J, Valerio CG. 1980. Observations on the web and behavior of *Wendilgarda* spiders (Araneae: Theridiosomatidae). *Psyche: A Journal of Entomology* **87(1–2)**:93–105 DOI 10.1155/1980/69153.

Cronin TW, Johnsen S, Marshall NJ, Warrant EJ. 2014. *Visual ecology*. Princeton: Princeton University Press.

Cumming MS, Wesołowska W. 2004. Habitat separation in a species-rich assemblage of jumping spiders (Araneae: Salticidae) in a suburban study site in Zimbabwe. *Journal of Zoology* **262(1)**:1–10 DOI 10.1017/s0952836903004461.

Dawkins R. 1982. *The extended phenotype*. Oxford: Oxford University Press.

Dumont CP, Drolet D, Deschênes I, Himmelman JH. 2007. Multiple factors explain the covering behaviour in the green sea urchin, *Strongylocentrotus droebachiensis*. *Animal Behaviour* **73(6)**:979–986 DOI 10.1016/j.anbehav.2006.11.008.

Duncan RP, Autumn K, Binford GJ. 2007. Convergent setal morphology in sand-covering spiders suggests a design principle for particle capture. *Proceedings of the Royal Society B: Biological Sciences* **274(1629)**:3049–3057 DOI 10.1098/rspb.2007.1039.

Eberhard WG, Agnarsson I, Levi HW. 2008. Web forms and the phylogeny of theridiid spiders (Araneae: Theridiidae): chaos from order. *Systematics and Biodiversity* **6(4)**:415–475 DOI 10.1017/s1477200008002855.

Foelix R. 2010. *Biology of spiders*. Oxford: Oxford University Press.

Gawryszewski FM. 2014. Evidence suggests that modified setae of the crab spiders *Stephanopis* spp. fasten debris from the background. *Zoomorphology* **133(2)**:205–215 DOI 10.1007/s00435-013-0213-4.

Gigliotti LC, Slotow R, Hunter LT, Fattebert J, Sholto-Douglas C, Jachowski DS. 2020. Habitat complexity and lifetime predation risk influence mesopredator survival in a multi-predator system. *Scientific Reports* **10**:1–10 DOI 10.1038/s41598-020-73318-3.

Gregorič M, Agnarsson I, Blackledge TA, Kuntner M. 2011. How did the spider cross the river? Behavioral adaptations for river-bridging webs in *Caerostris darwini* (Araneae: Araneidae). *PLOS ONE* **6(10)**:e26847 DOI 10.1371/journal.pone.0026847.

Gunnarsson B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. *The Journal of Animal Ecology* **59(2)**:743 DOI 10.2307/4892.

Hallas SEA, Jackson RR. 1986. Prey-holding abilities of the nests and webs of jumping spiders (Araneae, Salticidae). *Journal of Natural History* **20(4)**:881–894 DOI 10.1080/00222938600770651.

Hansell MH. 2005. *Animal architecture*. Oxford: Oxford University Press on Demand.

Herberstein ME. 2011. *Spider behaviour: flexibility and versatility*. Cambridge: Cambridge University Press.

Herberstein ME, Craig CL, Coddington JA, Elgar MA. 2001. The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biological Reviews* **75(4)**:649–669 DOI 10.1111/j.1469-185X.2000.tb00056.x.

Hill DE, Abhijith A, Krishna P, Ramesh S. 2019. Construction of orb webs as nocturnal retreats by jumping spiders (Araneae: Salticidae: cf. Anarrhotus) in southwestern India. *Peckhamia* **182(1)**:1–10.

Hill DE, Richman DB. 2011. The evolution of jumping spiders (Araneae: Salticidae): a review. *Peckhamia* **75**:1–7.

Hoefler CD, Jakob EM. 2006. Jumping spiders in space: movement patterns, nest site fidelity and the use of beacons. *Animal Behaviour* **71(1)**:109–116 DOI 10.1016/j.anbehav.2005.03.033.

Hultgren KM, Stachowicz JJ. 2009. Evolution of decoration in majoid crabs: a comparative phylogenetic analysis of the role of body size and alternative defensive strategies. *The American Naturalist* **173(5)**:566–578 DOI 10.1086/597797.

Humphreys W. 1992. Stabilimenta as parasols: shade construction by *Neogea* sp.(Araneae: Araneidae, Argiopinae) and its thermal behaviour. *Bulletin of the British Arachnological Society* **9**:47–52.

Jackson RR, Blest AD. 1982. The biology of *Portia fimbriata*, a web-building jumping spider (Araneae, Salticidae) from Queensland: utilisation of webs and predatory versatility. *Journal of Zoology* **196(2)**:255–293 DOI 10.1111/j.1469-7998.1982.tb03504.x.

Jackson RR, Nelson XJ, Sune GO. 2005. A spider that feeds indirectly on vertebrate blood by choosing female mosquitoes as prey. *Proceedings of the National Academy of Sciences of the United States of America* **102(42)**:15155–15160 DOI 10.1073/pnas.0507398102.

Jackson RR, Pollard SD. 1996. Predatory behavior of jumping spiders. *Annual Review of Entomology* **41(1)**:287–308 DOI 10.1146/annurev.en.41.010196.001443.

Jackson RR, Pollard SD. 2007. Bugs with backpacks deter vision-guided predation by jumping spiders. *Journal of Zoology* **273(4)**:358–363 DOI 10.1111/j.1469-7998.2007.00335.x.

Jackson RR, Wilcox RS. 1998. Spider-eating spiders: despite the small size of their brain, jumping spiders in the genus *Portia* outwit other spiders with hunting techniques that include trial and error. *American Scientist* **86**:350–357.

Khan MK. 2020. Bagworm decorations are an anti-predatory structure. *Ecological Entomology* **45**:924–928 DOI 10.1111/een.12876.

Langellotto GA, Denno RF. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* **139(1)**:1–10 DOI 10.1007/s00442-004-1497-3.

Lubin YD, Henschel JR. 1990. Foraging at the thermal limit: burrowing spiders (*Seothyra*, Eresidae) in the Namib desert dunes. *Oecologia* **84(4)**:461–467 DOI 10.1007/bf00328161.

Ma N, Yu L, Gong D, Hua Z, Zeng H, Chen L, Mao A, Chen Z, Cai R, Ma Y, Zhang Z, Li D, Luo J, Zhang S. 2020. Detritus decorations as the extended phenotype deflect avian predator attack in an orb-web spider. *Functional Ecology* **34(10)**:2110–2119 DOI 10.1111/1365-2435.13636.

Maia R, Gruson H, Endler JA, White TE. 2019. pavo 2: new tools for the spectral and spatial analysis of colour in r. *Methods in Ecology and Evolution* **10(7)**:1097–1107 DOI 10.1111/2041-210x.13174.

Mayani-Parás F, Kilner RM, Stoddard MC, Rodríguez C, Drummond H. 2015. Behaviorally induced camouflage: a new mechanism of avian egg protection. *American Naturalist* **186**:E91–E97 DOI 10.1086/682579.

Meehan CJ, Olson EJ, Reudink MW, Kyser TK, Curry RL. 2009. Herbivory in a spider through exploitation of an ant–plant mutualism. *Current Biology* **19**:892–893 DOI 10.1016/j.cub.2009.08.049.

Merilaita S, Lyytinen A, Mappes J. 2001. Selection for cryptic coloration in a visually heterogeneous habitat. *Proceedings of the Royal Society B Biological Sciences* **268**:1925–1929 DOI 10.1098/rspb.2001.1747.

Nakahira K, Arakawa R. 2006. Defensive functions of the trash-package of a green lacewing, *Mallada desjardinsi* (Neuroptera: Chrysopidae), against a ladybird, *Harmonia axyridis* (Coleoptera: Coccinellidae). *Applied Entomology and Zoology* **41**:111–115 DOI 10.1303/aez.2006.111.

Nentwig W. 1985. Social spiders catch larger prey: a study of *Anelosimus eximius* (Araneae: Theridiidae). *Behavioral Ecology and Sociobiology* **17**:79–85 DOI 10.1007/bf00299433.

Otto C. 2000. Cost and benefit from shield cases in caddis larvae. *Hydrobiologia* **436**:35–40 DOI 10.1023/a:1026589602313.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. *Available at https://www.R-project.org/*.

Richman DB, Jackson RR. 1992. A review of the ethology of jumping spiders (Araneae, Salticidae). *Bulletin of the British Arachnological Society* **9**:33–37.

Robinson MH, Robinson B. 1970. The stabilimentum of the orb web spider, *Argiope argentata*: an improbable defence against predators. *Canadian Entomologist* **102**:641–655 DOI 10.4039/Ent102641-6.

Robledo-Ospina LE, Escobar-Sarria F, Troscianko J, Rao D. 2017. Two ways to hide: predator and prey perspectives of disruptive coloration and background matching in jumping spiders. *Biological Journal of the Linnean Society* **122(4)**:752–764 DOI 10.1093/biolinnean/blx108.

Ross DM. 1971. Protection of hermit crabs (*Dardanus* spp.) from octopus by commensal sea anemones (*Calliactis* spp.). *Nature* **230(5293)**:401–402 DOI 10.1038/230401a0.

Ruxton GD, Stevens M. 2015. The evolutionary ecology of decorating behaviour. *Biology Letters* **11(6)**:20150325 DOI 10.1098/rsbl.2015.0325.

Rößler DC, Lotters S, Da Fonte LFM. 2020. Author declaration: have you considered equity, diversity and inclusion? *Nature* **584**:525–525 DOI 10.1038/d41586-020-02429-8.

Schneider CA, Rasband WS, Eliceiri KW. 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods* **9(7)**:671–675 DOI 10.1038/nmeth.2089.

Seymour RS, Hetz SK. 2011. The diving bell and the spider: the physical gill of *Argyroneta aquatica*. *Journal of Experimental Biology* **214(13)**:2175–2181 DOI 10.1242/jeb.056093.

Stevens M, Ruxton GD. 2019. The key role of behaviour in animal camouflage. *Biological Reviews* **94**:116–134 DOI 10.1111/brv.12438.

Thirunavukarasu P, Nicolson M, Elgar MA. 1996. Leaf selection by the leaf-curling spider *Phonognatha graeffei* (Keyserling) (Araneoidea: Araneae). *Bulletin of the British Arachnological Society* **10**:187–189.

Villanueva-Bonilla GA, Messas YF, Souza HS, Gonzaga MO, Brescovit AD, Vasconcellos-Neto J. 2020. Trunk structural complexity determines the diversity of bark-dwelling spiders in a tropical forest. *Ethology Ecology & Evolution* **33**:1–17 DOI 10.1080/03949370.2020.1830860.

Wicksten MK. 1986. Carrying behavior in brachyuran crabs. *Journal of Crustacean Biology* **6**:364 DOI 10.2307/1548176.

Wolff JO, Wierucka K, Uhl G, Herberstein ME. 2021. Building behavior does not drive rates of phenotypic evolution in spiders. *Proceedings of the National Academy of Sciences of the United States of America* **118(33)**:e2102693118 DOI 10.1073/pnas.2102693118.

World Spider Catalog. 2021. World spider catalog. Version 22.0. Natural History Museum Bern. *Available at http://wsc.nmbe.ch* (accessed 14 May 2021).

Zabka M. 2002. Salticidae (Arachnida: Araneae) from the oriental, Australian and Pacific regions, XV. New species of Astieae from Australia. *Records of the Australian Museum* **54(3)**:257–268 DOI 10.3853/j.0067-1975.54.2002.1365.

Zschokke S. 2002. Ultraviolet reflectance of spiders and their webs. *Journal of Arachnology* **30(2)**:246–254 DOI 10.1636/0161-8202(2002)030[0246:UROSAW]2.0.CO;2.

Chapter 3 - Decorated silk structures reduce the conspicuousness of unusual tree trunk resident spiders

Introduction

Decorative behaviour has been documented in different non-human species among both aquatic and terrestrial habitats (Ruxton & Stevens, 2015). Decorating by collecting environmental elements and placing them on their own bodies often provides animals with physical protection and may reduce detection by predators. For example, decorative crabs can visually conceal themselves with environmental materials and also repel predator attacks after detection by using pieces of chemically defended plants as decoration (Stachowicz & Hay, 1999; Hultgren & Stachowicz, 2008; Ruxton & Stevens, 2015). The bagworm *Eumeta crameri* carries portable shields that not only reduce the probability of attacks by the Asian ant weaver *Oecophylla smaragdina* upon contact but the shield also withstands the attacks protecting the bagworm inside (Khan, 2020).

Animals might also decorate built structures such as their homes (burrows and retreats), traps or displays. Of these three types of built structures, displays are the least frequently recorded function but have been described in detail in some well-known examples, such as the bowerbird's hut that functions as a courtship display. The birds collect natural and artificial items that they sort by type and colour to attract females to their bower (Madden, 2003; Larrivée & Buddle, 2010). Other built structures act as traps for prey. Functionally, traps should be inconspicuous to the intended prey target and decorations often disguise the presence of the trap, such is the case in some spider webs (Herberstein et al., 2000). Finally, homes, such as retreats and burrows, protect the occupants from environmental or biotic hazards (Hansell & Hansell, 2005) but despite being often suggested (Hansell, 1996), the validation of active decoration of homes is scarce (Stevens & Ruxton, 2019). For example, to the human eye, many bird nests resemble the surrounding vegetation, but this could be the result of the availability of materials in the environment (Bailey et al., 2015). Furthermore, without explicit testing, bird nests might still be detectable by viewers with different visual systems (Kemp et al., 2015). While the survival benefits of self-decoration have been established in a number of key species, the selective benefit of decorating built structures is not broadly established (Ruxton & Stevens, 2015).

Spiders produce diverse types of silk that can serve very different functions (Herberstein, 2011). Best known are the silken capture webs but silk is also used as protection for the eggs and for the building of retreats. In some instances, the capture web and the retreat are combined. Web-building spiders are also known to decorate their webs with environmental materials such as debris and prey carcasses or with silk elements (Herberstein et al., 2000).

Silk decorations in the webs of *Argiope* species are very conspicuous, consisting of large zig-zag bands in the centre of the orb-web. A rich body of literature exists on the function of these web decorations (Herberstein et al., 2000; Walter & Elgar, 2011, 2012). The fact that the silk reflects UV light suggests that one function is to attract flying prey (Herberstein et al., 2000; Théry & Casas, 2009). Other spiders decorate their webs with detritus (e.g. prey carcasses, moults and small leaf pieces). Such objects in the webs of *Cyclosa* spiders, for example, deflect the attacks from avian predators away from the spider body to the debris (Ma et al., 2020). Non-web building spiders, such as nursery, wolf or jumping spiders do not use silk to capture prey but to build protective structures for their eggs and young and in the case of jumping spiders as overnight or short-term retreats.

Recently we described for the first time, the building and decoration of silk retreats placed on the exposed surface of tree trunks by the jumping spider *Arasia mullion*. These spiders are sedentary inhabitants of the trunks from a narrow range of tree species, all characterised by a smooth bark resulting in a highly exposed habitat (Chapter 2). There, the spiders build silk retreats incorporating debris that they scratch from the surface of the trunks. The result is a silk sheet that appears to match the appearance of the tree trunk section that they occupy (at least to the human eye). Here, we test the hypothesis that the decorated silk retreats render the retreat less visible to potential prey and predators thereby providing beneficial defence and attack functions to the spiders. if the main function of the retreat decoration is camouflage, we expect increased prey encounters, and reduced predator encounters. The predictions from a camouflage hypothesis are that the decorated silk retreats reduce the conspicuousness of the silk as well as that of the spider within the retreat through the eyes of their (i) predators and (ii) their prey. To test these predictions, we first used spectrometry techniques to model the visual contrast of both the spiders and their silk retreats against the tree trunks they inhabit for potential prey and predator. Second, we conducted a field experiment to assess the impact of retreat visibility on approach rates by potential prey.

Methods

Study species and site

Arasia mullion Zabka, 2002 are small jumping spiders (Salticidae) to date only recorded in New South Wales (Zabka, 2002). The life history and phenology have recently been described (see Chapter 2). This study was conducted on the Macquarie University campus (Macquarie Park, NSW, Australia). Spectral data and videos were recorded in August and September 2019 respectively.

Spectral measurements

In order to assess the conspicuousness of the spiders and their retreats for ecologically relevant observers, we used reflectance spectra measurements. A complete set for discriminability comparisons was collected for an individual spider (prosoma and opisthosoma), the retreat it was occupying when collected and the area surrounding the retreat on the tree trunk surface (i.e., 1 cm radius from the silk retreat edge). We recorded a total of 24 comparison sets (= 24 individual spiders). We also included an unusual sample of non-decorated silk (retreats lacking the debris that covers retreats on trees). These samples were collected from a small group of spiders living on a concrete water tank (see details in chapter 2). Therefore, we were able to assess differences in silk reflectance due to the decorative debris.

Spectral data

The reflectance spectra measurements were obtained using a Jazz Ocean Optics spectrophotometer (Ocean Optics, Largo, FL, U.S.A.) with the following settings: integration time = 40 ms, boxcar width = 10, averaged scans = 10. We used a PX-2 pulse xenon light source and all measurements were relative to a white standard WS-1. The light source and probe were set at a 45 degrees angle. The spectral measurements for the retreats and tree trunk areas were taken on-site minimising environmental light as much as possible using a black velvet cloth to block incident light and the probe holder to keep a uniform 2mm distance for all samples. Spiders were collected from the trees and anaesthetized with CO_2 in the laboratory. Spectral measurements were then performed in the same way as for the previous sample types. The reflectance spectra were measured between 300 nm and 700 nm and averaged from three measurements.

Three sample measurements were taken for each individual subject. For the spiders, the light beam of the spectrophotometer was directed towards the centre area of the prosoma and opisthosoma. For the silk retreat, towards three points across the area covered with silk. And for the tree trunk, three points were haphazardly selected around the edge of the retreat within a 1cm radius.

Visual modelling

We used known spectral sensitivities for the photoreceptors of two classes of potential predators and one prey (Xavier et al., 2018; Ximenes & Gawryszewski, 2019). Birds and wasps have been recorded as important predators of spiders, while dipterans are common prey for many spider species. Among these groups, several species have the ability to perceive light in the UV part of the spectrum. Here we selected the known visual systems of two classes of potential predators and one prey. We used the blue tit *Cyanistes caeruleus* (as a proxy visual system for local bird predators) and the honeybee *Apis mellifera* (proxy to wasp vision) as models for potential predators of *A. mullion* spiders, and the fruit fly (proxy to potential prey vision). These visual systems have been studied in great detail and are common models for the study of visual perception.

For each of the measured patches in the silk retreats, the spiders and the tree backgrounds we calculated absolute quantum cone catch values with the chosen visual systems. Then we calculated the chromatic and achromatic contrasts of the silk retreats and the spiders against the tree trunk backgrounds to assess their overall conspicuousness to the potential observers using the receptor-noise limited model (Vorobyev & Osorio, 1998). This widely used method uses Weber fractions, a measure of signal-to-noise ratio in the physiological visual pathway of an animal, to assess the degree of discriminability between colours. We included in our analyses the standard day light D65 illuminant and the Von Kries transformation to account for the influence of the background in the discriminability assessment of this system (Maia et al., 2019).

The degree of discriminability between samples (ΔS) was modelled using "Just Noticeable Differences" (JND) units. A threshold varying from 1 to 3 JND units is commonly set to determine whether a given observer can discriminate between two different colours, values below the selected threshold are assumed to be indistinguishable (Drewniak et al., 2020; Brunton-Martin et al., 2021). Prior to our contrast analyses of colour (dS) and luminance (dL) we tested whether the colour samples from each subject type are statistically different from each other by performing a permutational multivariate analysis of variance (PERMANOVA). We followed up on this pipeline as recommended by Maia and White (2018) to better assess if colour contrasts are perceivable under meaningful biological contexts.

Field experiment

We further used video recordings to assess potential differences in the frequencies of insects approaching either an empty silk retreat, a hunting spider (spider partly covered by the silk retreat), and an exposed spider on the surface of the tree trunks. With this design we aimed to compare the function of the retreats and decoration against a hypothetical wandering individual or ancestral form that does not rely on the camouflage retreat.

A GoPro 7 camera was set on a tripod in front of a tree trunk with one of the following three subjects centred in the frame. First, empty silk retreats were found and inspected to confirm that no spider was inside before each recording (n = 8). Second, we located active hunting spiders and carefully set up the camera rig to avoid disturbance prior to the start of each video (n = 6). Finally, we collected spiders from a different set of silk retreats and anaesthetised them with CO_2. We then temporarily fixed this spider to the tree trunk with a small drop of non-toxic glue placed on the ventral side of its prosoma and recorded as exposed individuals (n = 7). At the end of the recording, we were able to free the spider from the glue and release it unharmed (but for one spider that was eaten by an ant). All spiders were subadult females. Each subject was recorded for approximately

1 hour. The videos were recorded throughout 7 days (2-4 October 2019 and 15-18 October 2019) between 9am and 12pm.

