Insect Systematics and Diversity, 8(4), 4; 2024, ixae019
https://doi.org/10.1093/isd/ixae019
Research

ENTOMOLOGICAL SOCIETY OF AMERICA
SHARING INSECT SCIENCE GLOBALLY
OXFORD

Conservation and Biodiversity

Disguise or surprise: spider antipredator adaptations as a function of the architecture of their webs

Andrea M. Haberkern[1,*], **Jessica C. Boles**[1], **Yi Lin Zhou**[1], **Luis F. Camacho**[1,2], **Antonio D. Brescovit**[3], **Leticia Avilés**[1,*]

[1]Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, BC, Canada, [2]Facultad de Ciencias Exactas y Naturales, Pontificia Universidad Católica del Ecuador, Quito, Ecuador, [3]Laboratório de Coleções Zoológicas, Instituto Butantan, São Paulo, SP, Brazil [*]Corresponding authors: Andrea M. Haberkern, email: ahab@zoology.ubc.ca; Leticia Avilés, email: laviles@zoology.ubc.ca

Subject Editor: Jacob Gorneau

Received on 1 June 2023; revised on 7 May 2024; accepted on 25 July 2024

Animals exhibit a variety of strategies to avoid predation; spiders are no exception. We explored whether web-building spiders that differ in the architecture of their webs exhibit morphologies or behaviors suggestive of antipredator strategies that trade-off with the degree of protection offered by their webs. Spiders build webs of 3 types: the more protected tangles and sheet-and-tangles, which are three-dimensional (3D), and the more exposed orbs, which are two-dimensional (2D), both with or without a refuge. We hypothesize that spiders whose webs offer greater protection—a 3D architecture or a refuge—will be less likely to be armored or brightly colored when compared to spiders without these protections. We collected data on 446 spiders and their webs in 2 lowland tropical rainforest sites. We show that 2D web builders with no refuges tended to be brightly colored (background contrasting) and spiny (spiky), whereas those with refuges tended to blend against the background of their refuges. 3D web builders, on the other hand, were neither cryptic nor brightly colored nor armored but were more likely to drop out of the web upon simulated predator contact. These results support the hypothesis that web-building spiders tend to be protected either through the architecture of their webs or their morphology and behavior, suggesting a trade-off between different types of antipredator strategies.

Key words: context-dependent evolution, predator–prey interaction, trade-off, antipredatory behavior, spider web

Introduction

Animals have evolved a variety of passive or active antipredator adaptations (Lima and Dill 1990, Pekár 2014) involving either morphology or behavior. Antipredator adaptations are a matter of life and death but also costly (Lima and Dill 1990). It is thus expected that the extent of these adaptations will depend on context, i.e., the degree of protection naturally afforded by an organism's environment or behavior. For example, birds that nest high in trees may have a greater level of protection than those that nest on the ground. Whereas choosing to nest high up on trees may in itself be an antipredator strategy, bird species with this habitat choice should be under less pressure to develop morphological or other types of behavioral antipredator adaptations (Montgomerie and Weatherhead 1988, Caro 2005, Lima 2009). Most strategies will also exhibit trade-offs with other aspects of fitness, including allocation of resources to other functions or to finding mates (Sih 1980, Lima and Dill 1990, Whiting et al. 2022). If an organism is well enough protected within environmental or behavioral parameters, it should forgo expensive morphological antipredator adaptations (Baird 2008, Crofts and Stankowich 2021).

An approach to studying rare events, such as predation, is to observe multiple species simultaneously in communities where varying contexts of protection are represented (Stanford 2002, Cadier et al. 2019). Documenting antipredator strategies in such communities can help test hypotheses concerning the role of context on antipredator strategies. Diurnal web-building spiders are particularly at risk of falling victim to visually oriented predators such as birds, lizards, damselflies, assassin bugs, mantids, predatory wasps, and other spiders (Rypstra 1984, Higgins 1992, Cloudsley-Thompson 1995, Blackledge and Wenzel 2001, Manicom et al. 2008, Eberhard 2020).