Results

Reflectance spectra

The spectral reflectances averaged for 24 silk retreats and tree trunk surfaces showed significant overlap in the 300 to 700 nm wavelength range. While the spiders (n = 24 for both prosoma and opisthosoma) did not overlap with either the tree trunk surface or the decorated silk retreat (Figure 1). Additionally, the average reflectance curve of the clear (non-decorated) silk (n = 5) differed the most from the decorated silk retreats and the tree trunk, particularly in the short wavelengths (300 - 450 nm).

Under the colour contrast discriminability comparisons, the decorated retreats are likely inconspicuous against the tree trunk surface with consistent values below 1 JND for every potential observer (bird, wasp, fly; Figure 2). Contrarily, the colour contrast of the spiders and the undecorated silk was consistently higher and above the discrimination threshold of 1 JND for all viewers. Achromatic discriminability showed that the decorated silk retreats varied within 1 and 3 JNDs for all observers while the spiders and the undecorated silk were significantly higher (Table 1).

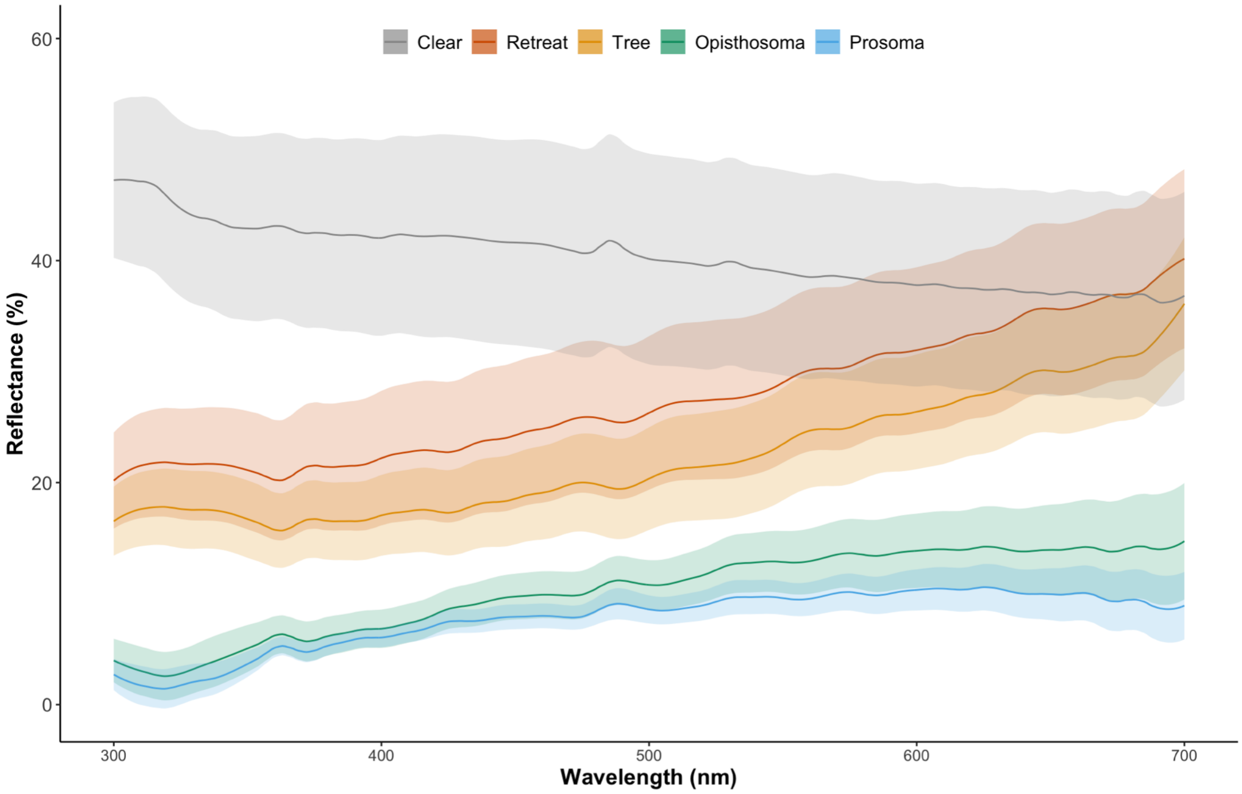
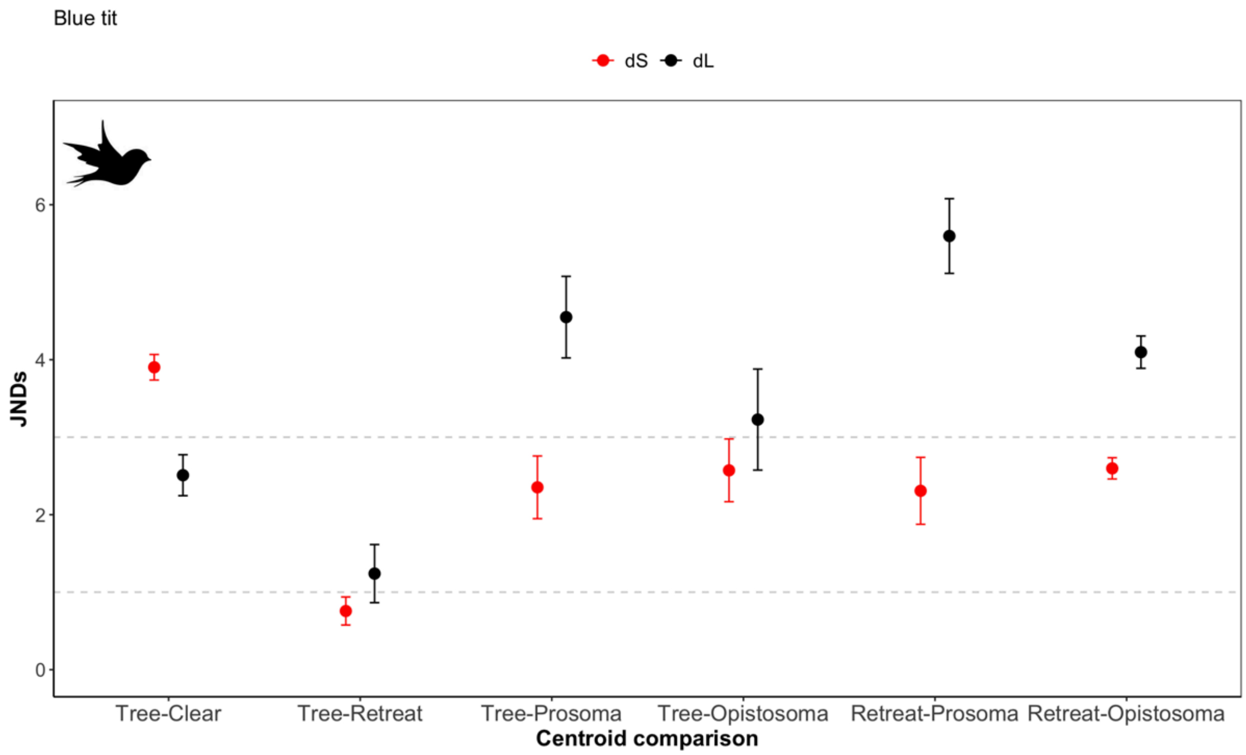
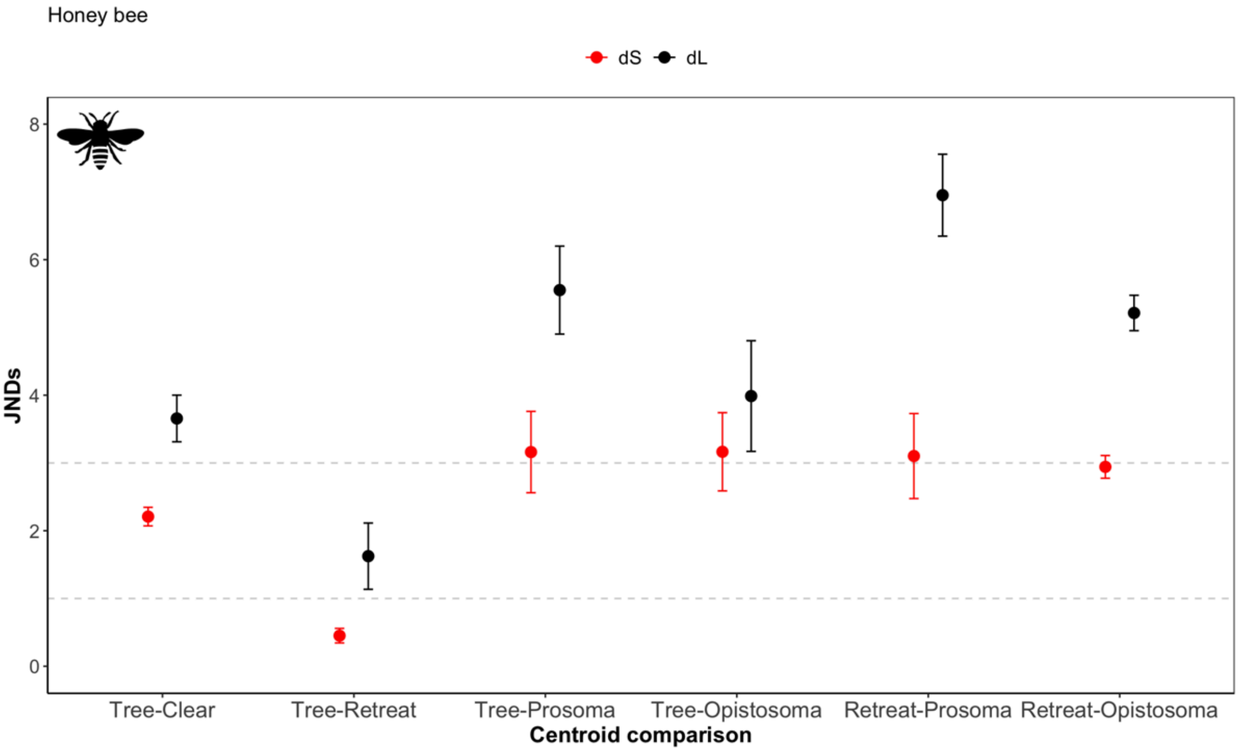


Figure 1. Mean reflectance spectra and standard deviation (shaded area) of non-decorated silk retreats (grey), decorated retreats (orange), the tree trunk surfaces (yellow), the spiders' opisthosoma (green) and the spiders' prosoma (blue).




Honey bee
dS
dL
JNDs
0
2
4
6
8
Tree-Clear
Tree-Retreat
Tree-Prosoma
Tree-Opistosoma
Retreat-Prosoma
Retreat-Opistosoma
Centroid comparison

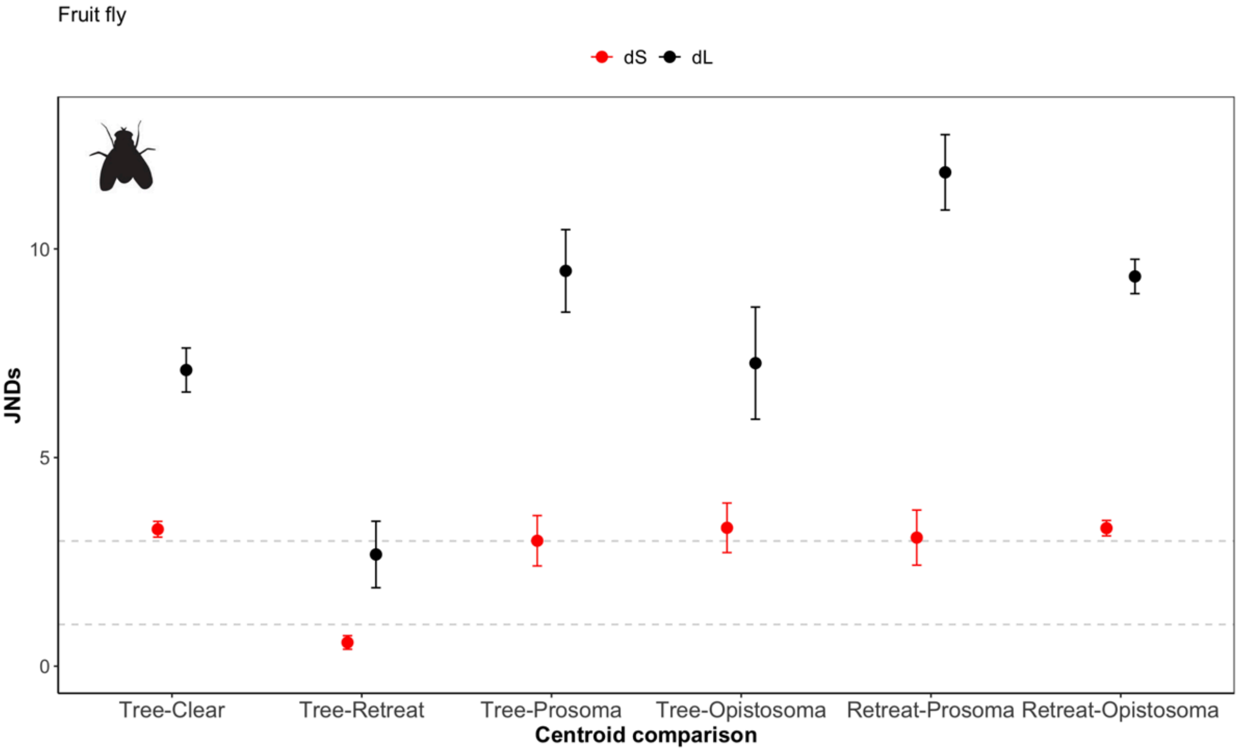

Fruit fly
dS
dL
JNDs
0
5
10
Tree-Clear
Tree-Retreat
Tree-Prosoma
Tree-Opistosoma
Retreat-Prosoma
Retreat-Opistosoma
Centroid comparison

Figure 2. Chromatic (red) and achromatic (black) contrasts between, non-decorated retreats (clear), decorated retreats, tree trunks and two spider body parts (prosoma and opisthosoma). Contrasts were calculated as perceived by three modelled visual systems, blue tit (A), honey bee (B) and fruit fly (C). Units for contrast are Just Noticeable Differences (JNDs), the bottom dotted line depicts 1 JND as the minimum contrast assumed to be perceptually detected by the observer. Top, dotted line depicts 3 JND, commonly considered a conservative contrast threshold under less-than-ideal lighting conditions.

Table 1. Contrast values between paired subjects were calculated for the three model observers of *Arasia mullion*, its silk retreats and the tree trunks that it inhabits. For chromatic contrasts (dS) and achromatic contrast (dL) the geometric mean, lower and upper confidence intervals are shown.

Blue tit

	dS			dL		
Comparison	mean	lower	upper	mean	lower	upper
Tree-Clear	3.902	3.737	4.067	2.509	2.245	2.774
Tree-Retreat	0.757	0.576	0.938	1.240	0.865	1.615
Tree-Prosoma	2.353	1.949	2.758	4.549	4.023	5.076
Retreat-Prosoma	2.308	1.8760	2.740	5.596	5.114	6.078
Tree-Opisthosoma	2.572	2.167	2.977	3.227	2.575	3.879
Retreat-Opisthosoma	2.598	2.461	2.735	4.097	3.889	4.306

Honey bee

	dS			dL		
Comparison	mean	lower	upper	mean	lower	upper
Tree-Clear	2.208	2.072	2.345	3.657	3.312	4.001
Tree-Retreat	0.451	0.344	0.559	1.625	1.135	2.114
Tree-Prosoma	3.161	2.561	3.761	5.551	4.901	6.110
Retreat-Prosoma	3.102	2.474	3.730	6.951	6.347	7.556
Tree-Opisthosoma	3.165	2.588	3.742	3.987	3.170	4.804
Retreat-Opisthosoma	2.942	2.775	3.110	5.213	4.952	5.474

Fruit fly

	dS			dL		
Comparison	mean	lower	upper	mean	lower	upper
Tree-Clear	3.282	3.093	3.471	7.097	6.569	7.625
Tree-Retreat	0.568	0.405	0.731	2.677	1.881	3.474
Tree-Prosoma	3.006	2.402	3.609	9.473	8.484	10.462
Retreat-Prosoma	3.081	2.420	3.742	11.835	10.93	12.738
Tree-Opisthosoma	3.316	2.722	3.910	7.262	5.918	8.606
Retreat-Opisthosoma	3.308	3.123	3.492	9.340	8.928	9.752

Field experiment: Insect landing

In total, we recorded 21 hours of observations, approximately 1 hour per subject, capturing 68 landings in total (Figure 3). Because the frequency of insect landings was highly dichotomous - some subjects had over 10 landings in an hour while others had none, we opted for a conservative analysis that compared the number of subjects in each treatment that were or were not visited by insects. We did not find a significant difference in the number of subjects that were visited within each subject type, decorated silk retreat, partly covered hunting spider and bare spider, X^2 (df = 2, n = 21) = 0.535, p = 0.765.

We also observed multiple instances where the spiders actively avoided contact with ants of different species. The spiders would retreat back into the silk cover and close the openings upond detection of the surrounding ants.

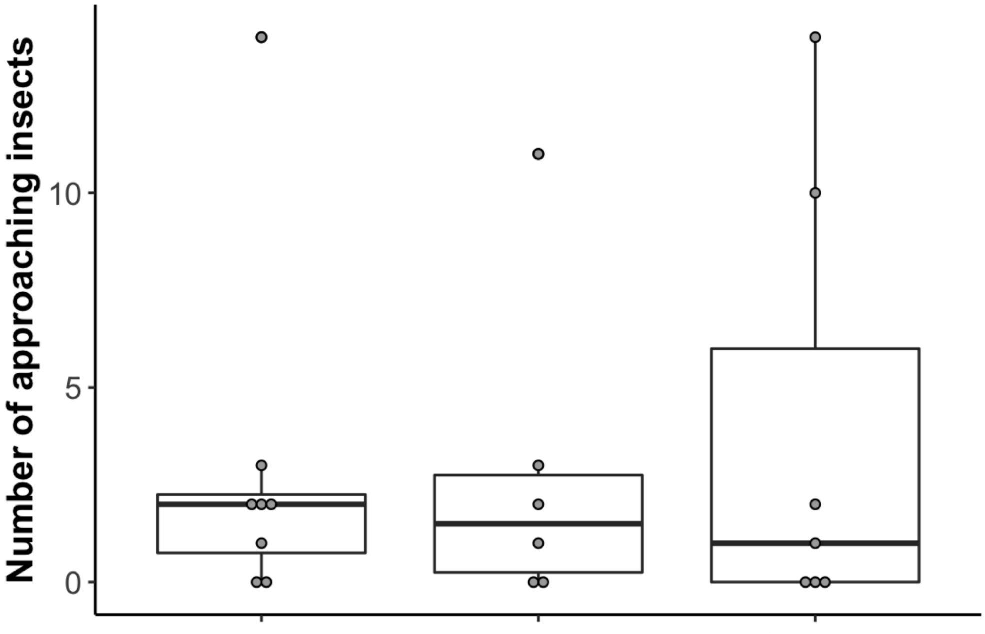


Figure 3. Approaching insects to each of the three types of subjects in the field experiment. The boxplots display 5th - 95th percentile and median. Retreat: empty silk retreat without a resident spider; Hunter: a spider with legs and prosoma protruding from the retreat; Spider: spider on a tree trunk without retreat.

Discussion

The aim of this study was to investigate the visibility of the decorations the arboreal jumping spider *Arasia mullion* places on its silk retreat. Specifically, we tested the hypothesis that decorating the silk reduces the visibility of the retreats against the trunk and also the visibility of the spider residing within the retreat. To test this hypothesis we used visual models of the spiders' potential prey and predators to evaluate the chromatic and achromatic contrast of decorated silk, non-decorated silk and the spiders against the exposed tree trunks. Furthermore, we evaluated the response of insects to decorated retreats and spiders outside the retreat using field observations.

The visual models showed that the debris decoration reduced both chromatic and achromatic contrast of the silk retreats, likely below a threshold of detectability for all three potential observers (bird and wasp predators and fly prey). However, we were not able to detect an effect on the likelihood of insects landing near a low contrast retreat or exposed spider based on 21 hours of observations.