Among those, the type of webs the spiders build may also influence predation risk. Although the primary function of spider webs is for prey capture, depending on their architecture, webs may also provide protection from predators as a secondary function (Eberhard 2019). Spiders build webs of many types, but most fall into 2 broad architectural categories (Rypstra 1983). Two-dimensional (2D) orbs tend to be flat and on a single plane, potentially leaving the spiders more exposed; three-dimensional (3D) webs, either a tangle of irregular silk, or a sheet-and-tangle with capture lines extending from a sheet, dome, or basket of dense silk (Fig. 1), should provide greater protection (Blackledge et al. 2002, Blamires et al. 2013, Su and Buehler 2020). Spider webs may also contain structures that serve as refuges or distractions, such as curled leaves; decoys the spider assembles from environmental materials; or conspicuous designs built from silk, such as stabilimenta (Bruce et al. 2005, Tseng and Tso 2009, Wang et al. 2022). Although there is debate on the primary function of such structures, there is sufficient evidence to suggest some of them may serve as barriers or to conceal the spider's location or identity from predators (Cloudsley-Thompson 1995, Blackledge 1999, Manicom et al. 2008, Eberhard 2019, 2020). It is thus expected that, within the context of varying web types and structures, the antipredator responses of diurnal spiders should also vary.

Web-building spiders thus present a clear opportunity to explore the role of context in the evolution of antipredator adaptations. Blackledge et al. (2002) suggested that 3D webs may have evolved as defensive structures against predatory wasps, as their cage-like 3D structure should provide more protection than the flattened structure of orb webs. Similarly, for sheet-and-tangle builders, it is expected that the sheet itself may act as a mechanical barrier to potential predators (Blamires et al. 2013, Su and Buehler 2020). Furthermore, web-building spiders may also choose specific microhabitats based on their web types (Blackledge et al. 2002, Robertson and Avilés 2018, Haberkern et al. 2020). 2D webs are typically built in open areas where there is enough space to accommodate the web (Blamires et al. 2007, Blackledge et al. 2011), leaving the spider potentially more exposed. 3D webs, on the other hand, tend to be built in more sheltered locations, such as against tree trunks or under leaves, either for structural support or protection from the rain (Blackledge et al. 2011, Robertson and Avilés 2018, Haberkern et al. 2020). As with differences in web structure, we expect differences in microhabitat use to lead to different predation risks, thus contributing to the evolution of diverse antipredator strategies.

We addressed the question of whether certain morphological and behavioral antipredator adaptations diurnal web-building spiders exhibit vary as a function of the architecture of their webs and the presence or absence of a refuge. Because spiders with 2D webs and no refuge are the most exposed, we predict that they will be more likely to invest in antipredator strategies, such as background contrasting coloration, such as aposematism, and protective structures, such as spines, and to exhibit offensive antipredator behavior, such as biting or attacking, compared to the 3D web types or orb webs with a refuge. Because of the greater protection afforded by a 3D architecture or a refuge, the latter type of spider may not benefit from paying the costs often associated with morphological antipredator adaptations. We, therefore, expect spiders with 3D webs or a refuge to exhibit either neutral (i.e., neither background contrasting nor background matching) or background matching coloration. Prior studies on spider antipredator adaptations have focused primarily on orb-weaving spiders, whereas the protective value of 3D webs has been considered mostly from a structural perspective (Eberhard 1990, 2020, Blackledge et al. 2002). Here, we examine the problem across all 3 main web types to test the hypothesis that morphological or behavioral antipredator adaptations evolve to the extent that the context requires them.

Materials and Methods

Study Sites and Data Collection

We collected data at 2 lowland tropical rainforest sites in Eastern Ecuador: the Jatun Sacha Biological Station (Napo Province, Ecuador, −0.99, −77.81; June–July 2018) and the Yasuní Research Station (Orellana Province, −0.67, −76.40; July–August 2019). The Jatun Sacha Biological Reserve (JS) consists of approximately 2,000 ha of Tropical Wet Forest at an approximate elevation of 420 m, has an average annual rainfall of 3,700 mm and an average annual temperature of 25 °C. Up to 70% of the JS reserve consists of primary forest. The Yasuní National Park (YS) consists of approximately 98,000 ha of primary Tropical Wet Forest at approximately 250 m in elevation, with an average annual rainfall of approximately 3,000 mm and an average annual temperature of 26 °C. We collected data on a total of 446 web-building spiders and their webs at 5 separate locations within each of the reserves, with at least a 500 m distance between any 2 locations. At each location, we collected data on spiders of at least 3 unique species per web type: orb, tangle, and sheet-and-tangle, as defined by Rypstra (1983). We did this to ensure a balanced design, so that our samples represented more of the web-building spider community present, and to minimize redundancy (see Haberkern et al. 2020 for more details). To maximize the representation of the web types and taxa, we included adults and juveniles, as well as males and females, in our sample. We collected data on spiders that were present and active in their webs at the time of data collection. Thus, webs of inactive nocturnal species, or those with missing or resting spiders, were not included. All field data collection was performed by A. M. Haberkern to ensure consistency.

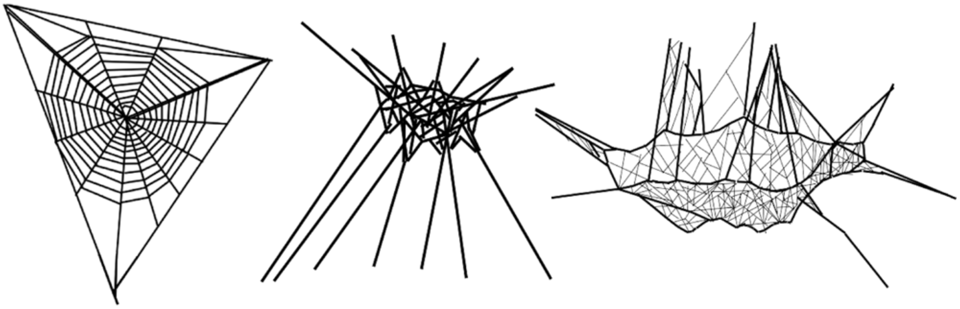

Fig. 1. Examples of different web types: (left) an orb web, (middle) a tangle web, and (right) a sheet-and-tangle web. Drawings from Straus et al. (2021).

Web and Spider Characteristics

For each web, we recorded its type (orb, tangle, sheet-and-tangle), angle relative to the ground (0°, 45°, 90°), dimensions (length × width, for orb webs; × height, for tangle and sheet-and-tangle webs, in mm), and capture lines height (cm) and angle (0°, 45°, 90°), for sheet-and-tangle webs; and type of refuge (none, stabilimentum, funnel, curled leaf, trash line, or decoys). We considered as *refugia* structures that the spiders build with their own silk (funnel, stabilimenta) or with outside materials (e.g., a curled leaf), specifically to hide or retreat to when disturbed; species where leaves or other structures were incidentally included in their nests, even if serving as secondary protection, were not considered as having a refuge. For each spider, we recorded its sex, instar (juvenile, adult), body length in mm (from the front of the chelicera to the tip of the abdomen), and position in/on its web (hub, on sheet, under sheet, periphery, in refuge).

Assessing Antipredator Morphology

In the field, we rated the spiders' degree of background matching vs. contrasting and of smoothness vs. spikiness using a scale from −2.5 (highest background matching) to +2.5 (highest background contrasting, 0 representing neutral) for the former (Fig. 3A) and from 0 (smoothest) to 5 (spikiest) for the latter (Fig. 3B). For this purpose, we prepared a priori a graphical guide of the trait states corresponding to the various scores (Fig. 3). For spikiness, we considered higher values to be antipredators in nature. For coloration, we considered both low and high values to represent antipredator investment, with spiders assigned values in the middle considered as making no investment in either blending or conspicuous coloration. We thus obtained a *coloration investment index* by taking averages (for a given species or genus) of absolute values of the coloration index on a scale between 0 (no investment) and 2.5 (high investment).

Assessing Antipredator Behavior

We assessed the spiders' response to a predator-like stimulus by gently touching the dorsal abdomen with a sturdy wire. We approached spiders from the side of the web on which it was sitting at approximately the same speed and angle to minimize variation across trials. We intended to simulate contact from a predator, with an approach slow enough not to startle the spider before contact. We created an arbitrary scale from −2 to +2 to assess the level of relative antipredator response of the spiders to the stimulus, with negative values representing defensive responses, 0 for neutral responses, and positive values for offensive responses (Table 1). We considered both offensive and defensive responses to be antipredator reactions.

Spider Identification

We preserved spiders in 95% ethanol in accordance with our research permits (2018: N° 011-018-IC-FLO-DPAN/MA; 2019: N°017-19 IC-FAU-DNB/MA). In the field, we identified specimens to the lowest possible taxonomic level and assigned each spider and web a unique code. In the laboratory, based on epigyna or pedipalp morphology and other morphological characteristics of the spiders and their webs, we assigned all specimens to morphospecies and, after cross-comparison, to a particular morphospecies. Specimens then received a morphospecies ID and a unique specimen number. Specimens were then assigned to families using the Brescovit et al. (2002) key to Amazonian spider families. We then used classic reviews for the families with the greatest diversity (Levi and Levi 1962, Levi 2002, Opell 2017) to assign morphospecies to genera.