We first found that non-decorated silk largely differs from decorated silk by having higher contrast in short wavelengths (blue to UV). This is maybe not so surprising because some silk types are known to be highly UV-reflective. The silk decorations built by several species of orb-web spiders *(e.g. Argiope* (Araneidae) and *Zosis* (Uloboridae)) reflect light, including UV, that makes them conspicuous to birds and bees against a green background (Bruce, Heiling & Herberstein, 2005). In *Argiope,* silk decorations are constructed from aciniform silk, the same silk that they use to wrap prey. This silk is particularly bright, unlike, for instance, the non-reflective sticky silk used in the capture threads of the orb-web (Herberstein et al., 2000). Jumping spiders commonly do not rely on capture webs, however, they do build silk retreats for resting (Richman & Jackson, 1992; Hill et al., 2019; Rößler et al., 2021). These retreats are thought to also utilise layers of aciniform silk (Wolff pers com.) and thus are possibly highly reflective. To our knowledge, this study is the first to characterise the reflectance spectrum of jumping spider silk retreats.

What is the selective consequence of decorating the silk retreat? Based on our modelling it seems to be a drastic reduction of contrast against the tree trunk background. Again, this makes sense because the spiders collect the debris from the tree trunk and specifically from their immediate surroundings (see Chapter 2). A comparable strategy is the use of soil to camouflage eggs on ground nests by the blue-footed booby *Sula nebouxii*. This behaviourally induced camouflage increases the survival of the eggs against other avian predators (Mayani-Parás et al., 2015). The selective advantage of the reduced visibility of the silk is likely to have similar potential for protection against predators as for aiding foraging. While retreats are commonly known for protective functions, in the particular "habitat" of tree trunks the gained cover can result advantageous in foraging contexts. Various types of insect prey are known to be able to see and alter their behaviour towards visible UV patches in orb-webs (Craig & Bernard, 1990; Herberstein et al., 2000; Blamires, Hochuli & Thompson, 2008). However, for *A. mullion* which sits against the tree trunk background this might not result in attraction of insects but in early detection by them. Thus, obscuring UV-reflection would result favourable. Against predators, the decorations might be hiding the bright undecorated silk against the surface of a UV-dull tree trunk. We know that the bright appearance of UV-reflective silk attracts predators such as praying mantises (Bruce, Herberstein & Elgar, 2001), predatory wasps (Cheng & Tso, 2007), and the spider-eating jumping spider *Portia labiata* (Zou et al., 2011). Furthermore, blue tits have been shown to use UV cues when foraging for otherwise cryptic insect prey (Church et al., 1998).

Unlike some of the debris decorations in uloborid webs that act as decoys, diverting an attack away from the spider body (Herberstein et al., 2000; Théry & Casas, 2009; Ma et al., 2020), *A. mullion* is either partially or completely covered by their silk retreats. Thus, the retreat is unlikely to function as a decoy, as any attack on the retreat is likely to also target the spider within. However, the retreat might act as a shield, and we have observed spiders seeking coverage within the silk retreats when objects, persons or animals (birds or large ants and bugs) approach them (see also Chapter 2). Once fully inside their retreats, the spiders use their forelimbs to close the openings. Unlike the decorated silk retreat, the spider body itself is chromatically and achromatically contrasting against the trunk for predator and prey observers. Thus, spending their entire life in a silk retreat reduces their exposure with the exception of the times they build or repair the retreats, hunt, search for females or select new retreat sites.

Despite the camouflaged nature of the silk retreat, there was no difference in the approach rates between decorated silk retreats and spiders without any. While we recorded over 21 hours of observations, we only ever captured 68 insects landing within the field of view. Most of these insects were very small, with body lengths between 1-2mm and therefore most likely to be prey rather than predators. Obviously, as with many other systems (Thompson, Jenkins & Bussell, 2000; Whitford, Freymiller & Clark, 2017), documenting predator-prey encounters and further predation events is very rare and in this case, our sampling effort was not large enough to detect an effect and should be regarded as preliminary. In the future a more comprehensive field experiment is needed to generate reliable results

Further studies under laboratory conditions with control over the number of landing prey are necessary to test the effect of the spider and their retreats on approaching prey. Furthermore, as the reduction of UV reflectance by decorating the silk is likely to be linked to predation avoidance, tests with co-occurring predators will be pertinent. For example, in our study sites, we frequently observed mud dauber wasps (Sphecidae), who are known predators of spiders. They capture and store their prey spiders in mud pods to feed their offspring (Perveen & Shah, 2013; Powell & Taylor, 2017). If they are in fact hunting *A. mullion,* we should be able to find them in these mud pods.

Our study documents a rare occurrence of retreat camouflage. While there are many examples of animal construction offering physical protection, camouflage for the most part is limited to animal bodies or trap structures. What is even more intriguing is that we discovered this phenomenon in jumping spiders, who are not known to build long-lasting retreats. Whether this behaviour has evolved to the particular constraints of the tree trunk environment or is also found in other environments remains to be discovered.

References

Bailey IE, Muth F, Morgan K, Meddle SL, Healy SD. 2015. Birds build camouflaged nests. *The Auk* 132:11–15.

Blamires SJ, Hochuli DF, Thompson MB. 2008. Why cross the web: decoration spectral properties and prey capture in an orb spider (*Argiope keyserlingi*) web. *Biological Journal of the Linnean Society* 94:221–229.

Bruce MJ, Heiling AM, Herberstein ME. 2005. Spider signals: are web decorations visible to birds and bees? *Biology Letters* 1:299–302.

Bruce MJ, Herberstein ME, Elgar MA. 2001. Signalling conflict between prey and predator attraction. *Journal of Evolutionary Biology* 14:786–794.

Brunton-Martin A, Nichols M, Gaskett A. 2021. Assessing kea perception of cereal baits using modelling of spectral reflectance. *New Zealand Journal of Ecology* 45:1-9.

Cheng R-C, Tso I-M. 2007. Signaling by decorating webs: luring prey or deterring predators? *Behavioral Ecology* 18:1085–1091.

Church SC, Bennett ATD, Cuthill IC, Partridge JC. 1998. Ultraviolet cues affect the foraging behaviour of blue tits. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 265:1509–1514.

Craig CL, Bernard GD. 1990. Insect attraction to ultraviolet-reflecting spider webs and web decorations. *Ecology* 71:616–623.

Drewniak ME, Briscoe AD, Cocucci AA, Beccacece HM, Zapata AI, Moré M. 2020. From the butterfly's point of view: learned colour association determines differential pollination of two co-occurring mock verbains by *Agraulis vanillae* (Nymphalidae). *Biological Journal of the Linnean Society* 130:715–725.

Hansell MH. 1996. The function of lichen flakes and white spider cocoons on the outer surface of birds' nests. *Journal of Natural History* 30:303–311.

Hansell M, Hansell MH. 2005. *Animal Architecture*. OUP Oxford.

Herberstein ME. 2011. *Spider Behaviour: Flexibility and Versatility*. Cambridge University Press.

Hill DE, C. AAP, Krishna P, Ramesh S. 2019. Construction of orb webs as nocturnal retreats by jumping spiders (Araneae: Salticidae: cf. *Anarrhotus*) in southwestern India. *Peckhamia*

182:1–10.

Hultgren KM, Stachowicz JJ. 2008. Alternative camouflage strategies mediate predation risk among closely related co-occurring kelp crabs. *Oecologia* 155:519–528.

Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall J, Whiting MJ. 2015. An integrative framework for the appraisal of coloration in nature. *The American Naturalist* 185:705–724.

Khan MK. 2020. Bagworm decorations are an anti-predatory structure. *Ecological Entomology* 45:924–928.

Larrivée M, Buddle CM. 2010. Scale dependence of tree trunk spider diversity patterns in vertical and horizontal space. *Écoscience* 17:400–410.

Madden JR. 2003. Bower decorations are good predictors of mating success in the spotted bowerbird. *Behavioral Ecology and Sociobiology* 53:269–277.

Maia R, Gruson H, Endler JA, White TE. 2019. pavo 2: New tools for the spectral and spatial analysis of colour in r. *Methods in Ecology and Evolution* 10:1097–1107.

Maia R, White TE. 2018. Comparing colors using visual models. *Behavioral Ecology* 29:649–659.

Mayani-Parás F, Kilner RM, Stoddard MC, Rodríguez C, Drummond H. 2015. Behaviorally-induced camouflage: a new mechanism of avian egg protection. *The American Naturalist* 186:E91–E97.

Ma N, Yu L, Gong D, Hua Z, Zeng H, Chen L, Mao A, Chen Z, Cai R, Ma Y, Zhang Z, Li D, Luo J, Zhang S. 2020. Detritus decorations as the extended phenotype deflect avian predator attack in an orb-web spider. *Functional Ecology* 34:2110–2119.

Perveen F, Shah M. 2013. Nest Architectural patterns by three wasp species (*Vespa velutina, Polistes flavus* and S*celiphron formosum*) with reference to their behavior. *International Journal of Tropical Insect Science* 5:IJIS–S10737.

Powell EC, Taylor LA. 2017. Specialists and generalists coexist within a population of spider-hunting mud dauber wasps. *Behavioral Ecology* 28:890–898.

Richman DB, Jackson RR. 1992. A review of the ethology of jumping spiders (Araneae). *Bulletin of the British Arachnological Society* 9:33–37.

Rößler DC, De Agrò M, Biundo E, Shamble PS. 2021. Hanging by a thread: unusual nocturnal resting behaviour in a jumping spider. *Frontiers in Zoology* 18:23.

Ruxton GD, Stevens M. 2015. The evolutionary ecology of decorating behaviour. *Biology Letters* 11:20150325.

Stachowicz JJ, Hay ME. 1999. Reducing predation through chemically mediated camouflage: Indirect effects of plant defenses on herbivores. *Ecology* 80:495–509.

Stevens M, Ruxton GD. 2019. The key role of behaviour in animal camouflage. *Biological Reviews* 94:116–134.

Théry M, Casas J. 2009. The multiple disguises of spiders: web colour and decorations, body colour and movement. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 364:471–480.

Thompson RC, Jenkins SR, Bussell JA. 2000. A method for recording predator–prey encounters between crabs and limpets using wax replicas. *Journal of the Marine Biological Association of the United Kingdom* 80:633–638.

Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society of London. Series B, Biological Sciences* 265:351–358.

Walter A, Elgar MA. 2011. Signals for damage control: web decorations in *Argiope keyserlingi* (Araneae: Araneidae). *Behavioral Ecology and Sociobiology* 65:1909–1915.

Walter A, Elgar MA. 2012. The evolution of novel animal signals: silk decorations as a model system. *Biological Reviews* 87:686–700.

Whitford MD, Freymiller GA, Clark RW. 2017. Avoiding the serpent's tooth: predator–prey interactions between free-ranging sidewinder rattlesnakes and desert kangaroo rats. *Animal Behaviour* 130:73–78.

Xavier GM, Brito VLG, Gonzaga MO. 2018. Colour matching in an orb-web spider: a twig-masquerading species as seen by potential predators. *Journal of Zoology* 306:48–57.

Ximenes NG, Gawryszewski FM. 2019. Prey and predators perceive orb-web spider conspicuousness differently: evaluating alternative hypotheses for color polymorphism evolution. *Current Zoology* 65:559–570.

Zabka M. 2002. Salticidae (Arachnida: Araneae) from the Oriental, Australian and Pacific regions, XV. New species of Astieae from Australia. *Records of the Australian Museum* 54:257–268.

Chapter 4 - Colour patterns of tree-trunk two-tailed spiders (Hersiliidae) against different backgrounds and viewer distances

Introduction

Camouflage is a textbook example of how natural selection has shaped the appearance of animals and is often referred to as the most common form of antipredator defence for prey species (Stevens & Merilaita, 2009a; Skelhorn & Rowe, 2016; Cuthill, 2019). More recently it has been recognised as being of great importance for many predators (Pembury Smith & Ruxton, 2020), avoiding detection by prey.

For camouflage to effectively hinder detection by observers, the animal's appearance interacts with its background and with the particular properties of the visual system of the observer (Stevens & Merilaita, 2009a; Cuthill, 2019). For instance, background matching as the better known and more frequent camouflage strategy is achieved when the colour (specific wavelengths in the spectrum of light) (Kelber, Vorobyev & Osorio, 2003; Cronin et al., 2014) and the patterning (shape and frequency distribution of colours) (Caves, Brandley & Johnsen, 2018) cannot be distinguished between the camouflaged animal and that of its immediate environment (i.e. the background).

On relatively uniformly coloured backgrounds, it might be sufficient to attain a single body colour tone that matches the background to remain undetected. For instance, the green and brown colour morphs of praying mantids (*Mantis religiosa*) preferentially occupy green and brown vegetation, respectively (Di Cesnola, 1904; Battiston & Fontana, 2010), which results in higher survival rates due to reduced bird attacks (Di Cesnola, 1904). The assumption is that bird predators did not detect the presence of the insect because it did not contrast sufficiently against the background colour.

In habitats where the backgrounds are more complex, effective camouflage might also involve matching the complex array of background colours and patterns (the shape, size and frequency distribution of colours). For example, many species of moths rest on the surfaces of tree trunks during the day when visually hunting predators like birds are active (Kettlewell, 1955; Sargent, 1966; Grant & Howlett, 1988; Kang et al., 2014). The trunk surfaces have complex colour patterns, and the moths match those (Kang et al., 2014). In some instances, even if the colour and pattern match is weak, animals can achieve concealment when the arrangement of colours distorts the shape of the body. This is called disruptive colouration and makes the animal unrecognisable either because of strong contrast in the colouration patterning that disrupts their recognizable shape (Stevens & Cuthill, 2006; Stevens & Merilaita, 2009b) or the pattern results in only some parts of the body contrasting against the background (Kang et al., 2014; Stevens & Ruxton, 2019). Despite how impressive the matching of colours and patterns can be to the human eye, the functional importance of the appearance of any camouflaged animal depends on the relevant receiver's colour vision and visual acuity, which might be substantially different to humans.

The perception of camouflage depends on the type and amount of colour receptors in the eyes of the observer (Kelber, Vorobyev & Osorio, 2003; Osorio & Vorobyev, 2008) and the type and size of the eyes, the viewing distance and any resulting combinations which define the observer’s visual acuity (Cronin et al., 2014; Caves, Brandley & Johnsen, 2018). In terms of colour vision, different types of receptors in the eyes capture specific wavelengths of the electromagnetic spectrum (Osorio & Vorobyev, 2008; Kelber & Osorio, 2010). Thus, for colour vision to occur, the animal must have at least two different types of colour receptors with different spectral sensitivity (Kelber & Osorio, 2010; Kemp et al., 2015). There is considerable variation in the composition of visual receptors in animals (Troscianko et al., 2009; Kelber & Osorio, 2010) and the majority of these deviate from the human perception of colour which is based on three receptors sensitive to red, green and blue light. Most mammals only have two types of receptors, with the exception of some primate species that share a similar combination of receptors with humans (Mollon, 1989). While other animals like bees, wasps and some birds also have three receptors, these might have different spectral sensitivity. For instance, honey bees lack red colour receptors but have green, blue and ultraviolet UV receptors (Briscoe & Chittka, 2001; Kelber, Vorobyev & Osorio, 2003; Koshitaka et al., 2008). Ultraviolet vision aids bees in detecting flower signals only visible in the UV part of the spectrum. Finally, some species of birds, fish and insects have four or even more specific receptor types (Osorio & Vorobyev, 2008). Among butterflies, species have been described with five and up to eight different receptors (Briscoe & Chittka, 2001; Kelber, Vorobyev & Osorio, 2003; Koshitaka et al., 2008) while the mantis shrimp has 12 (Thoen et al., 2014). For an in-depth review of colour receptor diversity see (Kelber, Vorobyev & Osorio, 2003). It is not clear what the impact of having more than four receptors is - potentially it could enable a refined colour perception or an expansion of the range of perceived colours (Kelber & Osorio, 2010; Thoen et al., 2014). Considering the variation in colour receptors between different animal species, it can be problematic to generalise from one visual system to another (Kemp et al., 2015).

In addition to colour perception, vision is also affected by the spatial arrangement with respect to shape, size, distribution and frequency of colour patterns. Thus, the ability to resolve spatial detail - visual acuity, is as important as colour perception for animals in how they interact with the biotic and abiotic elements in the environment (Troscianko et al., 2009; Skelhorn & Rowe, 2016). While humans have great visual acuity, this ability is not shared by many animals and is surpassed by some (Caves, Brandley & Johnsen, 2018).

Resolving spatial detail is commonly measured as the number of lines that can be distinguished within one degree of the visual field and it is expressed as units of cycles per degree (cpd). In other words, 30 cpd means the observer can detect 30 lines within one degree of the visual field while a species with an acuity of 140 cpd can distinguish 140 lines per degree of the visual field. Thus, the greater the number of cycles per degree the greater the ability to distinguish detail. The range in visual acuity can vary by orders of magnitude across species (Cronin et al., 2014). Humans sit pretty high on this scale, with a visual acuity of 60 cpd, only surpassed by a few species of predatory birds (Caves, Brandley & Johnsen, 2018). Among raptors, the wedge-tailed eagle *Aquila audax* scores the highest acuity of 140 cdp. However, for most birds values are below 30 cpd with a median of 11 cdp. By contrast, the vast majority of published acuity values for insects are below 1.0 cpd (98%) with a median acuity of only 0.25 cpd (Caves, Brandley & Johnsen, 2018).

A significant component of the variation in visual acuity among animals can be attributed to anatomical or intrinsic traits, such as the type and the size of the eyes. Camera and compound type eyes are the dominant types of eyes, but are functionally quite distinct. The camera eye is a single optical unit consisting of a lens and an external cornea. These elements focus the light onto the retina where the visual receptors are. Camera eyes are the main type of eyes in vertebrates, but are also present in some invertebrates, such as octopus and spiders (Cronin et al., 2014).

Compound eyes are made of multiple optical units (ommatidia), each one contains a lens that passes light through a tubular structure onto a small group of receptor cells. Compound eyes are abundantly found in insects, crustaceans and some chelicerates (Cronin et al., 2014). In comparison, even if a compound eye is of the same size as a camera eye, the acuity of the compound eyes will be lower. This is because the multiple smaller lenses (up to 3000 ommatidia per eye in house flies; (Sukontason et al., 2008) are affected by a form of blurring of the image that results from the light waves moving through the small eye tubes. Thus, the combination of eye type and size generally accounts for the observed variation in visual acuity (see figure 1).

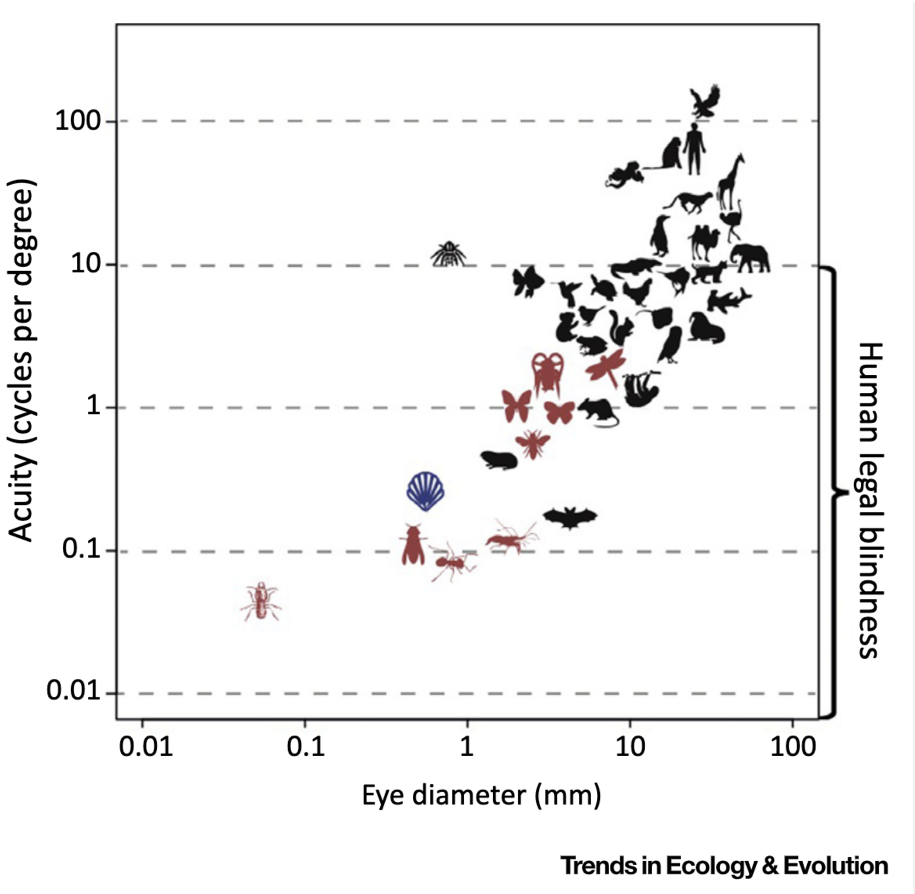


Figure 1. Taken from Caves, Brandley & Johnsen, 2018. Relationship between eye diameter and visual acuity. The intersection between eye diameter and acuity is placed in the center of each animal shape. Eye types denoted by colour, Camera (Black), Compound (Red), and Mirror (Blue). Additional details are found in Table S1 of the original publication.