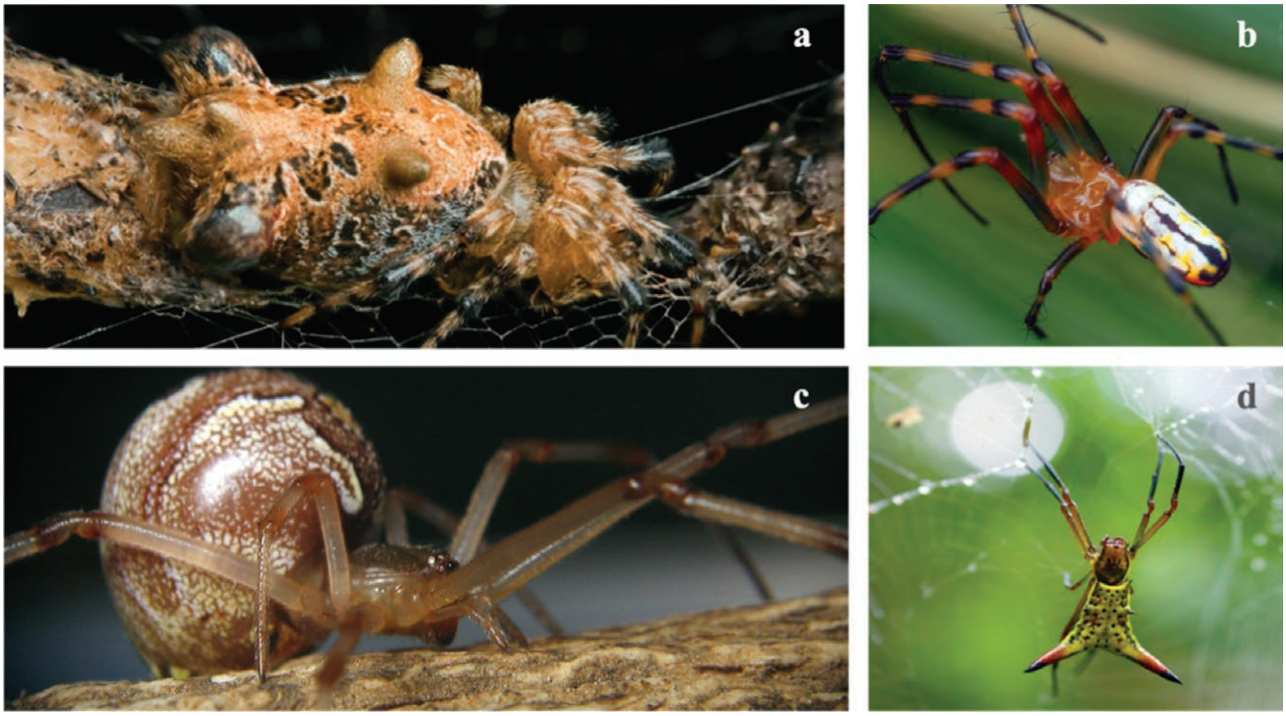

Fig. 2. Example spider taxa of different coloration and smooth vs. spiked morphologies: A) background matching *Cyclosa* sp. (Araneidae) sitting on a trash line in the middle of her orb web, B) background contrasting of a brightly colored *Leucauge* sp. (Tetragnathidae, orb weaver), C) smooth-bodied *Latrodectus* sp. (Theridiidae, tangle), D) spiney-bodied (and brightly colored) female *Micrathena* sp. (Araneidae, orb weaver). Photos: João Burini (primalshutter.com), manipulated solely for the purpose of clarity.

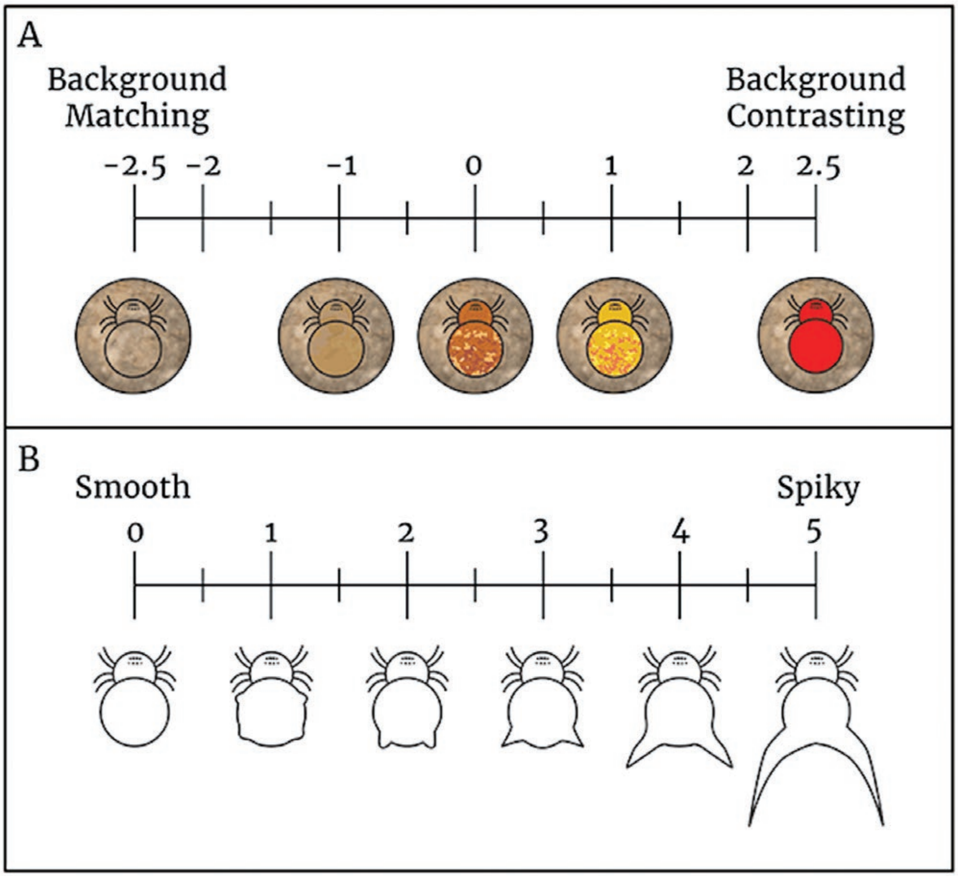

Fig. 3. Cartoon depictions to illustrate the relative scales used to rate A) background matching vs. background contrasting or B) smoothness vs. spikiness. A) A spider is assigned −2.5 on the background matching scale when it is obviously cryptic, being nearly indistinguishable from its background, a −1 when it more or less matches its background but does not appear to be cryptic; 0, when it neither matches nor contrasts its background, appearing neutral in color; 1, when it has small specs of contrasting color or is slightly red or yellow in coloration; and a 2.5 when its body highly contrasts its background (i.e., obvious aposematism). B) On the spikiness scale, 0 is given to a smooth-bodied spider with no visible bumps and an abdomen that is soft in appearance; 1, to a spider that is mostly smooth but may have slight bumps or appear thicker-bodied; 2, when bumps on the abdomen are apparent; 3 when spikes are obvious but small; 4, when spikes are both obvious and large; and 5, the spider is heavily armored with very large spikes. The spiders shown in Fig. 2 would have been rated as follows: Fig. 2a, -2.5 for coloration, Fig. 2b, 2.5 for coloration; Fig. 2c, 0 for spikiness; Fig. 2d, 5 for spikiness.

Table 1. Explanation of spider responses to predator stimuli. Negative values were considered defensive behaviors, and positive values were considered offensive behaviors

Value	Response to stimuli
−2	Spider drops from web (defensive antipredator response)
−1	Spider flees from web without dropping (defensive antipredator response)
0	Spider does not react, or only curls or flinches (neutral antipredator response)
+1	Spider shakes the web or performs a threat display
+2	Spider attacks by attempting to bite or by biting

The material has been deposited in the arachnological collections of the Instituto Butantan, São Paulo (IBSP, curator: A.D. Brescovit) and the Museo Ecuatoriano de Ciencias Naturales, Quito (MECN, curators: D. Fernández and E. Freire).

Analyses

With genera as the units of analysis, we used general linear mixed models (GLMM) to assess the effect of web type (orb, tangle, or sheet-and-tangle) and the presence/absence of a refuge on 3 morphological and one behavioral response variables. All models had spider body size as a covariate and morphospecies nested within genera as random effects. Genera that were polymorphic for these traits were represented in more than one web type-refuge category. We did not include an interaction between web type and refuge in the models as in preliminary analyses; this term did not have a significant effect on any of the variables. The morphological response variables were degree of background matching vs. contrasting (scale −2.5 to +2.5), investment in antipredator coloration (absolute value from either negative or positive scores), and level of smoothness vs. spikiness (scale 0–5) (Table 2, models A–C). In analyses of the morphological variables, there were 194 morphospecies in 55 genera represented, with morphospecies whose genus could not be identified grouped in a single "unknown" genus per family and web type-refuge category.