The species-specific ecology may also be reflected in visual acuity. For example, predators have greater acuity than non-predators and species that live in spatially complex habitats have greater acuity than those in relatively simpler habitats (Caves, Brandley & Johnsen, 2018). Finally, acuity is distance dependent as details become more discriminable at closer range and acuity is reduced as light scatters with increasing distance. Therefore, the ability to discern detail decreases when the animal moves further away from the subject (Marshall, 2000; Caves, Brandley & Johnsen, 2018).

We are now in an excellent position to assess both colour perception and visual acuity for non-human animals through reasonably affordable optical equipment (Troscianko & Stevens, 2015; van den Berg et al., 2020) coupled with computational modelling (Stevens et al., 2006; Arias et al., 2020). These approaches allow us to estimate how animals perceive objects of interest such as predators or prey.

In the context of camouflage, a full appreciation of how a camouflaged animal is viewed, needs to integrate the observer's colour perception and acuity within the relevant ecological context (Merilaita, Scott-Samuel & Cuthill, 2017; Caves, Brandley & Johnsen, 2018), which is often difficult and complex. For example, the natural light of the viewing scene might include wavelengths in the UV as well as the visible spectrum, which can be difficult to replicate under laboratory conditions. Assessing the discriminability of camouflaged animals under natural conditions is equally difficult. While it addresses the issue of natural light, approaching live animals in the field often results in disturbance and consequent movement. This movement may also displace the animal from their relevant backgrounds, which is likely to impact the assessment of camouflage.

Here we have identified an excellent study animal to investigate how predators might assess its level of camouflage. Hersiliidae spiders occupy tree trunks and to the human eye, are superiorly camouflaged (Figure 2). They remain immobile for long periods of time on the surface of tree trunks where their presence remains hidden by their body camouflage (at least to the human eye) (Baehr & Baehr, 1987). The tree trunk habitat offers limited cover, therefore, Hersiliidae spiders are likely to be under selection to avoid detection or recognition by predators and prey. Such a system is ideal to address questions about the impact that visual acuity has on the perception of background matching.

Here we use a novel set of computational methods for the analysis of colour and pattern in conjunction with one another. The Quantitative Colour Pattern Analysis (QCPA) framework allows us to combine several physiological attributes of animal visual systems including photoreceptor spectral sensitivities, receptor noise levels and receptor abundances, spatial acuity and viewing distance to model visual perception generating a large set of quantitative outputs. We used the numerical outputs from the QCPA framework to assess how hersilid spiders are visually perceived against different backgrounds, from different viewing distances by an ecologically relevant observer.

Our primary aim was to assess how a relevant predator observer with a visual system fundamentally different from human vision perceives the Hersillidae camouflage. For this, we studied two different species of Hersiliidae spiders (*Tamopsis brisbanensis* and *Tamopsis fickertii*) that differed in appearance to the human eye and occupied different tree types. We used multispectral digital images to model the colour, luminance and patterning of the spiders and their backgrounds as perceived by the visual systems of potential prey and predators at a range of distances that are considered ecologically relevant.

First, we hypothesise that Hersiliidae spiders occupy the background that produces the most favourable camouflage, and if this is true then we predict that the selected background has the lowest contrast values, a random spot on the same tree has second lowest, and finally that a nonselected tree would have the highest contrast. And second, the relative contrast against the background is higher at closer distances, and therefore differences between patterns would decrease with distance.

Methods

Study species

Tamopsis fickertii L. Koch, 1876 and *Tamopsis brisbanensis* Baehr & Baehr, 1987 Hersiliidae are sympatric residents of tree trunks in eastern Australia. Despite being potentially able to occupy the same trees, each of these two species are commonly found on trees with distinct appearances. *T. brisbanensis* sits on pale coloured Eucalyptus species with smooth bark, such as *Eucalyptus saligna* and *Eucalyptus tereticornis*, while *T. fickertii* is commonly found in trees, such as *Eucalyptus resinifera* and *Eucalyptus microcorys* with long striped crevices that generate a high contrast appearance (Figure 2). Other than taxonomic descriptions of these species, little is known about their biology (Baehr & Baehr, 1987).

Figure 2. Left, *Tamopsis brisbanensis* has a relatively homogeneous colouration pattern that matches the smooth appearance of the *Eucalyptus saligna* trees. Right, *Tamopsis fickertii* has a more complex colouration pattern and sits on the rough and also a visually more complex surface of *Eucalyptus resinifera* trees.

The observed species of Hersiliidae occupy trees do not completely hide behind or below the shallow depressions or crevices in the tree trunk. Instead, the spiders remain on plain sight (uncovered) during the daytime and exposed to visual predators. While active at night, I do not expect their potential predators to be driven by sight. Nocturnal predators are likely to be guided by non-visual cues, therefore we selected diurnal vertebrates as models for predators (described below).

Sites and time

This study was conducted in the summer months (November-February) of 2019. Four different sites where populations of *T. fickertii* and *T. brisbanensis* occur were located and surveyed in the Sydney area. In addition to the Macquarie University campus (-33.7741271, 151.1094476), we surveyed three urban recreational parks, Centennial Park (-33.893214, 151.235694), Bicentennial West Pymble park (-33.7635419, 151.1354318) and Blenheim Park (-33.795361, 151.135417). The four sites consisted of a mix of stretches of lawn and patches of trees and understory. We surveyed these sites on sunny and warm days, avoiding the rain and extreme heat.

At each site, tree trunks were haphazardly inspected for the presence of Hersiliid spiders from the base of the tree and up to 2 meters in height. When a spider was found the surrounding trees were also inspected. Within our study sites, we commonly observed a single spider on the surveyed tree trunk except for larger trees, where occasionally up to two spiders were found, in which case, we included both in our dataset (details below).

Individuals of each species were found occupying specific tree species with either smooth or rough bark. *Tamopsis fickertii* occupied tree bark with a “rough” appearance and *T. brisbanensis* occupied tree bark with a “smooth” appearance. A total of 50 Hersiliidae spiders were recorded and photographed in the four locations utilised in this study (*Tamopsis fickertii* (rough), n = 30; *Tamopsis brisbanensis* (smooth), n = 20). However, in order to generate a comparable set of analyses and to minimise confounding factors, we only analysed data coming from a single tree species per surface type. For the rough bark we selected only *Eucalyptus resinifera* and for the smooth bark we selected only *Eucalyptus saligna*. Thus, our final sample sizes were: *T. fickertii* (rough), n = 9 and *T. brisbanensis* (smooth), n = 18. Other tree species were excluded from the analyses given the low number of trees we were able to record which resulted insufficient for statistical testing.

Multi-spectral photographs

We assessed the perception of the spiders’ camouflage by prey and predator model observers with different visual systems and at different distances. For this, we used standardised multispectral images of both hersillid species relative to the distinct tree trunk surfaces they occupied. First, we took pictures of the spiders using a Nikon D7000 camera (converted to full-spectrum) with a UV transmitting EL-Nikkor 80 mm f/5.6 lens attached. Two pictures were taken for each individual subject, one to include the ultraviolet (~ 300–400 nm) and the other the human visible part of the spectrum (~400 to 700 nm). For the UV-photograph, we used a Baader Venus UV pass and for the visible spectrum, we attached a Baader UV/IR filter to the lens. In each photo, we included a 5% reflectance standard as well as a scale.

Each pair of photographs was processed and combined following the methods by Troscianko (2015) to generate multispectral files with reflectance values of the spiders and their natural backgrounds. We used the Multispectral Image Calibration and Analysis Toolbox (MICA) to process and convert the multispectral images to quantum catch files. Further we used its analytical extension Quantitative Pattern Colour Analysis (QCPA) to perform colour and pattern analysis including spatial acuity and viewing distance corrections (Troscianko & Stevens, 2015; van den Berg et al., 2020).

This method allows us to estimate reflectance values for every pixel in the images and further convert these into the particular cone catch values of selected observers. For each image, we manually delimited two regions of interest, the body of the spider (including legs) and the immediate surrounding background at two distances from the spider (one and two body lengths).

All photographs in our study were taken around noon time +/- 2 hours, and only under the shade to avoid the direct sunlight casting shadows over the subjects. Since the specific local predators are not known, we used available information about visual systems of relevant visual sensitivities and models. As predators, we used the blue tit *Cyanistes caeruleus* with its species-specific Webber fraction (Silvasti, Valkonen & Nokelainen, 2021).
In the Sydney area, I observed multiple instances of the noisy miner (*Manorina melanocephala*) hovering and capturing insect prey from the surface of tree trunks (Aceves-Aparicio A, pers. obs.). Thus, posing as a potential vertebrate predator in the same trees occupy by the Hersiliida spiders studied in this chapter.

QCPA data domains

This analysis generates a large number of metrics that fall into four broad domains: Colour adjacency, visual contrast, boundary strength, colour local edge and luminance local edge.

Colour Adjacency Analysis (CAA) generates geometric attributes of the spatial arrangement of colour patterns of a given subject or scene. These are estimated from frequencies of colour change in a transition matrix. This analysis generates a total of 37 metrics.

Visual Contrast Analysis (VCA) generates metrics that describe the perceived contrast for colour and luminance of the object and its background. Calculating weighted means of chromatic and achromatic elements (colour and luminance elements of the image) by their spatial distribution (the relative abundance of these elements in the image). This analysis generates a total of 45 metrics.

Boundary Strength Analysis (BSA) is an extension of the CAA. These metrics utilise the transition matrices previously created to measure properties of boundaries between adjacent patches in a visual scene. Thus, chromatic and achromatic properties together with patch size, and abundance define the edges which ultimately impact visual perception. This analysis generates a total of 45 metrics.

Local Edge Intensity Analysis (LEIA) is a novel way to quantify boundary properties. Edge intensity is measured as colour and luminance contrast between each pixel and its surrounding neighbours (along vertical, horizontal and diagonal axes). This provides a biologically relevant estimation of local edges in an image. The analysis generates two separate outputs, one for chromatic attributes and one for achromatic attributes. This analysis generates a total of 15 metrics for colour and 15 for luminance.

Potential perception of the QCPA domains by observers
CAA. Could be perceived as differences in patterns complexity, from the richness of elements in the colour pattens to the similarity to adjacent patterns.

VCA. The perception of either a highly contrasty pattern as opposed to a smooth uniform pattern.

BSA. This is focused on the resulting contrast at the edge were the elements of a pattern meet. BSA takes into account both colour and luminance.

LEIA. Unlike BSA, here the edge contrast between elements of a pattern might are presented separately assessing colour contrast and luminance contrast. This is likely to be perceived differently depending the viewing distance of the observer.

QCPA metric validation

Before we proceed with the QCPA metrics we tested their suitability in discriminating between rough and smooth surface types (both spiders and tree backgrounds). We used Regularised Discriminant Analysis (RDA), which improves the estimation and classification accuracy when the number of input variables exceeds the number of observations (subjects/samples) (Friedman, 1989). Each metric was first normalised to within a 0 -1 range using the *caret* R package (Kuhn, 2008). We then prepared a training set from a subset (80%) of our total samples. We set the surface type as grouping class, where rough surfaces correspond to *T. fickertii* and *Eucalyptus resinifera*, while smooth surfaces to *T. brisbanensis* and *Eucalyptus saligna*. The RDA analysis showed high discrimination power between the surface types for backgrounds and spiders that decreases with increasing viewing distance (see supplementary). Based on these results we proceeded with utilising the QCPA metrics.

Statistics

We ran multiple Kruskal-Wallis tests to compare the domains' metric values of the surface types (rough, smooth) and spiders against tree backgrounds at each given viewing distance. For the comparisons between scenarios, we ran a Pairwise Wilcoxon Rank Sum test for the domains' averaged absolute difference between spiders and the tree backgrounds. We used the Benjamini-Hochberg correction for multiple comparisons (Benjamini & Hochberg, 1995). All statistical analyses were conducted in (R Core Team, 2022).

Results

Below we present a three-step approach to the results. We first present the comparison of the colours and patterns using the five QCPA data domains (see above) between rough (*T. fickertii*) and smooth (*T. brisbanensis*) spiders as well as smooth and rough bark backgrounds. Second, we compared the average colours and patterns of spiders against their matching background (rough spider against rough background and smooth spider against smooth background). Third, we compare the average colours and patterns of spiders against a matching, non-matching and unrelated background. We consider these metrics at seven different viewing distances (2-80cm) using the visual system of the blue tit (species) as the model predator viewer.

Rough VS Smooth type

Colour Adjacency Analysis (CAA)

We found significant differences in colour adjacency metrics (the geometric properties of colour patterning) between the rough and smooth spiders mostly at close distances (2 to 10cm and 50cm). While for the rough and smooth tree trunk backgrounds, the differences only were non-significant in the longest viewing distance. This means that the perception of differences between the geometric properties of colour patterning between the two spider and surface types varies distinctly with viewing distances (Figure 3, Table 1).

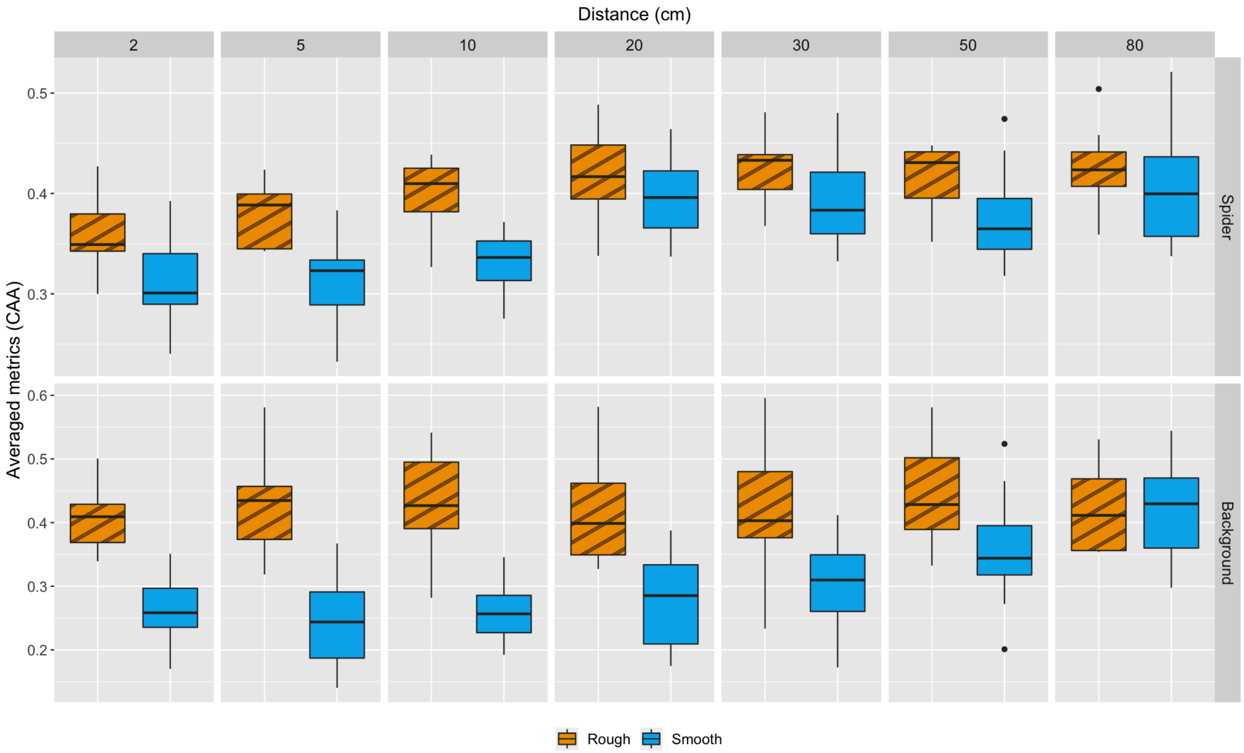


Figure 3. Boxplots of the averaged metrics of the QCPA Colour Adjacency data domain for rough (yellow) and smooth (blue) spiders (*T. fickertii* and *T. brisbanensis*, respectively) and tree bark backgrounds (rough: yellow; smooth: blue) from seven different viewer distances (2-80cm).

Table 1. Colour adjacency analysis comparing the rough and smooth surface types between *T. fickertii* and *T. brisbanensis* spiders respectively, and the colour adjacency between the rough and smooth tree backgrounds at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Spider		Background	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	6.61	0.010	16.51	<0.001
5	13.34	<0.001	16.51	<0.001
10	12.60	<0.001	14.10	<0.001
20	2.07	0.150	12.23	<0.001
30	3.82	0.051	8.30	0.004
50	5.60	0.018	5.84	0.016
80	1.36	0.243	0.00	0.959

Visual Contrast Analysis (VCA)

The visual contrast between the elements of colour patterns did not differ significantly between rough and smooth spiders at any viewing distance. When considering the visual contrast between the two tree backgrounds, we found significant differences only at the closest viewing distances, 2-5cm. Overall, we observed higher contrast values for the tree backgrounds at close viewing distance. Values for the two spider species remained relatively constant with increasing viewing distance, while for tree trunk backgrounds, the contrast decreased with viewing distance (Figure 4, Table 2).

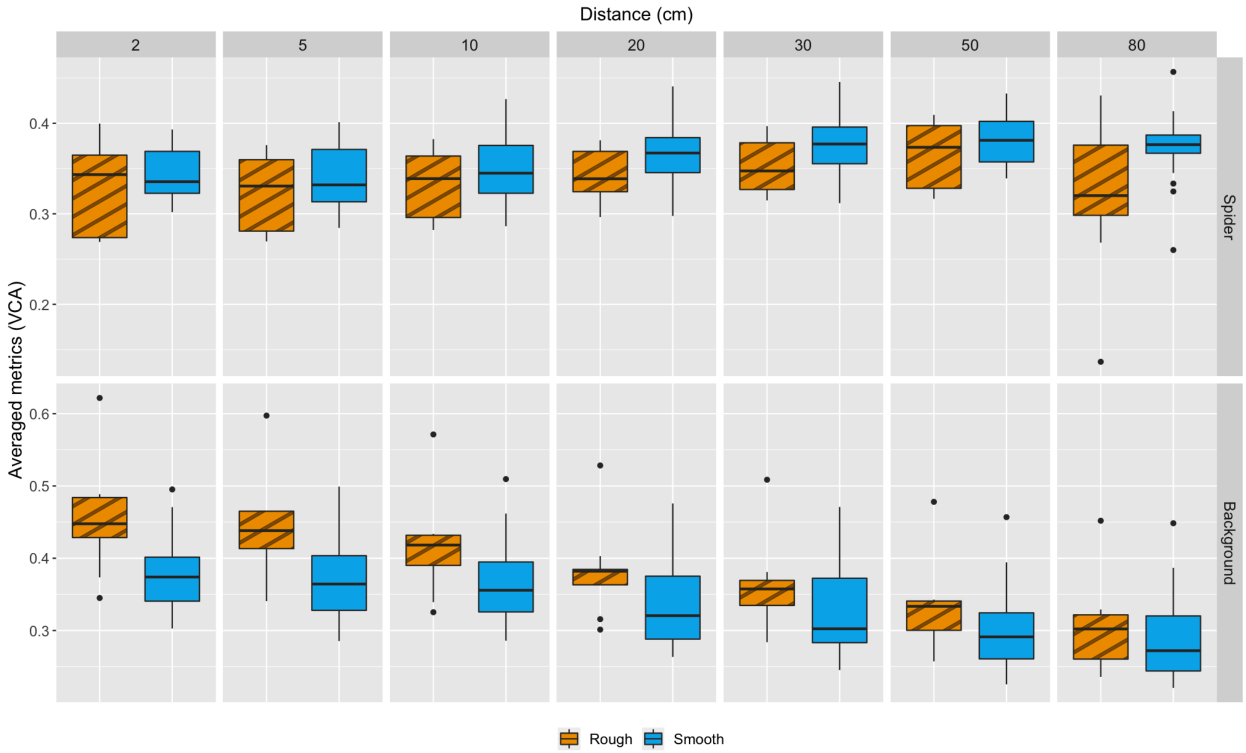


Figure 4. Boxplots of the averaged metrics of the QCPA Visual Contrast data domain for rough (yellow) and smooth (blue) spiders (*T. fickertii* and *T. brisbanensis*, respectively) and tree bark backgrounds (rough: yellow; smooth: blue) from seven different viewer distances (2-80cm).