The behavioral antipredator response—drops, flees, flinch, shakes, attacks—converted to an index from −2 to +2, from most defensive to most aggressive (Table 1), was analyzed as a function of a synthetic variable that combined web type and refuge category in a numeric scale (0–5) from least to most protection (Table 2). As assigning the level of protection can be somewhat arbitrary, we used 3 alternative sequences for the web type-refuge categories, all assuming that webs with a 3D structure offered more protection

Table 2. Result of general linear mixed models assessing the effect of web type and the presence or absence of a refuge, after controlling for body length on the coloration, spikiness, and response to a simulated predator attack in web-building spiders of the Ecuadorian Amazon. All models used morphospecies nested within genus as random effects. Web type estimates are in comparison to orb webs. Models D–F consider 3 different sequences in the level of protection resulting from a 3D web architecture and the presence or absence of a refuge. *P*-values <0.05 in bold

Response variable	Fixed factor	Estimate ± Std. error	Chi-squared	***P*-value**
Model A				
Coloration index	Web type		4.19	0.12
	Tangle	0.37 ± 0.21		
	Sheet-tangle	0.36 ± 0.27		
	Web refuge	−0.79 ± 0.15	25.80	**<0.01**
	Spider length (mm)	0.41 ± 0.15	7.24	**0.01**
Model B				
Coloration investment index	Web type		10.88	**<0.01**
	Tangle	−0.40 ± 0.14		
	Sheet-tangle	−0.24 ± 0.18		
	Web refuge	0.26 ± 0.11	5.27	**0.02**
	Spider length (mm)	0.26 ± 0.11	5.33	**0.02**
Model C				
Spikiness index	Web type		33.51	**<0.01**
	Tangle	−1.04 ± 0.18		
	Sheet-tangle	−0.38 ± 0.24		
	Web refuge	−0.16 ± 0.13	1.48	0.22
	Spider length (mm)	0.50 ± 0.12	16.83	**<0.01**
Antipredator response index	Protection index (0–5)*			
Model D	o, o+, t, t+, st, st+	−0.19 ± 0.10	3.49	0.06
Model E	o, o+, t, st, t+, st+	−0.20 ± 0.10	4.06	**0.04**
Model F	o, o+, st, st+, t, t+	−0.22 ± 0.08	7.60	**0.01**

*Abbreviations for the web type-refuge category sequences: o = orb; o+ = orb + refuge: o = orb; o+ = orb + refuge; t = tangle, t+ = tangle + refuge; st = sheet-and-tangle; st+ = sheet-and-tangle + refuge.

than 2D webs (see models D–F, Table 2). Thus, orb webs and orb webs with refuge were given a value of 0 or 1, respectively, and either sheet-and-tangle webs with a refuge (Models D and E) or tangle webs with a refuge (Model F), a value of 5 (Table 2). In these analyses, 57 morphospecies in 33 genera were represented.

Analyses were carried out in R v3.2.2 software (R Core Team 2021). We used packages *glmmTMB* (Brooks et al. 2017) for GLMM construction, *car* (Fox and Weisberg 2019) for *P*-value calculations; and *ggplot2* (Wickham 2016), *ggpubr* (Kassambara 2020), and *lemon* (Edwards et al. 2020) for figure design.

Limitations

The comment by German biologist Jakob von Uexküll (von Uexküll 1920, cited in Caves et al. 2019) that "the real thing is that there is no real world but as many worlds as species" emphasizes the fact that animals perceive the world in unique ways as a function of their particular sensory physiology, neural processing, and ecology. In this study, we assessed spider antipredator adaptations with the human eye, as ours was a broad field survey of entire web-building spider communities (we have data for additional communities along an elevation gradient, J. Boles et al. in prep). Human vision, however, differs from that of other organisms, including that of the predators of web-building spiders, in various ways. The results of our study, therefore, should be considered with caution. For instance, humans can only perceive wavelengths in the visual range, but some spider predators also perceive ultraviolet (UV) (Withgott 2000). We may thus be missing cases of color contrasting patterns only visible in the UV spectrum, which could explain, for instance, our coding of some spiny araneid genera, such as *Aspidolasius* or *Wagneriana*, as color-matching (Supplementary Fig. S5). Colors in the visible spectrum are nonetheless relevant to spider predators, including lizards (Pérez and Font 2014), birds (Withgott 2000), and some insects (Peitsch et al. 1992, Tibbetts 2002). Corcobado et al. (2016), for instance, found that wasps, an important group of spider predators, use both the UV and low-resolution visible spectrum when hunting spiders and can differentiate spider coloration even in the absence of UV detection. The patterns in the visible spectrum we report here are thus a relevant subset of what spider predators perceive.