Table 2. Visual contrast analysis comparing the rough and smooth surface types between *T. fickertii* and *T. brisbanensis* spiders respectively, and the colour adjacency between the rough and smooth tree backgrounds at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Spider		Background	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	0.45	0.504	6.35	0.012
5	0.96	0.328	5.60	0.018
10	1.06	0.304	3.82	0.051
20	3.43	0.064	3.24	0.072
30	3.06	0.080	1.93	0.165
50	1.17	0.280	2.07	0.150
80	2.38	0.123	0.68	0.411

Boundary Strength Analysis (BSA)

High values of the boundary strength metric indicate higher contrast in the boundaries/edges between colour patches. For spiders, we found significant differences at two viewing distances, 2 and 50cm. While for the tree trunk backgrounds, the differences were significant between the 2 and 30cm viewing distances (Figure 5, Table 3). In general, for both spiders and tree backgrounds, the rough type showed higher boundary contrast.

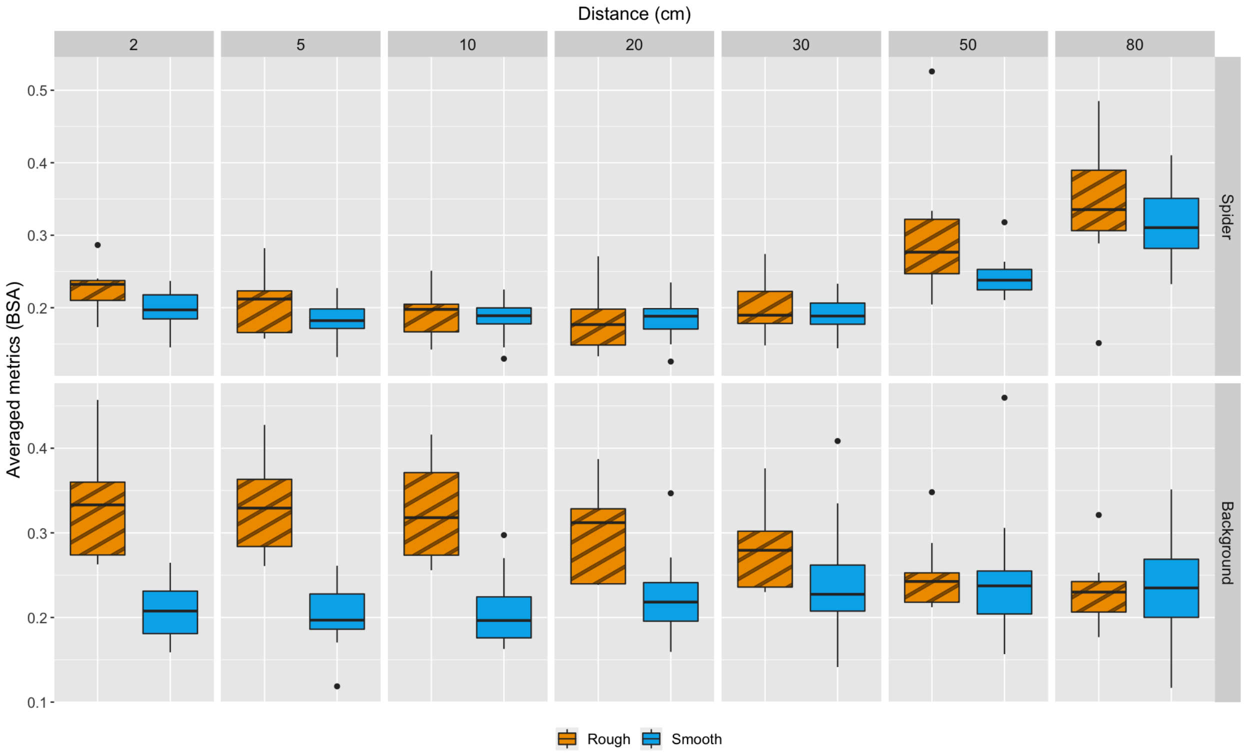


Figure 5. Boxplots of the averaged metrics of the QCPA Boundary Strength data domain for rough (yellow) and smooth (blue) spiders (*T. fickertii* and *T. brisbanensis*, respectively) and tree bark backgrounds (rough: yellow; smooth: blue) from seven different viewer distances (2-80cm).

Table 3. Boundary Strength analysis comparing the rough and smooth surface types between *T. fickertii* and *T. brisbanensis* spiders respectively, and the colour adjacency between the rough and smooth tree backgrounds at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Spider		Background	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	5.12	0.024	16.93	<0.001
5	2.07	0.150	16.93	<0.001
10	0.02	0.877	14.88	<0.001

20	0.52	0.471	8.90	0.003
30	0.07	0.797	4.45	0.035
50	4.02	0.045	0.86	0.355
80	0.79	0.374	0.07	0.797

Local Edge Intensity Analysis

Similarly to the boundary strength analysis, the local edge intensity analysis (LEIA) measures contrast at the edge (boundary) between patches in a given colour pattern. The first component measures this contrast chromatically (LEIA - Colour) and the second, achromatically (LEIA - luminance).

LEIA - Colour

For both spiders and tree backgrounds, we found significant differences in boundary colour contrast between rough and smooth spiders at short viewing distances, between 2 and 5 cm for spiders and 2 to 20 cm for the trees (Figure 6, Table 4).

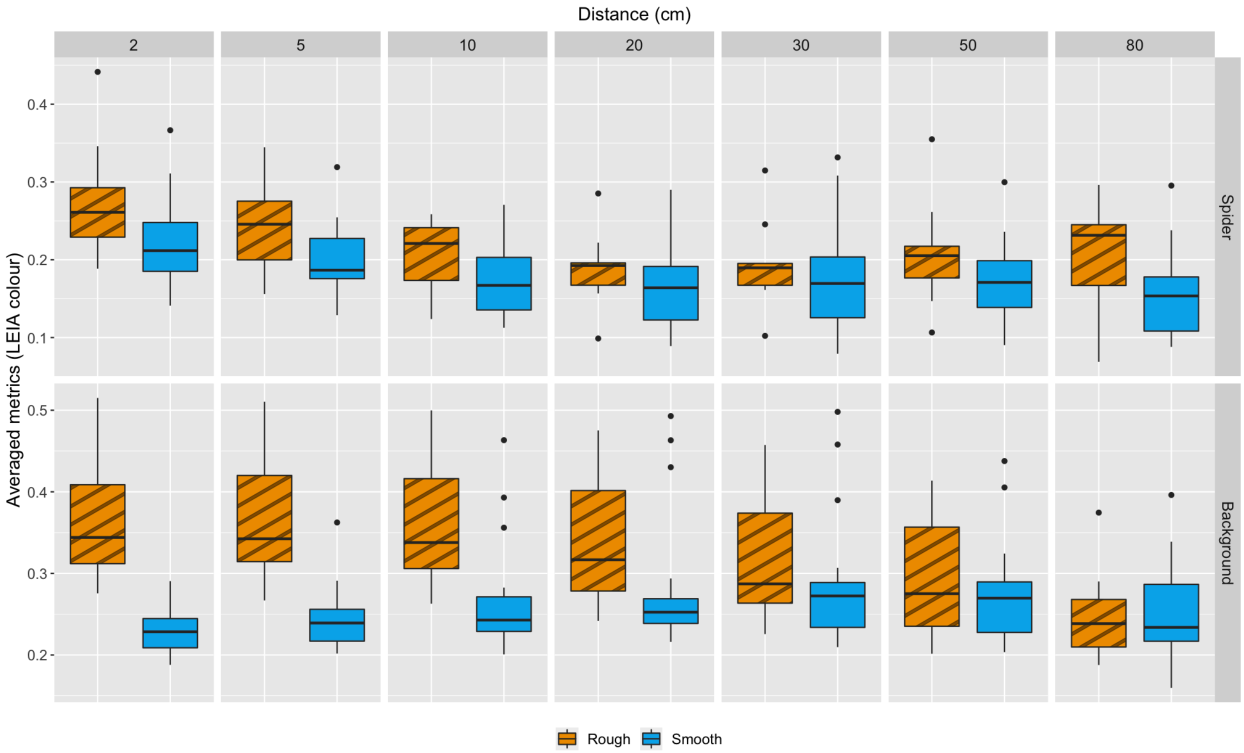


Figure 6. Boxplots of the averaged metrics of the QCPA LEIA (colour) data domain for rough (yellow) and smooth (blue) spiders (*T. fickertii* and *T. brisbanensis*, respectively) and tree bark backgrounds (rough: yellow; smooth: blue) from seven different viewer distances (2-80cm).

Table 4. Local edge intensity analysis (colour) comparing the rough and smooth surface types between *T. fickertii* and *T. brisbanensis* spiders respectively, and the colour adjacency between the rough and smooth tree backgrounds at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Spider		Background	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	4.45	0.035	16.51	<0.001
5	4.67	0.031	13.71	<0.001
10	3.43	0.064	8.90	0.003
20	1.28	0.258	4.45	0.035
30	1.28	0.258	1.06	0.304
50	1.52	0.217	0.32	0.572
80	3.62	0.057	0.13	0.719

LEIA - Luminance

The perception of boundary luminance contrast significantly differed between the rough and smooth spiders with the rough type having higher contrast than the smooth type at all viewing distances. Backgrounds had significantly higher contrast at short viewing distances (2-5cm), with no difference at 10-20cm viewing distance followed by an inversion, where smooth backgrounds had a significantly higher boundary luminance contrast from 30 to 80cm (Figure 7, Table 5).

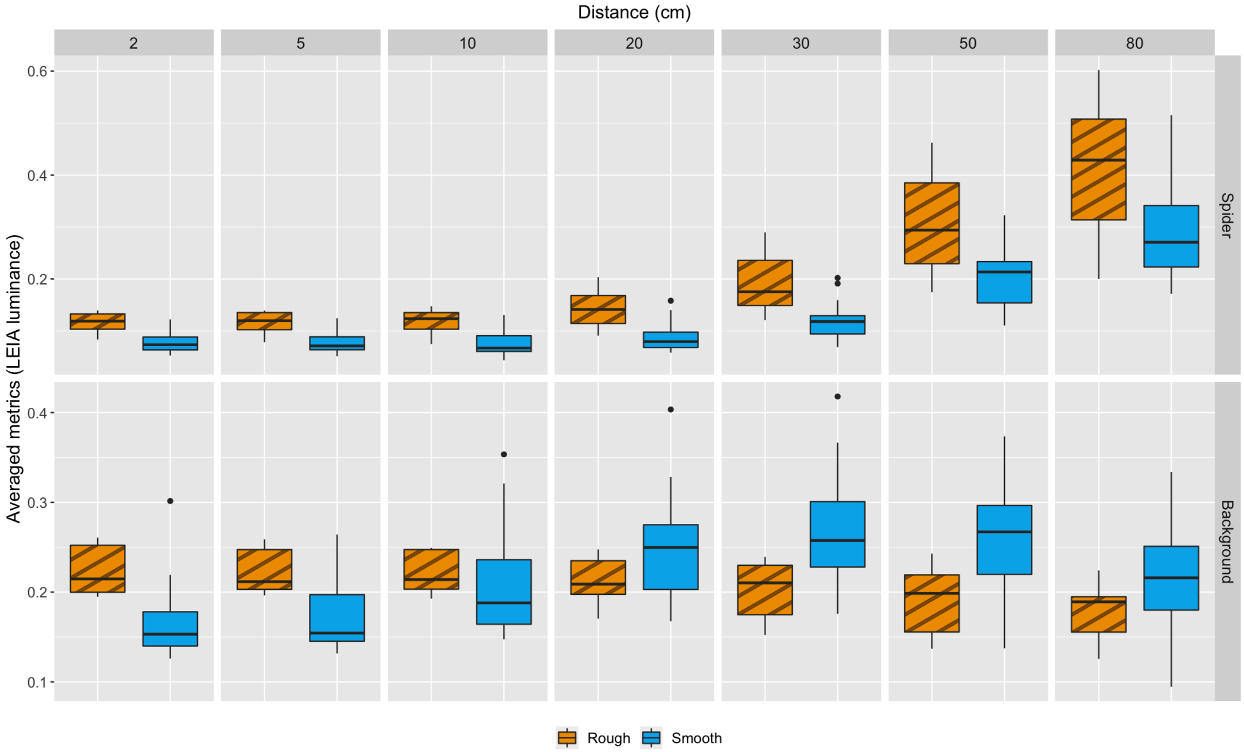


Figure 7. Boxplots of the averaged metrics of the QCPA LEIA (luminance) data domain for rough (yellow) and smooth (blue) spiders (*T. fickertii* and *T. brisbanensis*, respectively) and tree bark backgrounds (rough: yellow; smooth: blue) from seven different viewer distances (2-80cm).

Table 5. Local edge intensity analysis (luminance) comparing the rough and smooth surface types between *T. fickertii* and *T. brisbanensis* spiders respectively, and the colour adjacency between the rough and smooth tree backgrounds at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Spider		Background	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	12.23	<0.001	11.88	0.001
5	11.18	0.001	8.00	0.005
10	10.17	0.001	2.07	0.150
20	10.84	0.001	2.71	0.100
30	9.52	0.002	6.88	0.009
50	6.61	0.010	7.71	0.005
80	4.23	0.040	4.23	0.040

Spider VS Background

Here we compare the five QCPA data domains between spiders and backgrounds within each surface type (smooth and rough) at seven viewing distances.

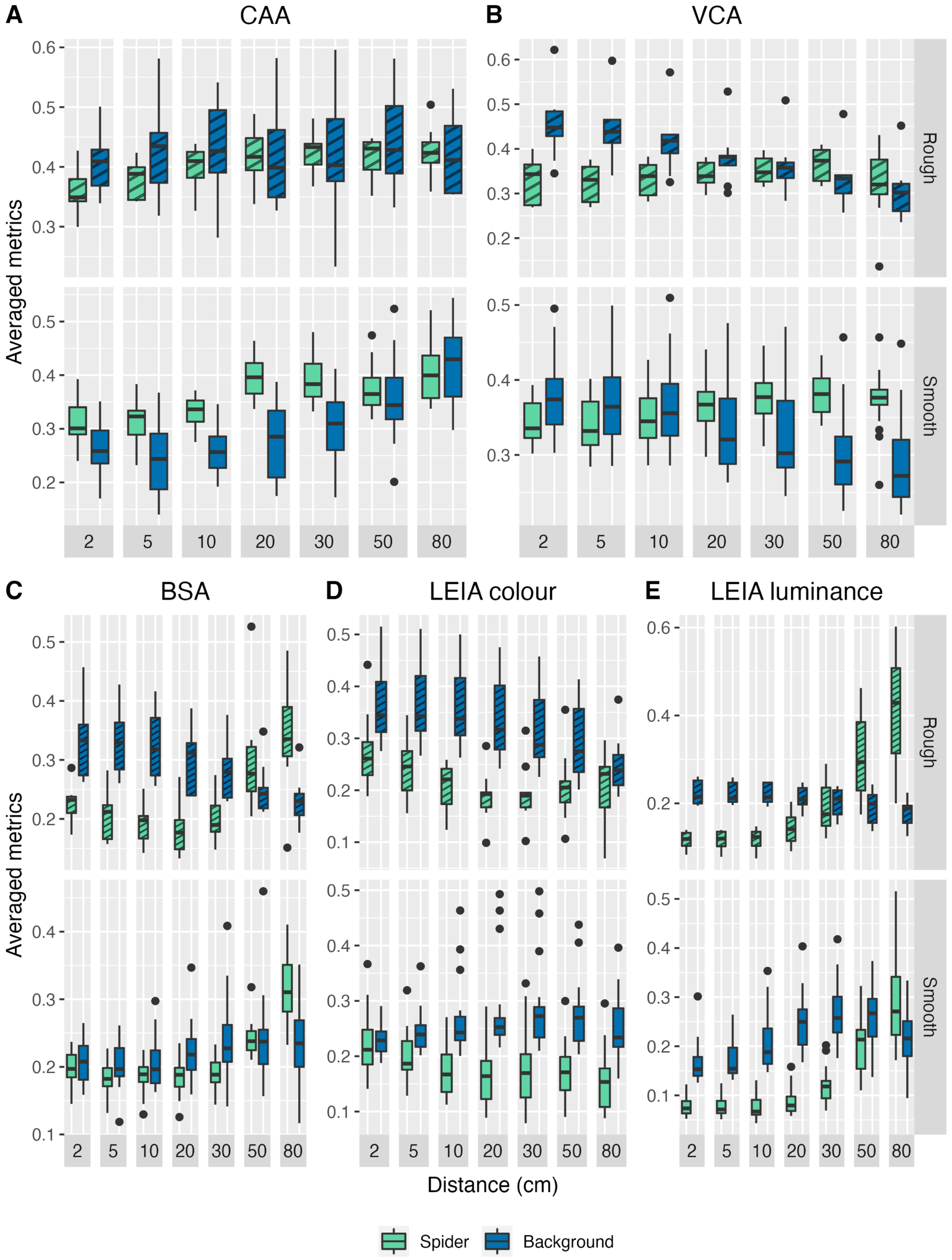


Figure 8. Boxplots of the averaged metrics of the QCPA data domains: A, Colour Adjacency; B, Visual Contrast; C, Boundary Strength; D, Local Edge Intensity (colour); E, Local Edge Intensity (luminance). In each panel, the boxplots compare the spiders (yellow) and tree backgrounds (blue) within surface types, rough and smooth, which correspond to the matching spider species *T. fickertii* and *T. brisbanensis* respectively. Comparisons are modelled for seven different viewing distances (2-80cm).

Colour Adjacency Analysis (CAA)

For rough spiders against rough background, we did not find significant differences in colour adjacency metrics (the geometric properties of colour patterning) at any viewing distance. For smooth spiders against smooth backgrounds, differences between spiders and tree backgrounds were significant at shorter viewing distances (2-30cm). Within this range, the perceivable diversity of colour patterning was higher for spiders than for tree trunk backgrounds (Figure 8A, Table 6).

Table 6. Colour adjacency analysis comparing spiders against their tree backgrounds within surface types (rough and smooth) at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Rough		Smooth	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	3.60	0.058	7.58	0.006
5	1.42	0.233	12.33	<0.001
10	1.03	0.310	16.15	<0.001
20	0.00	0.965	19.62	<0.001
30	0.02	0.895	17.44	<0.001
50	0.10	0.757	0.90	0.343
80	0.45	0.501	0.48	0.486

Visual Contrast Analysis (VCA)

The colour pattern contrast was significantly higher for rough backgrounds than for rough spiders at short viewing distances (2-10cm). The colour pattern contrast was significantly lower for the smooth spiders than for the smooth tree backgrounds at a 2cm viewing distance while at longer viewing distances (20-80cm) this trend was inverted and significant (Figure 8B, Table 7).

Table 7. Visual contrast analysis comparing spiders against their tree backgrounds within surface types (rough and smooth) at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Rough		Smooth	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	9.83	0.002	5.48	0.019
5	8.75	0.003	2.40	0.121
10	7.74	0.005	0.53	0.467
20	2.39	0.122	4.10	0.043
30	0.00	0.965	7.40	0.007
50	2.12	0.145	13.01	<0.001
80	0.70	0.402	11.89	0.001

Boundary Strength Analysis (BSA)

The boundary contrast between spiders and tree backgrounds was significantly different for rough and smooth types across most viewing distances. The exceptions were 50cm for the rough type and 2, 10 and 50cm for the smooth type. At longer viewing distances the boundary contrasts increased faster for both types of spiders than for their respective tree backgrounds (Figure 8C, Table 8).

Table 8. Boundary strength analysis comparing spiders against their tree backgrounds within surface types (rough and smooth) at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Rough		Smooth	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	10.96	0.001	0.63	0.429
5	11.56	0.001	4.90	0.027
10	12.79	<0.001	1.03	0.311
20	10.39	0.001	9.03	0.003
30	8.24	0.004	8.84	0.003
50	1.42	0.233	0.44	0.506
80	5.33	0.021	14.41	<0.001

LEIA - Colour

The colour boundary contrast was significantly lower for spiders than for the tree backgrounds of both surface types and across most viewing distances. The exceptions were 80cm for the rough type and 2cm for the smooth type (Figure 8D, Table 9).

Tabel 9. LEIA colour analysis comparing spiders against their tree backgrounds within surface types (rough and smooth) at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Rough		Smooth	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	5.07	0.024	0.96	0.327
5	8.24	0.004	9.23	0.002
10	12.79	<0.001	15.64	<0.001
20	10.96	0.001	17.97	<0.001
30	9.28	0.002	17.18	<0.001
50	5.90	0.015	17.71	<0.001
80	0.86	0.354	17.44	<0.001

LEIA - Luminance

The luminance boundary contrast was significantly different between spiders and tree backgrounds of both surface types (rough and smooth) and across most distances, except for 30cm for the rough type. Luminance boundary contrast increased for both spider types from the 20cm viewing distance, but not for the tree backgrounds. At the longest viewing distance of 80cm, the contrast was higher for the rough spiders compared with the smooth spiders (Figure 8E, Table 10).

Table 10. LEIA luminance analysis comparing spiders against their tree backgrounds within surface types (rough and smooth) at seven viewing distances using Kruskal-Wallace tests (h-statistic). Sample size, rough = 9 (spiders and background); smooth = 18 (spiders and background). Degrees of freedom for all tests = 1.

	Rough		Smooth	
Distance (cm)	h-statistic	P (corrected)	h-statistic	P (corrected)
2	12.79	<0.001	26.27	<0.001
5	12.79	<0.001	26.27	<0.001

10	12.79	<0.001	26.27	<0.001
20	9.83	0.002	26.27	<0.001
30	0.44	0.508	24.67	<0.001
50	6.79	0.009	8.29	0.004
80	12.17	<0.001	5.78	0.016

Scenario Comparison

A specific camouflage prediction that we set out in the introduction was that contrasts between the spider and the tree background would be lowest where each spider was located (matching), increasing against a random patch on the same tree type (non-matching) and greatest against a ‘foreign’ background from a different tree type that is usually not utilised by the spider species (unrelated).

Given our study design, we could calculate the absolute difference between the estimated metrics for spiders and the tree trunk backgrounds in three different scenarios. The first scenario is the difference between the spiders and the particular background where each spider was located (matching). The second scenario is the difference between spiders and a randomly chosen background sample from the same surface type excluding its own occupied background (nonmatching). The third scenario is the difference between the spiders and a randomly chosen background sample from the opposite surface type - i.e. smooth spider vs rough background and rough spider vs smooth background (unrelated).

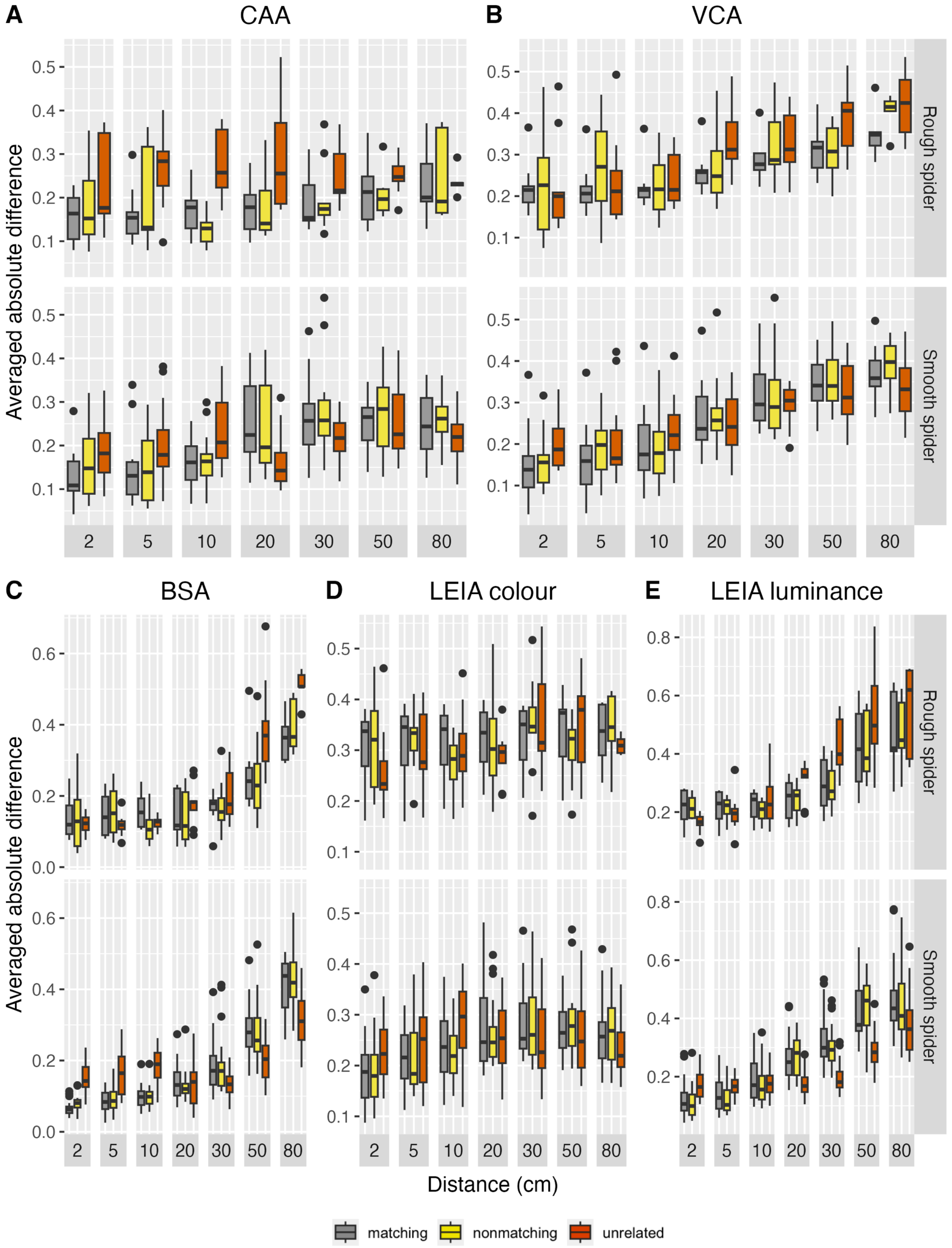


Figure 9. Boxplots of the absolute difference between spiders and backgrounds within the metrics of the QCPA data domains: A, Colour Adjacency; B, Visual Contrast; C, Boundary Strength; D, Local Edge Intensity (colour); E, Local Edge Intensity (luminance). In each panel, the boxplots compare three different background scenarios: matching - spiders against the backgrounds they were found on (yellow); non-matching - spiders against a background of the same surface type (blue); unrelated - spiders against a background type (smooth or rough) that is different to their

own surface type (green). Comparisons are modelled for seven different viewing distances (2-80cm) for each spider species - *T. fickertii* (rough) and *T. brisbanensis* (smooth).

Colour Adjacency Analysis (CAA)

The differences in Colour Adjacency (CAA) metrics describe the diversity of colour pattern elements. For rough spiders, the background scenario had a significant effect on colour adjacency, specifically, rough spiders on unrelated backgrounds (ie smooth backgrounds) had a significantly higher pattern diversity 10cm and marginally at 20cm compared with the matching and non-matching background scenarios. The other distances were not significant (Figure 9A, Table 11).

For the smooth spiders, the background scenario also had a significant effect on colour adjacency, with unrelated backgrounds being significantly different to the other background scenarios at most distances (2, 5, 10 and 20cm). Additionally, the unrelated scenario was not significantly different to the non-matching background at close distances (2 & 5 cm) (Figure 9A, Table 12).

Visual contrast Analysis (VCA)

Overall, we found few differences between the background scenarios and viewing distances for the VCA metrics, which describe the visual contrast between the elements of a given colour pattern. For rough spiders, the unrelated background was marginally significantly different from the unmatched background at 20 cm only (Figure 9B, Table 11).

For the smooth spiders, the visual contrast against the unrelated background (smooth spider against a rough background) was significantly higher than that of the non-matched and matched backgrounds at 2cm. By contrast at 80cm viewer distance, the visual contrast was lower against non-matching backgrounds compared with the unrelated background (Figure 9B, Table 12).

Boundary Strength Analysis (BSA)

The Boundary Strength (BSA) metrics describe the edge contrast within the colour patterns of the spiders and the background. We found a significantly higher contrast between the rough spiders and the unrelated background (smooth background) at 50 and 80cm, but not among any other distances or background scenarios (Figure 9C, Table 11).

The difference in boundary strength of the smooth spider against the unrelated background scenario was significantly higher than the other two scenarios at close viewing distances (2-10cm). At the closest viewing distance (2cm) the boundary contrast difference between spiders and the non-matching backgrounds was higher than for spiders on their matching backgrounds. At the longest viewing distances (30-80cm), this pattern reversed with the difference of the unrelated scenario being significantly lower than the matching and non-matching scenario (Figure 9C, Table 12).

LEIA-Colour

LEIA describes the edge colour contrast within patches of the colour patterning in spiders and backgrounds. For rough spiders, we did not find any significant differences between the three background scenarios at any viewing distance (Figure 9D, Table 11). While for the smooth spiders, the difference against the unrelated scenario was significantly higher than the non-matching scenario at 10cm and all other scenarios and distances were not significant (Figure 9D, Table 12).

LEIA-Luminance

LEIA luminance describes the achromatic edge contrast within patches of the colour patterning in spiders and backgrounds. We found a significantly lower contrast in rough spiders on unrelated bark backgrounds compared with non-matching backgrounds at 2cm. Conversely, at the 20 and 30cm viewing distances, the differences in luminance edge contrast were significantly higher in unrelated compared with non-matching backgrounds (Figure 9E, Table 11). For the smooth spiders, the difference in luminance edge contrast was significantly higher against unrelated backgrounds (i.e. rough tree backgrounds) than the other two background scenarios at 2cm and higher than the non-matching category at 5cm. Between 20 and 50cm viewing distances the luminance contrast difference was significantly lower for spiders on unrelated backgrounds than the other background scenarios while at 80cm this difference was only significant against the matching background (Figure 9E, Table 12).

It is helpful to point out that the comparisons of matching with non-matching backgrounds were non-significant for almost all distances in smooth and rough spiders - the only exception being boundary strength at 2cm for smooth spiders.

Table 11. Results of the pairwise Wilcoxon Rank Sum test comparing the different background scenarios for rough spiders, *T. fickertii*. We only listed pairwise comparisons if the Kruskal-Wallace model indicated a significant (<0.05) or marginal (=/<0.06) difference in the metrics of the QCPA domains for the triad (comparing the three background scenarios).

Domain	Distance (cm)	Comparison	P (corrected)
CAA	10	unrelated - matching	0.008
	10	unrelated - nonmatching	<0.001
	20	unrelated - matching	0.060
	20	unrelated - nonmatching	0.060
VCA	20	unrelated - matching	0.056
BSA	50	unrelated - matching	0.037
	50	unrelated - nonmatching	0.037
	80	unrelated - matching	0.048
	80	unrelated - nonmatching	0.048
LEIA luminance	2	unrelated - nonmatching	0.017
	20	unrelated - matching	0.037
	20	unrelated - nonmatching	0.037
	30	unrelated - matching	0.021
	30	unrelated - nonmatching	0.017

Table 12. Results of the pairwise Wilcoxon Rank Sum test comparing the different background scenarios for smooth spiders, *T. brisbanensis*. We only listed pairwise comparisons if the Kruskal-Wallace model indicated a significant (<0.05) or marginal (=/<0.06) significant difference in the metrics of the QCPA domains for the triad (comparing the three background scenarios).

Domain	Distance (cm)	Comparison	P (corrected)
CAA	2	unrelated - matching	0.005
	5	unrelated - matching	0.039
	10	unrelated - matching	0.028
	10	unrelated - nonmatching	0.028
	20	unrelated - matching	0.002
	20	unrelated - nonmatching	0.008
VCA	2	unrelated - matching	0.035
	2	unrelated - nonmatching	0.056
	80	unrelated - nonmatching	0.035

BSA	2	nonmatching - matching	0.047
	2	unrelated - matching	<0.001
	2	unrelated - nonmatching	<0.001
	5	unrelated - matching	<0.001
	5	unrelated - nonmatching	<0.001
	10	unrelated - matching	<0.001
	10	unrelated - nonmatching	<0.001
	30	unrelated - matching	0.056
	30	unrelated - nonmatching	0.056
	50	unrelated - matching	0.002
	50	unrelated - nonmatching	0.005
	80	unrelated - matching	0.002
	80	unrelated - nonmatching	0.001
LEIA colour	10	unrelated - nonmatching	0.024
LEIA luminance	2	unrelated - matching	0.009
	2	unrelated - nonmatching	0.002
	5	unrelated - nonmatching	0.007
	20	unrelated - matching	<0.001
	20	unrelated - nonmatching	<0.001
	30	unrelated - matching	<0.001
	30	unrelated - nonmatching	<0.001
	50	unrelated - matching	<0.001
	50	unrelated - nonmatching	<0.001
	80	unrelated - matching	0.035

Discussion

Here we utilised a novel analytical method to investigate the nature of camouflage in hersilid spiders that typically sit against tree trunks (Baehr & Baehr, 1987). To the human observer, the spider on the tree trunk appears superbly camouflaged. Our study takes advantage of two sympatric Hersiliidae species that differ in their colouration patterns and occupy rather different niches. Specifically, they occupy different tree species with either very smooth or very rough bark. Here we aimed to quantitatively assess differences in colouration patterns between the two different spider species, the two different backgrounds as well as the spiders against the background. This will help us to understand the role of colour patterns in the cryptic appearance as perceived by a potential predator. Our analyses support the overall hypothesis we posed in the introduction that each species is most cryptic against the background that it naturally occupies.

We took an unconventional analytical approach that goes beyond estimating how the colour or luminance of spiders contrasts against their backgrounds. We applied the QCPA framework that was developed by van den Berg et al (2020) and has been argued to be a modern pipeline for the study of colour patterns (Mason & Bowie, 2020; Yang et al., 2021). The novelty of this approach is that it combines colour, luminance, pattern and estimated viewer acuity with the option of factoring different viewer distances into the analysis (van den Berg et al., 2020). In addition, this analytical tool also comes with a user-friendly interface that collapses several laborious steps. To date, this framework has had some discussion in the literature regarding its potential value (Mason & Bowie, 2020; Yang et al., 2021), but it is yet to be extensively tested with real biological systems. However, QCPA and MICA are more often used in combination for their different sets of built-in tools for image processing and visual modelling rather than applying the complete pipeline for the quantification of colouration patterns -for examples see, (Rodríguez-Morales et al., 2021; McLellan, Scott-Samuel & Cuthill, 2021; Trapp & Fernández-Juricic, 2022).

Some of the current notable examples include quantifying background matching in Sahara-Sahel desert rodents (Nokelainen et al., 2020) and the quantification of sexual dimorphism in jumping spiders (Zhou et al., 2021). The QCPA was also applied to “debunk” the myth that giant pandas (*Ailuropoda melanoleuca*) are highly conspicuous in their natural habitats. Instead, pandas seem to match elements of their surroundings at closer distances while their colouration generates a high edge disruption at longer viewing distances (Nokelainen et al., 2021). Finally, this methodological framework was highly praised for its potential to open novel avenues of research for extensively studied colour systems such as bird plumages. Specifically, the ease of access to sophisticated analyses for colour, luminance and its spatial distribution (ie. colour patterning) allows the exploration of novel ecological questions as well as classic evolutionary hypotheses (Mason & Bowie, 2020).

In the application of the QCPA, we made the following observations regarding its usability. This method generates a large number (in excess of 158) of colour, pattern and luminance metrics from multispectral digital images. This amount of metrics is quite challenging and difficult to manage, as many of the metrics within or across domains are strongly correlated. Depending on the underlying shared parameters, some metrics might covary either positively or negatively while still containing useful information and are thus not redundant. The number of metrics that covary and the nature of the correlation depends on the underlying data and taxa. Van den Berg et al. (2020) caution about comparing the perception of colour patterns by highly divergent taxa.

It is difficult to evaluate the suitability of the metrics due to the complex underlying algorithms and assumptions, which are available in the extensive supplementary of the original paper (van den Berg et al., 2020). Nevertheless, the user is confronted with a large set of metrics involving complex formulae and with only minor differences between the metrics (eg., estimated and relative

Simpson and Shannon diversity indexes). The authors leave it up to the user to determine the best fit of selected variables or the methods to collapse these variables to accommodate the particular research question of interest. At this stage, this methodology requires more user uptake to validate the strengths and weaknesses of these metrics across visual systems and to explore ways of selecting QCPA metric outputs.

Our approach was not to select and analyse individual metrics, but to combine them all within the five data domains (Colour Adjacency, Visual Contrast, Boundary Strength, and Local Edge Intensity Analyses - colour and luminance variants). The upside of this was that we considered all metrics without inflating the number of comparisons (type I error). The downside is that we lose perspective on which specific metric contributes to any observed overall difference. Other studies selected either just specific data domains and compared the metrics within these independently (Nokelainen et al., 2021) or just selected very specific outputs from the analytical tools (Mason & Bowie, 2020). Zhou et al. (2021) utilised dimension reduction via multivariate analysis (Principal Components Analysis, PCA) to collapse variables from the VCA and BSA domains into a manageable number of variables for direct comparisons.

There is no doubt that we could have spent many more weeks and months exploring different ways of analysing this vast set of metrics, in the absence of a trialled frame of reference or general consensus. We do hope that our approach will instigate other researchers to further refine the utility of the QCPA. Despite these complexities, we believe that QCPA offers great advantages that, unlike most other available methods, allow us to pull together different dimensions involved in visual perception of the world of colour.

Colour pattern analyses

In this study, we focused on the colour patterns on the bodies of spiders and their immediate background against the tree trunk surface. The elements that make up these patterns include colour (chromatic) and luminance (achromatic), the size of these chromatic and achromatic patches and the boundaries between them. The Colour Adjacency and Visual Contrast metrics describe these elements within a pattern, excluding the boundaries where elements meet. The Boundary Strength and Local Edge Intensity (colour and luminance) on the other hand describe metrics at the boundaries, where colour patches meet (van den Berg et al., 2020).

Based on human perception, the rough spider and bark surface appeared richer in patterns from which we perceived a higher contrast. On the other hand, the smooth spider and bark surface contained more homogenous pattern elements and appeared less contrasting. Thus, under human visual perception these two surfaces appear readily discriminable, while the spiders seem relatively camouflaged against their relevant background (e.g. smooth spider against smooth bark). However, this might not be true for the ecologically relevant observers of Hersiliidae spiders in this system.

Surface type comparison

Generally, rough surfaces showed higher geometric diversity and complexity of their colour patterns than smooth surfaces (CAA). However, we found that the elements that describe the overall contrast of the colour patterns varied distinctly between the surface types. While the contrast within a colour pattern was not different between rough and smooth surfaces (VCA), the contrast between colour patterns (i.e. boundaries - the zone where colour patterns meet) was more effective in separating the two types of surface (BSA, LEIA-colour and LEIA-luminance).

Spider to background comparison

When comparing spiders against tree backgrounds we found different trends between the rough and smooth types. Rough spiders better matched the geometric attributes of their rough backgrounds than smooth spiders against smooth backgrounds (CAA). Similarly, within-colour pattern element contrast was better matched between rough spiders and backgrounds, while smooth spiders generally contrasted the background elements (VCA). Despite these differences in within-colour pattern elements between the two spiders and their backgrounds, both spiders differed largely from their backgrounds in the between-colour pattern elements (boundary) contrast (combined in BSA and in LEIA colour and luminance).

The question here is, whether receivers pay more attention to differences within or between colour patterns. Both are likely to rely on different visual mechanisms. For instance, low contrast patterns could better match the background, rendering the subject cryptic and difficult to detect (Merilaita & Lind, 2005; Troscianko et al., 2009). While high contrast patterns, instead will break the shape of the subject and thus prevent recognition (Cuthill et al., 2005; Stevens & Merilaita, 2009b). At this stage, we have no behavioural data to evaluate the salience of these pattern elements, but experiments using artificial prey have shown that high contrast disruptive patterns in the outline of moths' shape reduce detection against heterogenous backgrounds and thus confer protection on a wider range of environments. On the other hand, reduced detection via strategies of colour matching are background specific and thus more restrictive (Schaefer & Stobbe, 2006). This becomes more important when considering the viewing distance of the observer. Specifically, within-colour pattern contrasts are more likely to be detected only at short viewing distances while between-colour pattern contrasts could be detectable at longer viewing distances (Osorio & Vorobyev, 2005; Kang, Kim & Jang, 2016).

The effect of viewing distance

As argued above, viewing distance will impact the perception of colour patterns and is directly related to visual acuity and the resulting perception of fine detail (Osorio & Vorobyev, 2005; Barnett & Cuthill, 2014; Nokelainen et al., 2021). As humans, we are familiar with our own visual limitations with respect to discerning details with increasing distance. For instance, we have all experienced that text becomes harder to read as we move away from a sign or a screen.

In nature, the effect of viewing distance on the ability of animals to perceive details has important ecological implications. For example, active foraging predators first need to locate/recognise potential prey in their environments before directing their focus and movement towards it. Thus, the predator can only detect its prey at a minimal visual acuity, which will increase as it moves closer, facilitating an accurate attack (Cronin et al., 2014; Caves, Brandley & Johnsen, 2018).

We originally predicted that the difference between surface types (smooth, rough) and spiders against their background would decrease with viewing distance in all domains. However, we did not find a single consistent trend along with viewing distances. Instead, we saw all combinations of increase and decrease in metrics across different domains.