It is also possible that some of the patterns we perceive as "contrasting" may be perceived to be less so by predators due to visual sensitivity and acuity differences relative to humans. Sensitivity and acuity differences, however, may occur even among species of the same taxon: web-building spiders, for instance, are generally known for their poor visual acuity (Clemente et al. 2005, Morehouse et al. 2017), in contrast to spiders that actively hunt without a web, such as genera in the Salticidae (jumping spiders), Ctenidae (wandering

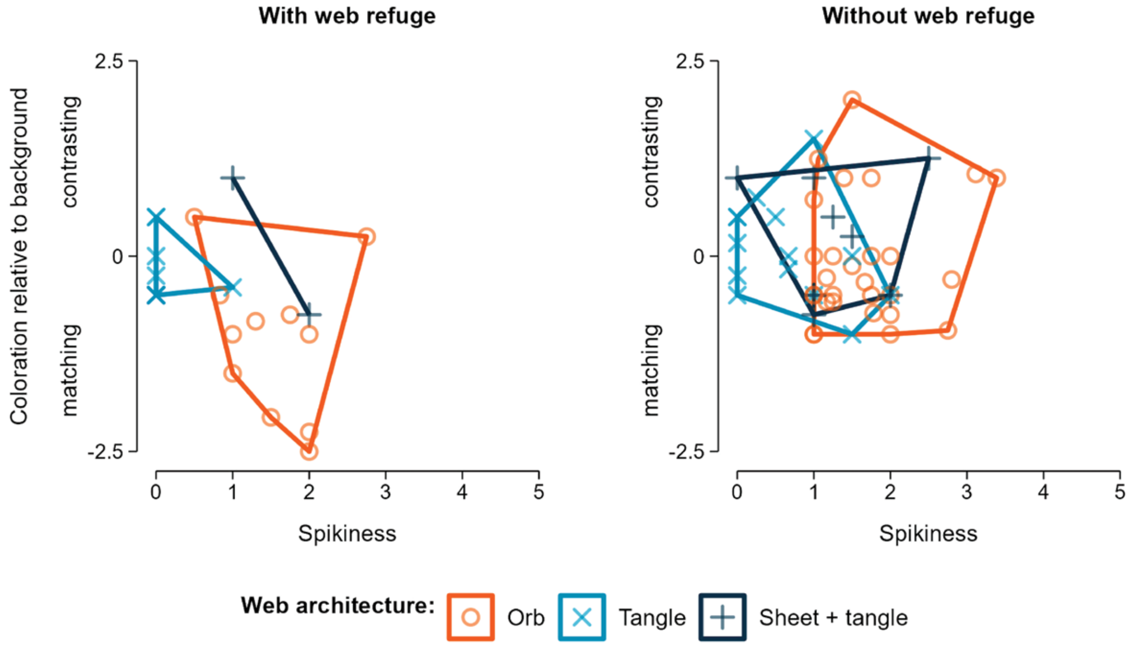

Fig. 4. Association between web type (orb, tangle, sheet-and-tangle) and the presence or absence of a refuge on the level of coloration background matching or contrasting and the level of spikiness in web-building spider communities in the Ecuadorian Amazon. Data points represent the average across species of a single genus within each web type category. See Supplementary Fig. S2 for families and genera represented in the graphs.