The differences between the two tree trunk surfaces decreased for all domain metrics with increasing viewing distance, except for boundary luminance contrast (LEIA-luminance). This means when a bird views the two trees from a distance, the boundaries of the colour patterns would be the most conspicuous aspect. However, when we compared spider species, the effect of viewing distance was not consistent across the domains. The within-colour pattern contrast did not differ between spider species at any viewing distance. On the contrary, the luminance contrast of the boundaries did differ at all distances. This suggests, our selected bird visual system has a limited ability to distinguish differences between the individual elements in the colour patterns of both spider species. However, the edge of the elements in the body of the rough spider were more salient than those on the smooth spider.

Critical from an anti-predatory perspective is how spiders are viewed against their background from a distance. Rough spiders were better matched in the within-colour patterns with their backgrounds than the smooth spiders throughout the full range of modelled viewing distances. However, the between-colour pattern contrasts were stable, even when viewed at increasing distances for both spider species. The boundary colour contrast of both spiders was consistently lower than that of the tree backgrounds but unaffected by viewing distance. Conversely, boundary luminance contrast increased with viewing distance for both spider species. So, in sum, the contrasts of colour patterns created by spiders against the tree backgrounds are very complex, the different colour domains are not acting synergistically with viewing distance, contrary to how we might intuitively assume based on our own visual experience. Moreover, how a bird viewer might integrate this complex information or whether some visual information is more salient than others is not known. Nevertheless, our results identify the elements of colour pattern contrasts that could be manipulated in behavioural tests with bird viewers. For example, one could create prey models with variably contrasting luminance boundary edges and test their detectability from a range of viewing distances.

Some studies have manipulated the level of colour matching and disruptive patterning on the wings of artificial moth prey to evaluate predation by birds (Cuthill et al., 2005), others manipulated the spatial frequency of salient signals (aposematic coloured stripes) in caterpillars (Tullberg, Merilaita & Wiklund, 2005; Barnett, Cuthill & Scott-Samuel, 2018).

Different studies independently showed that the position and contrast of colour patterns are interrelated and their perception is affected by distance. For instance, at a given viewing distance, any visual system reaches its limit to distinguish independent lines and even aposematic signals can turn into camouflage that blends with the surroundings (Barnett, Cuthill & Scott-Samuel, 2018). Alternative, highly contrasting patterns can render the outline shape of animals (either moths or giant pandas) unrecognisable, an effect that increases with distance. The disruptive marks become more salient at greater distances and prevent recognition of the rest of the body.

Scenario comparison

Finally, we utilised the QCPA data to estimate absolute differences in the domain metrics between spiders and backgrounds under three different scenarios - spiders against their home background, against a random background of their respective surface type (e.g. smooth spider against a smooth tree) and against a different surface type (e.g. smooth spider against a rough tree). Overall, we predicted the least contrast for spiders against their home background and the greatest contrast against a different surface type.

Overall, according to our prediction, we found that the difference between spiders and backgrounds was greater when the background did not match the spider’s surface type (i.e., when a rough spider sat on a smooth background or a smooth spider sat on a rough background). However, within the same surface type, it did not seem to matter where the spider was sitting on the tree, as long as the surface type matched. This is surprising because we observed that these hersillid spiders show great microsite fidelity - we observed the same individual occupying the identical position on a tree for several days and even weeks. The literature on hersillids is mostly focused on their taxonomy and with very few descriptions of their behaviour on the tree trunk (Baehr & Baehr, 1987; Metwally, Mowaf & Mohafez, 2001; Rheims & Brescovit, 2004) and no research published to date that describes their site selection. There are several, non-visual explanations to explain this remarkable site fidelity. First, they may have invested silk in preparing the substrate for occupation. The jumping spider *Arasia mullion* is unusually sedentary on the surface of tree trunks where they spend hours building and decorating their silk retreats (Aceves-Aparicio et al., 2022). Second, they may minimise movement to reduce predator detection (Stevens & Ruxton, 2019), and finally, they may have selected optimal microclimates on the tree surface (Prinzing, 2001; Villanueva-Bonilla et al., 2021).

Our data also suggest that rough spiders are generalists in terms of camouflage as they did equally well against smooth and rough surfaces. Smooth spiders on the other hand seemed to better reduce their overall conspicuousness when occupying smooth trees but not rough trees. This might predict that rough spiders can occupy a greater range of trees than smooth spiders. Indeed, we recorded rough spiders on intermediately smooth trees on several occasions but never found any smooth spiders against rougher trees. Clearly, more extensive surveys are required to confirm these observations.

Conclusion

In conclusion, the QCPA approach has great potential in linking spatial elements of colour patterns with viewer identity and viewing distance into a single analysis. It generates a rich tapestry of data that can however be overwhelming to the user. Critically, the analysis generates predictions of how viewers might perceive complex colour patterns, that ultimately require the establishment of thresholds based on behavioural tests with relevant viewers. In this context, hersillid spiders offer an excellent study model because of the complexity and variation of their body colouration and their tree backgrounds.

References

Aceves-Aparicio A, McLean DJ, Wild Z, Schneider JM, Herberstein ME. 2022. Novel decorating behaviour of silk retreats in a challenging habitat. *PeerJ 10:e12839*.

Arias M, Tedore C, Elias M, Leroy L, Madec C, Matos L, Renoult JP, Gomez D. 2020. Deep neural network and field experiments reveal how transparent wing windows reduce detectability in moths. *bioRxiv*. DOI: 10.1101/2020.11.27.401497.

Baehr B, Baehr M. 1987. The Australian Hersiliidae (Arachnida: Araneae): Taxonomy, phylogeny, zoogeography. *Invertebrate Systematics* 1:351.

Barnett JB, Cuthill IC. 2014. Distance-dependent defensive coloration. *Current Biology* 24:R1157–8.

Barnett JB, Cuthill IC, Scott-Samuel NE. 2018. Distance-dependent aposematism and camouflage in the cinnabar moth caterpillar (*Tyria jacobaeae*, Erebidae). *Royal Society Open Science* 5:171396.

Battiston R, Fontana P. 2010. Colour change and habitat preferences in *Mantis religiosa*. *Bulletin of Insectology* 63:85–89.

Benjamini Y, Hochberg Y. 1995. Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society* 57:289–300.

van den Berg CP, Troscianko J, Endler JA, Marshall NJ, Cheney KL. 2020. Quantitative Colour Pattern Analysis (QCPA): A comprehensive framework for the analysis of colour patterns in nature. *Methods in Ecology and Evolution* 11:316–332.

Briscoe AD, Chittka L. 2001. The evolution of color vision in insects. *Annual Review of Entomology* 46:471–510.

Caves EM, Brandley NC, Johnsen S. 2018. Visual acuity and the evolution of signals. *Trends in Ecology & Evolution* 33:358–372.

Cronin TW, Johnsen S, Marshall NJ, Warrant EJ. 2014. *Visual ecology*. Princeton University Press.

Cuthill IC. 2019. Camouflage. *Journal of Zoology* 308:75–92.

Cuthill IC, Stevens M, Sheppard J, Maddocks T, Párraga CA, Troscianko TS. 2005. Disruptive coloration and background pattern matching. *Nature* 434:72–74.

Di Cesnola AP. 1904. Preliminary note on the protective value of colour in *Mantis religiosa*. *Biometrika* 3:58–59.

Friedman JH. 1989. Regularized Discriminant Analysis. *Journal of the American Statistical Association* 84:165–175.

Grant B, Howlett RJ. 1988. Background selection by the peppered moth (*Biston betularia* Linn.): individual differences. *Biological Journal of the Linnean Society* 33:217–232.

Kang C, Kim YE, Jang Y. 2016. Colour and pattern change against visually heterogeneous backgrounds in the tree frog *Hyla japonica*. *Scientific Reports* 6:22601.

Kang C, Stevens M, Moon J-Y, Lee S-I, Jablonski PG. 2014. Camouflage through behavior in moths: the role of background matching and disruptive coloration. *Behavioral Ecology* 26:45–54.

Kelber A, Osorio D. 2010. From spectral information to animal colour vision: experiments and concepts. *Proceedings* of the *Royal Society of London. Series B, Biological Sciences* 277:1617–1625.

Kelber A, Vorobyev M, Osorio D. 2003. Animal colour vision--behavioural tests and physiological concepts. *Biological Reviews* 78:81–118.

Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshall J, Whiting MJ. 2015. An integrative framework for the appraisal of coloration in nature. *The American Naturalist* 185:705–724.

Kettlewell HBD. 1955. Selection experiments on industrial melanism in the Lepidoptera. *Heredity* 9:323–342.

Koshitaka H, Kinoshita M, Vorobyev M, Arikawa K. 2008. Tetrachromacy in a butterfly that has eight varieties of spectral receptors. *Proceedings* of the *Royal Society of London. Series B, Biological Sciences* 275:947–954.

Kuhn M. 2008. Building Predictive Models in R Using the caret Package. *Journal of Statistical Software* 28:1–26.

Marshall NJ. 2000. Communication and camouflage with the same “bright” colours in reef fishes. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences* 355:1243–1248.

Mason NA, Bowie RCK. 2020. Plumage patterns: Ecological functions, evolutionary origins, and advances in quantification. *The Auk* 137:1-29.

McLellan CF, Scott-Samuel NE, Cuthill IC. 2021. Birds learn to avoid aposematic prey by using the appearance of host plants. *Current Biology* 31:5364–5369.

Merilaita S, Lind J. 2005. Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proceedings* of the *Royal Society of London. Series B, Biological Sciences* 272:665–670.

Merilaita S, Scott-Samuel NE, Cuthill IC. 2017. How camouflage works. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences* 372. DOI: 10.1098/rstb.2016.0341.

Metwally AM, Mowaf MH, Mohafez MA. 2001. Biological aspects of *Hersilia caudata* Savigny, 1825 (Arachnida: Araneida: Hersiliidae). *Serket* 7:108 113.

Mollon JD. 1989. “Tho’she kneel'd in that place where they grew…” The uses and origins of primate colour vision. *The Journal of Experimental Biology* 146:21–38.

Nokelainen O, Brito JC, Scott-Samuel NE, Valkonen JK, Boratyński Z. 2020. Camouflage accuracy in Sahara-Sahel desert rodents. *The Journal of Animal Ecology* 89:1658–1669.

Nokelainen O, Scott-Samuel NE, Nie Y, Wei F, Caro T. 2021. The giant panda is cryptic. *Scientific Reports* 11:21287.

Osorio D, Vorobyev M. 2005. Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proceedings* of the *Royal Society of London. Series B, Biological Sciences* 272:1745–1752.

Osorio D, Vorobyev M. 2008. A review of the evolution of animal colour vision and visual communication signals. *Vision Research* 48:2042–2051.

Pembury Smith MQR, Ruxton GD. 2020. Camouflage in predators. *Biological Reviews* 95:1325–1340.

Prinzing AJ. 2001. Use of shifting microclimatic mosaics by arthropods on exposed tree trunks. *Annals of the Entomological Society of America* 94:210–218.

R Core Team. 2022. R: A Language and Environment for Statistical Computing.

Rheims CA, Brescovit AD. 2004. Revision and cladistic analysis of the spider family Hersiliidae (Arachnida, Araneae) with emphasis on Neotropical and Nearctic species. *Insect Systematics & Evolution* 35:189–239.

Rodríguez-Morales D, Tapia-McClung H, Robledo-Ospina LE, Rao D. 2021. Colour and motion affect a dune wasp's ability to detect its cryptic spider predators. *Scientific Reports* 11:15442.

Sargent TD. 1966. Background Selections of geometrid and noctuid Moths. *Science* 154:1674–1675.

Schaefer HM, Stobbe N. 2006. Disruptive coloration provides camouflage independent of background matching. *Proceedings* of the *Royal Society of London. Series B, Biological Sciences* 273:2427–2432.

Silvasti SA, Valkonen JK, Nokelainen O. 2021. Behavioural thresholds of blue tit colour vision and the effect of background chromatic complexity. *Vision Research* 182:46–57.

Skelhorn J, Rowe C. 2016. Cognition and the evolution of camouflage. *Proceedings* of the *Royal Society of London. Series B, Biological Sciences* 283:20152890.

Stevens M, Alejandro Párraga C, Cuthill IC, Partridge JC, Troscianko TS. 2006. Using digital photography to study animal coloration. *Biological Journal of the Linnean Society* 90: 211-237.

Stevens M, Cuthill IC. 2006. Disruptive coloration, crypsis and edge detection in early visual processing. *Proceedings* of the *Royal Society of London. Series B, Biological Sciences* 273:2141–2147.

Stevens M, Merilaita S. 2009a. Animal camouflage: current issues and new perspectives. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences* 364:423–427.

Stevens M, Merilaita S. 2009b. Defining disruptive coloration and distinguishing its functions. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences* 364:481–488.

Stevens M, Ruxton GD. 2019. The key role of behaviour in animal camouflage. *Biological Reviews* 94:116–134.

Sukontason KL, Chaiwong T, Piangjai S, Upakut S, Moophayak K, Sukontason K. 2008. Ommatidia of blow fly, house fly, and flesh fly: implication of their vision efficiency. *Parasitology Research* 103:123–131.

Thoen HH, How MJ, Chiou T-H, Marshall J. 2014. A different form of color vision in mantis shrimp. *Science* 343:411–413.

Trapp R, Fernández-Juricic E. 2022. How visual system configuration can play a role in individual recognition: a visual modeling study. *Animal Cognition* 25:205–216.

Troscianko T, Benton CP, Lovell PG, Tolhurst DJ, Pizlo Z. 2009. Camouflage and visual perception. *Philosophical transactions of the Royal Society of London. Series B, Biological Sciences* 364:449–461.

Troscianko J, Stevens M. 2015. Image calibration and analysis toolbox - a free software suite for objectively measuring reflectance, colour and pattern. *Methods in Ecology and Evolution* 6:1320–1331.

Tullberg BS, Merilaita S, Wiklund C. 2005. Aposematism and crypsis combined as a result of distance dependence: functional versatility of the colour pattern in the swallowtail butterfly larva. *Proceedings* of the *Royal Society of London. Series B, Biological Sciences* 272:1315–1321.

Villanueva-Bonilla GA, Messas YF, Souza HS, Gonzaga MO, Brescovit AD, Vasconcellos-Neto J. 2021. Trunk structural complexity determines the diversity of bark-dwelling spiders in a tropical forest. *Ethology Ecology & Evolution* 33:108–124.

Yang C, Wang J, Lyu N, Lloyd H. 2021. Comparison of digital photography and spectrometry for evaluating colour perception in humans and other trichromatic species. *Behavioral Ecology and Sociobiology* 75:151.

Zhou W, Yu L, Kwek BZW, Ge J, Zeng H, Li D. 2021. Sexual selection on jumping spider colour pattern: investigation with a new quantitative approach. *Behavioral Ecology* 32:695–706.

Supplementary materials

Data and code for analysis available at:

https://github.com/PonchoAceves/hersiliidae_mq

Thesis conclusions

Main aims

In this thesis, I aimed to analyse and describe the ecological strategies, specifically the predatory and anti-predatory strategies, of tree-trunk spiders. While considerable previous work on tree trunks has focused on the diversity of the inhabiting species (Nicolai, 1993; Rosen, 2000; Heterick, Majer & Recher, 2001; Majer, Recher, Heterick, & Postle, 2001; Proctor et al., 2002; Bickel & Tasker, 2004), the intricate relationship between tree trunks as a specific niche and the species inhabiting them has not often been given much attention (but see (but see Bulbert, Herberstein & Cassis, 2014).

At first, it may seem counterintuitive to consider tree trunks as a habitat that can provide the resources to sustain prolonged occupation as tree trunks are highly exposed to both abiotic and biotic elements and have limited nutritional resources for herbivores (Nicolai, 1986; Gunnarsson, 1990; Rodgers & Kitching, 1998; Proctor et al., 2002; Villanueva-Bonilla, Salomão & Vasconcellos-Neto, 2017). With limited physical cover, exposure to wind, rain and sun radiation can potentially impose considerable physiological costs (Nicolai, 1986). Similarly, exposure to predators but also visibility to potential prey is likely to be high on tree trunks due to the lack of cover and background complexity. This would particularly affect mesopredators such as spiders.

Despite the potential limitations associated with tree trunks, I identified three species of spiders that permanently reside on tree trunks and that are highly specialised in reducing detection and in capturing prey effectively. To my best knowledge, some of the strategies used by these spiders were described in detail here for the first time.

My approach

I decided to embark on a PhD journey where I could progress my personal interest in understanding the natural history of animals in the wild while expanding my scientific skillset and academic research vision. I started with a solid knowledge of Mexican spiders (Rao & Aceves-Aparicio, 2012; Aceves-Aparicio et al., 2018), including initial observations of tree trunk Hersiliidae and moved to Australia where the diversity of Hersiliidae spiders is considerable (Rheims & Brescovit, 2004).

I swiftly launch myself into exploring my new environment, new city/country/continent. I set out my search with an expectation to find hersiliids, but then made unexpected discoveries of other unique inhabitants of tree trunks, spiders building and living in decorated silk retreats (aka “blankies”) and the nocturnal ant-hunting by the “ant-slayer”. These discoveries transformed my research from investigating “camouflage against tree trunks" to “how do tree trunk spiders exploit their habitat?”.

I first made careful and prolonged observations in the field to develop specific questions about life on tree trunks. Then I started by asking the following questions: 1) how can spiders make a living in this habitat with apparently limited resources compared to the canopies or the ground? and 2) how do these spiders overcome the risks of limited cover to hide from visual detection?

To capture the finer details of the predatory and anti-predatory behaviour of these three species of tree trunk spiders, I used a variety of high-tech methodologies and modelling tools - such as high-speed videography, spectrophotometry, multi-spectral photography and distinct visual modelling computational methods. Throughout the chapters in my thesis, I find particularly interesting the variability in strategies to deal with this same problem in different ways, such as nocturnal behaviour, permanent retreats and sophisticated camouflage colour patterns.

Predatory strategies

Spiders are the largest group of predators (Coddington & Levi, 1991; Nyffeler & Birkhofer, 2017) and considerable research focuses on their predator strategies (Barrantes & Eberhard, 2007; Herberstein, 2011; Pekár & Toft, 2015; Michálek et al., 2018). How spiders that permanently occupy tree trunks access sufficient prey, was a particular research question in my thesis and has not been studied extensively, but for notable examples of camouflage (Gawryszewski, 2014) and gliding behaviour (Yanoviak, Munk & Dudley, 2015). Tree trunks can be considered as connective “highways” between ground and canopies for wandering prey or as landing sites for flying insects (Proctor et al. 2002) and thus provide potential prey to spiders that utilise the trunk in such a transient manner.

I discovered the extraordinary predatory behaviour of the ant slayer (Chapter 1) after a fortuitous observation of a predation event at dusk, whilst walking back home across campus. I found a large *Camponotus* ant hanging off a silk thread with a small spider feeding on it. After closer inspection of the tree trunk, I noticed another spider sitting flat against the trunk. This led to the question, how did this tiny spider manage to overcome such a large and dangerous ant? This casual observation instigated an intensive field study that combined high-speed footage, prey manipulation and video tracking. From these observations, it is clear that 1) the intricate predatory sequence is adapted to a vertical environment and 2) it exploits a seemingly unlimited resource of prey - nocturnal ants that move up the tree trunk to forage in the tree canopy. Hunting ants is not uncommon in theridiid spiders, but most do so on the ground with or without a web (Liu et al., 2016; Eberhard, 2020). How and why the ant slayer moved onto trunks is unclear, but the selective advantage could be 1) safer vertically positioning against large and dangerous prey that allows a quick escape by simply dropping to the ground or 2) access to more prey that is concentrated on trunks.

I observed an alternative strategy on the same tree trunks in a jumping spider, *Arasia mullion, which* also provides indirect information about how they might adapt their predatory behaviour to the tree trunk environment (Chapters 2 and 3). I observed that these jumping spiders remained unusually sedentary within their silk retreats that are constructed against the surface of tree trunks. Typically, jumping spiders are very mobile moving swiftly through the environment. After studying a large population of *A. mullion* for 18 months, I documented the construction and decoration of the retreats with bark debris from the immediate surroundings. I modelled the likely effect of decoration in reducing the visibility of the silk to potential observers, including approaching prey. When foraging, these spiders are visually triggered by nearby prey, such as small flies or other insects, lunging at the prey from the retreat. However, not all prey elicited this behaviour, when the spiders detected ants, they showed a more aversive reaction, retreating and hiding below the silk retreat.

The silk retreats seem to be the key element resulting in the unusual stationary behaviour. The observed sedentary lifestyle is likely the result of reliance on the benefits provided by their decorated silk retreat and the risk of exposure when moving outside the retreat. The retreat construction entails the investment of energy in terms of silk production, building behaviour, and the collection of debris. However, once built the retreat acts as a hunting tent that hides the presence of the spider and from which it launches its attack on potential prey.

Retreat building is used by most jumping spiders but these are usually hidden, short-lived and left behind during foraging activities (Hoefler & Jakob, 2006; Hill et al., 2019). By contrast, the high abundance of *A. mullion* spiders and their retreats likely points to the success of these more or less permanent retreats. Potential costs associated with this strategy are yet to be discovered, as are potential trade-offs resulting from the shift from active foraging to a sit-and-wait strategy. For instance, intra-specific competition for prey and/or space (Marshall & Rypstra, 1999; Miyashita, 2001) in this habitat is a possibility, given the challenging conditions of the tree trunk habitat.

The third tree-trunk inhabitant that I studied was the hersiliid spiders (Chapter 4). These spiders are thought to only capture wandering prey on the surface of tree trunks and deploy background matching to reduce recognition by potential prey (Baehr & Baehr, 1987). While my analyses of the degree of crypsis in hersiliids did not consider a prey perspective due to time limitations, I believe I am still able to extrapolate some generalities from the results based on predator vision.

It is likely that the better match to the home background detected under potential predator vision may also hold for prey vision, as there are some similarities in colour receptors between potential prey and predators, such as visual sensitivities in the UV, blue and green spectrum of light (Briscoe & Chittka, 2001; Vorobyev, Marshall & Osorio, 2001; Osorio & Vorobyev, 2008). However, as explained before, the ability to discriminate a given subject from its background does not only depend on colour perception but on the interaction of colour with visual acuity (Merilaita, Scott-Samuel & Cuthill, 2017; Caves, Brandley & Johnsen, 2018). Spiders could potentially be better at background matching under insect prey vision, which has a lower resolution than some of their potential predators, such as birds (Caves, Brandley & Johnsen, 2018). Thus, insects landing on the tree trunks are less likely to detect a hersiliid spider.

However, our visual models have generated a testable set of predictions regarding the visibility of hersiliid spiders against tree trunks. This now needs to be explicitly tested. For instance, do spiders with lower visual contrast capture more prey? To answer this question, camera traps could be used to detect naturally occurring prey capture events in spiders occupying different backgrounds. Furthermore, to identify the actual and relevant prey for hersiliids, molecular techniques could aid in their identification from gut content (Krehenwinkel et al., 2017).

Anti-predatory strategies

Despite spiders occupying a predominant position among predators, spiders are also potential prey of many other invertebrate and vertebrate predators (Herberstein, 2011). Not surprisingly, in spiders, we can find outstanding defence mechanisms, such as rolling scapes (dune spiders flip sideways with their legs curled to roll down smooth sand dunes;(Henschel, 1990), decoys (eg. using debris in the web to divert predator attacks; (Ma et al., 2020), mimicry (e.g. ant mimicry; (Cushing, 1997; McLean, Cassis & Kikuchi, 2019) and camouflage (Ma et al., 2020); see (Cloudsley-Thompson, 1995) for a review.

Anti-predatory strategies are likely affected by habitat complexity - commonly a greater structural complexity (i.e., higher abundance and/or diversity of elements in a given environment) is associated with greater protection from predatory detection and attacks (Langellotto & Denno, 2004). In my thesis, my focus was on the mechanisms that spiders on tree trunks could potentially utilise to deal with the lack of visual and physical cover on tree trunks. Diurnal spider residents of tree trunks are faced with the challenge of reducing visually detected by predators (as well as prey). Particularly relevant in this thesis is the diversity of strategies to avoid visually guided predators. These range from behavioural avoidance (nocturnality), the construction of camouflaged silk retreats and background matching of body colouration.

Hiding in retreats

Two of my thesis chapters discuss the adaptive value of the decorative behaviour of *A. mullion* as camouflage for its silk retreats on exposed tree surfaces (Chapters 2 and 3). *Arasia mullion* hunts during the day while partially covered by layers of silk and bark debris. The results of visual contrast modelling suggest that the colour matching and reduction of the UV reflectance on the silk retreat would render the spider “invisible” while residing within the retreat. Even when they are partially protruding from the retreat while they hunt it is likely that the decorated retreat disrupts the shape of the spider leading to disruptive camouflage (Stevens et al., 2006; Webster et al., 2013). The promising results from the visual modelling now require testing in controlled field experiments that measure the approach of visually guided predators to spiders within and outside their protective retreat.

Additionally, testing predator responses to non-decorated and decorated retreats could reveal the degree to which UV reflectance affects the conspicuousness of silk (see examples of UV-reflection in crab spiders (Heiling, Herberstein & Chittka, 2003; Heiling et al., 2005). and the specificity of the camouflage provided by surrounding bark debris. A possible experimental set-up could be similar to previous work on crab spiders, where spiders were tethered to flowers of different colours generating different contrast levels (Rodríguez-Gironés & Maldonado, 2020).

While I was not able to conduct such an experiment within the timeline of my PhD, I did observe that ants seem to be a threat to *A. mullion*. In our prey approach experiment (see above) we prevented the experimental group from accessing their retreat and one of those spiders was killed by *Crematogaster* ants. This might indicate that silk retreats also act as a physical barrier to predators such as ants.

Camouflage

My final chapter looked at camouflage against tree trunks by hersiliid spiders. By far the most common anti-predatory strategy in animals is camouflage facilitated by body colouration and patterns that elude visual detection by predators (Merilaita, Scott-Samuel & Cuthill, 2017; Cuthill, 2019). In spiders, camouflage is probably best understood in crab spiders. Some species are known to sit-and-wait on flowers that minimise colour contrast (i.e., match the colour of the spider) for potential prey to approach (Heiling et al., 2005). While other crab spiders on tree trunks are equipped with microsetae that collect and retain bark debris on their bodies rendering them highly camouflaged against the tree trunk (Gawryszewski, 2014). Thus, both strategies prevent detection by visually guided viewers, such as prey and predators. However, a common constraint on the efficacy of camouflage is the variation in background colour patterns in nature. Animals that match a highly specific background are thus restricted to that particular habitat while generalist colour patterns might risk insufficient matching to multiple backgrounds (Houston, Stevens & Cuthill, 2007; Merilaita, Tuomi & Jormalainen, 2008; Stevens & Ruxton, 2018). One way to mitigate background variation is the ability to change body colour - such as in crab spiders (Oxford & Gillespie, 1998). Other ways that avoid these constraints include forming highly contrasting colour patterns that do not reduce detection but prevent recognition of the animal (e.g. disruptive colouration (Robledo-Ospina et al., 2017)).

It has been anecdotally noted that hersillid spiders show colouration patterns that match those of their backgrounds across the tropical regions of the world (Baehr & Baehr, 1987; Rheims &

Brescovit, 2004). In my thesis, I utilised two species of Hersiliidae spiders that occupy tree trunks that are either lacking complex patterns (smooth trunks) or are highly patterned (rough trunks) and I analysed and compared the spider colouration patterns relative to the tree background. This family of spiders is an excellent system for comparing the reliance on camouflage strategies as the vast majority of the species sit-and-wait for passing prey on tree trunks. The results of my study using visual modelling from digital multi-spectral images suggest that even species of Hersiliidae living in the same area (sometimes only a few metres apart) vary in specific colour pattern traits resulting in a better blend against the particular tree trunk.

The separation in the use of particular niches -tree trunk types, points to the likely ability of each hersiliid species to choose a particular background to settle on. The short distances between trees with different trunk types (smooth and rough) are likely reachable by the spiders, either via ballooning as spiderlings or via silk bridging as adults. Thus, spiders would have a random chance of landing on a matching or non-matching tree. My own field observations of the Mexican hersiliid *Neotama mexicana* indicate that they move along tree trunks and branches at night, whereby they could potentially reach other, non-matching trees. Nocturnality could possibly enable relocations while avoiding visually guide predators.

Alternatively, the observed strict niche separation of the two hersiliid species could result from strong selective predatory pressure for good background matching and site fidelity of spiderlings to their hatching site. Hersiliid spiders could potentially stay in an individual tree for their entire lifetime, thus active choice is not involved.

While the visual modelling data are strongly suggesting species-specific background matching, further controlled behavioural experiments are necessary to directly test the ability of prey and predators to detect the hersiliid spiders at different contrast thresholds such as against different backgrounds and over a range of viewing distances (see examples Barnett et al., 2016; Barnett, Cuthill & Scott-Samuel, 2018).

Behavioural predator avoidance - nocturnality

While I did not make any direct observations of anti-predatory behaviour in the Australian ant slayer (*E. umbilicata*), nocturnal activity is generally regarded as a response to evading diurnal predators (Cloudsley-Thompson, 1995; Soutar & Fullard, 2004; Pekár, 2014). During the day the ant slayer remains inactive in crevices. As I have not witnessed any predator attacks on these spiders, the identity of such predators is entirely unknown at this stage.

My study on spiders that live on tree trunks allowed me to discover intriguing and diverse strategies of prey capture, camouflage and animal constructions. From a distance - tree trunks seem deprived of life, but a closer inspection revealed complex lifestyles and interactions that deserve closer attention as these expand previously known systems whilst also discovering novel systems.

Most of my thesis focused on the discovery and description of these complex lifestyles, but there was not enough time to undertake manipulative experiments that explicitly tested the effect of each strategy on the fitness outcome of these species. Despite this, my thesis achieves a rich and integrative overview of functional diversity amongst tree trunk fauna. Three predators occupying the same apparently simple habitat evolved different and for the most part unique solutions to the challenges faced as both predators and prey. The strategies of the Australian ant-slayer (*E. umbilicata* - Theridiidae) and *A. mullion* (Salticidae) are seemingly novel adaptations derived from ancestral attributes, while in the hersiliids, the exploitation of tree trunks appears basal for the entire family (Baehr & Baehr, 1987). While one might expect that these three species could compete with each other over resources, as they sometimes occupied the same tree, my casual observations indicate that there are several other species of jumping spiders and huntsman spiders that can also be found on the same tree trunks. Clearly, tree trunks have much more to offer than meets the eye and tree trunk spiders are an intriguing study system where further research is needed to understand the often complex interaction of this diverse community of predators.

Personally, despite the mental and emotional strain of a pandemic (being in lock-down in two different countries, unable to conclude my field work aspirations), I found great value in learning about discovering and describing novel strategies through a rigorous naturalist approach: developing a series of ordered questions and applying methodologies to answer them; integrating teams of colleagues with expertise in different fields, and learning from their particular methods and techniques (e.g., high-speed videography, computational video tracking and programming, visual modelling from traditional spectrometry and modern digital imagery). Ultimately, the enthusiastic response of conference delegates and paper reviewers to novel behaviour was affirming the value of detailed natural history studies.

References

Aceves-Aparicio A, Tapia-McClung H, Macías-Ordóñez R, Rao D. 2018. Subsocial spiders in space and time: A fine scale approach to the dynamics of dispersal. *Ethology* 124:458–467.

Baehr B, Baehr M. 1987. The Australian Hersiliidae (Arachnida : Araneae): Taxonomy, phylogeny, zoogeography. *Invertebrate Systematics* 1:351-437.

Barnett JB, Cuthill IC, Scott-Samuel NE. 2018. Distance-dependent aposematism and camouflage in the cinnabar moth caterpillar (*Tyria jacobaeae*, Erebidae). *Royal Society Open Science* 5:171396.

Barnett JB, Redfern AS, Bhattacharyya-Dickson R, Clifton O, Courty T, Ho T, Hopes A, McPhee T, Merrison K, Owen R, Scott-Samuel NE, Cuthill IC. 2016. Stripes for warning and stripes for hiding: spatial frequency and detection distance. *Behavioral Ecology* 28:373–381.

Barrantes G, Eberhard WG. 2007. The evolution of prey-wrapping behaviour in spiders. *Journal of Natural History* 41:1631–1658.

Bickel DJ, Tasker EM. 2004. Tree trunk invertebrates in Australian forests: conserving unknown species and complex processes. *Conservation of Australia's Forest Fauna* 888–898.

Briscoe AD, Chittka L. 2001. The evolution of color vision in insects. *Annual Review of Entomology* 46: 471–510.

Bulbert MW, Herberstein ME, Cassis G. 2014. Assassin bug requires dangerous ant prey to bite first. *Current Biology* 24:R220-R221.

Caves EM, Brandley NC, Johnsen S. 2018. Visual acuity and the evolution of signals. *Trends in Ecology & Evolution* 33:358–372.

Cloudsley-Thompson JL. 1995. A review of the anti-predator devices of spiders. *Bulletin of the british arachnological society* 10:81–96.

Coddington JA, Levi HW. 1991. Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* 22:565–592.

Cushing PE. 1997. Myrmecomorphy and myrmecophily in spiders: A review. *The Florida entomologist* 80:165–193.

Cuthill IC. 2019. Camouflage. *Journal of Zoology* 308:75–92.

Eberhard W. 2020. *Spider Webs: Behavior, Function, and Evolution*. University of Chicago Press.

Gawryszewski FM. 2014. Evidence suggests that modified setae of the crab spiders *Stephanopis* spp. fasten debris from the background. *Zoomorphology* 133:205–215.

Gunnarsson B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. *The Journal of Animal Ecology* 59:743–752.

Heiling AM, Chittka L, Cheng K, Herberstein ME. 2005. Colouration in crab spiders: substrate choice and prey attraction. *The Journal of experimental biology* 208:1785–1792.

Heiling AM, Herberstein ME, Chittka L. 2003. Crab-spiders manipulate flower signals. *Nature* 421:334–334.

Henschel. 1990. Spiders wheel to escape. *South African journal of science*.

Herberstein ME. 2011. *Spider Behaviour: Flexibility and Versatility*. Cambridge University Press.

Heterick BE, Majer J, Recher H. 2001. A checklist of canopy, bark, soil and litter fauna of the Darling Plateau and adjacent woodland near Perth, Western Australia, with reference to the conservation of forest and woodland fauna. *Curtin University School of Environmental Biology Bulletin* 21:1–35.

Hill DE, C. AAP, Krishna P, Ramesh S. 2019. Construction of orb webs as nocturnal retreats by jumping spiders (Araneae: Salticidae: cf. Anarrhotus) in southwestern India. *Peckhamia* 182:1–10.

Hoefler CD, Jakob EM. 2006. Jumping spiders in space: movement patterns, nest site fidelity and the use of beacons. *Animal behaviour* 71:109–116.

Houston, Stevens, Cuthill. 2007. Animal camouflage: compromise or specialize in a 2 patch-type environment? *Behavioral ecology* 18(4):769-775.

J.D. Majer, H.F. Recher, B.E. Heterick, and A.C. Postle. 2001. The canopy, bark, soil and litter invertebrate fauna of the Darling Plateau and adjacent woodland near Perth, Western Australia, with reference to the diversity of forest and the woodland invertebrates. *Pacific conservation biology* 7:229–239.

Krehenwinkel H, Kennedy S, Pekár S, Gillespie RG. 2017. A cost-efficient and simple protocol to enrich prey DNA from extractions of predatory arthropods for large-scale gut content analysis by Illumina sequencing. *Methods in ecology and evolution* 8:126–134.

Langellotto GA, Denno RF. 2004. Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* 139:1–10.

Liu J, May-Collado LJ, Pekár S, Agnarsson I. 2016. A revised and dated phylogeny of cobweb spiders (Araneae, Araneoidea, Theridiidae): A predatory Cretaceous lineage diversifying in the era of the ants (Hymenoptera, Formicidae). *Molecular phylogenetics and evolution* 94:658–675.

Marshall SD, Rypstra AL. 1999. Spider competition in structurally simple ecosystems. *The Journal of arachnology* 27:343–350.

Ma N, Yu L, Gong D, Hua Z, Zeng H, Chen L, Mao A, Chen Z, Cai R, Ma Y, Zhang Z, Li D, Luo J, Zhang S. 2020. Detritus decorations as the extended phenotype deflect avian predator attack in an orb-web spider. *Functional ecology* 34:2110–2119.

McLean DJ, Cassis G, Kikuchi DW. 2019. Insincere flattery? Understanding the evolution of imperfect deceptive mimicry. *The quarterly review of biology,* 94(4), 395-415.

Merilaita S, Scott-Samuel NE, Cuthill IC. 2017. How camouflage works. *Philosophical Transactions of the Royal Society B: Biological Sciences* 372(1724): 20160341.

Merilaita S, Tuomi J, Jormalainen V. 2008. Optimization of cryptic coloration in heterogeneous habitats. *Biological journal of the Linnean Society* 67:151–161.

Michálek O, Řezáč M, Líznarová E, Symondson WOC, Pekár S. 2018. Silk versus venom: alternative capture strategies employed by closely related myrmecophagous spiders. *Biological journal of the Linnean Society.* 126:545–554.

Miyashita T. 2001. Competition for a limited space in kleptoparasitic Argyrodes spiders revealed by field experiments. *Population Ecology* 43:97–103.

Nicolai V. 1986. The bark of trees: thermal properties, microclimate and fauna. *Oecologia* 69:148–160.

Nicolai V. 1993. The arthropod fauna on the bark of deciduous and coniferous trees in a mixed forest of the Itasca State Park, MN, USA. *Spixiana* 16:61–69.

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.

Osorio D, Vorobyev M. 2008. A review of the evolution of animal colour vision and visual communication signals. *Vision research* 48:2042–2051.

Oxford GS, Gillespie RG. 1998. Evolution and ecology of spider coloration. *Annual review of entomology* 43:619–643.

Pekár S. 2014. Comparative analysis of passive defences in spiders (Araneae). *The Journal of animal ecology* 83:779–790.

Pekár S, Toft S. 2015. Trophic specialisation in a predatory group: the case of prey-specialised spiders (Araneae). *Biological reviews* 90:744–761.

Proctor HC, Montgomery KM, Rosen KE, Kitching RL. 2002. Are tree trunks habitats or highways? A comparison of oribatid mite assemblages from hoop-pine bark and litter. *Australian journal of entomology* 41:294–299.

Rao D, Aceves-Aparicio A. 2012. Notes on the ecology and behavior of a subsocial spider *Anelosimus baeza* (Araneae: Theridiidae) in Mexico. *The journal of arachnology* 40(3), 325-331.

Rheims CA, Brescovit AD. 2004. Revision and cladistic analysis of the spider family Hersiliidae (Arachnida, Araneae) with emphasis on Neotropical and Nearctic species. *Insect systematics & evolution* 35:189–239.

Robledo-Ospina LE, Escobar-Sarria F, Troscianko J, Rao D. 2017. Two ways to hide: predator and prey perspectives of disruptive coloration and background matching in jumping spiders. *Biological journal of the Linnean Society.* 122:752–764.

Rodgers DJ, Kitching RL. 1998. Vertical stratification of rainforest collembolan (Collembola: Insecta) assemblages: description of ecological patterns and hypotheses concerning their generation. *Ecography* 21:392–400.

Rodríguez-Gironés MA, Maldonado M. 2020. Detectable but unseen: imperfect crypsis protects crab spiders from predators. *Animal behaviour* 164:83–90.

Rosen K. 2000. Collembolan Species Turnover Within Araucarian Vine Forest of South-East Queensland. Griffith University.

Soutar AR, Fullard JH. 2004. Nocturnal anti-predator adaptations in eared and earless Nearctic Lepidoptera. *Behavioral ecology* 15:1016–1022.

Stevens M, Cuthill IC, Windsor AMM, Walker HJ. 2006. Disruptive contrast in animal camouflage. *Proceedings of the Royal Society B: Biological Sciences* 273: 2433-2438.

Stevens M, Ruxton GD. 2018. The key role of behaviour in animal camouflage. *Biological reviews* 94(1): 116-134.

Villanueva-Bonilla GA, Salomão AT, Vasconcellos-Neto J. 2017. Trunk structural traits explain habitat use of a tree-dwelling spider (Selenopidae) in a tropical forest. *Acta Oecologica* 85:108–115.

Vorobyev M, Marshall J, Osorio D. 2001. Colourful objects through animal eyes. *Color Research & Application: Endorsed by Inter Society Color Council, The Colour Group (Great Britain), Canadian Society for Color, Color Science Association of Japan, Dutch Society for the Study of Color, The Swedish Colour Centre Foundation, Colour Society of Australia, Centre Français de la Couleur* 26(S1), S214-S217.

Webster RJ, Hassall C, Herdman CM, Godin J-GJ, Sherratt TN. 2013. Disruptive camouflage impairs object recognition. *Biology letters* 9:20130501.

Yanoviak SP, Munk Y, Dudley R. 2015. Arachnid aloft: directed aerial descent in neotropical canopy spiders. *Journal of the Royal Society Interface* 12:0534.