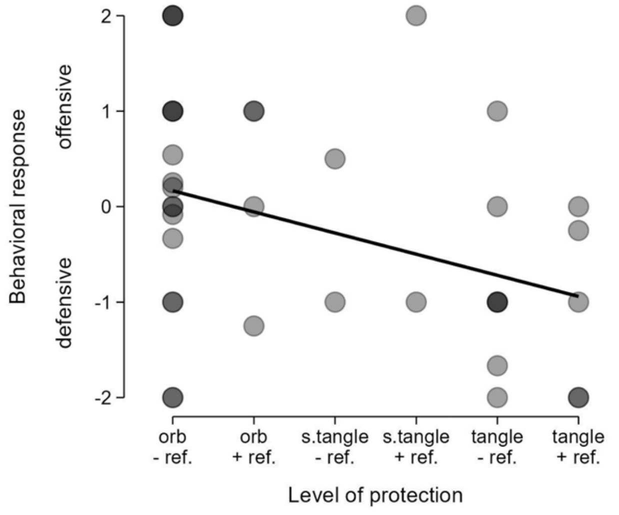

Fig. 5. Correlation between a spider's behavioral response (defensive vs. offensive) to simulated predator contact and the degree of protection expected from the architecture of their webs and the presence or absence of a refuge in a Neotropical web-building spider community. The level of protection is assumed to increase from the most exposed orb webs without a refuge to the presumably better-protected tangle webs with a refuge (Model F, Table 2). See Supplementary Fig. S3 for families and genera represented in the graph.

spiders), Lycosidae (wolf spiders), and Oxyopidae (lynx spiders) (Kovoor et al. 2008, Clemente et al. 2010, Morehouse et al. 2017). Jumping spiders, in particular, are unique among invertebrate predators in their ability to maintain acuity for a range of light sensitivities, thus potentially being able to hunt in the varied microhabitats web-building spiders occupy (Morehouse et al. 2017, Haberkern et al. 2020). Therefore, although human vision is associated with high visual acuity, it is a fair assumption that such sensitivity may be matched, or exceeded, by some of the spider predators, especially those that are both diurnal and engage in visually guided predatory tasks.

More sophisticated methods would thus be needed to better determine how the various types of predators perceive specific spider antipredator adaptations. This could include spectrophotometry and visual modeling to expand the perceived range into the UV end of the spectrum (e.g., Robledo-Ospina and Rao 2022), methods that use color classification to measure the degree of crypsis or conspicuousness against backgrounds in different light conditions (e.g., Endler 1990), or software that converts photographs into images that reflect a taxon's specific parameters of visual acuity (e.g., Caves and Johnsen 2018). We thus suggest that our findings can serve as a starting point for investigations that use some of these more sophisticated and targeted techniques to determine which specific predators these spider antipredator adaptations may be designed for.

Results

In general, spiders with greater spikiness and background contrasting coloration tended to be larger than spiders without these characteristics (significance of spider size for the spikiness index: $\chi^2 = 16.83$, $P < 0.01$; for the coloration index: $\chi^2 = 7.24$, $P = 0.01$) (Table 2, models A and C). After controlling for spider size, orb-weaving genera had a higher spikiness index than genera with 3D webs, with those in tangle webs being the least spiky ($\chi^2 = 33.51$, $P < 0.01$; Est. ± SE relative to orb webs, tangle: −1.04 ± 0.18; sheet-and-tangle: −0.38 ± 0.24) (Table 2, model C; Fig. 4). On the other hand, whether a spider's coloration matched or contrasted with its background did not depend on web type ($\chi^2 = 4.19$, $P = 0.12$) but rather on the presence or absence of a refuge ($\chi^2 = 25.80$, $P < 0.01$) (Table 2, model A). Spiders without a refuge had the most background contrasting coloration, whereas those with a refuge were more likely to match their background (Table 2, model A; Fig. 4). The degree of coloration investment in either background matching or contrasting depended on both web type ($\chi^2 = 10.88$, $P < 0.01$) and refuge presence ($\chi^2 = 5.27$, $P = 0.02$). Orb weavers exhibited higher antipredator investment than sheet-and-tangle weavers, which in turn showed more investment than tangle weavers (Table 2, model B). Larger spiders tended to be more brightly colored and spikier, with overall greater investment in apparent antipredator adaptations ($\chi^2 = 5.33$, $P < 0.02$, Table 2). In terms of their behavior, genera with a greater level of protection from their webs or refugia were more likely to exhibit defensive behaviors, such as fleeing or dropping from the web upon a simulated predator contact, than less protected species (Table 2, models D–F; Fig. 5).

Discussion

We found that diurnal spiders with potentially different levels of predation risk as a function of the geometry of their webs and the presence or absence of a refuge differed in terms of their antipredator physical and behavioral characteristics. Specifically, orb weavers without a refuge tended to be more brightly colored and spiky, whereas the more protected 3D web builders, with or without a refuge, tended to be smooth and more neutral in coloration. Orb weavers with a refuge, in contrast, tended to exhibit a coloration that blended against the refuges they built. Behaviorally, spiders with potentially greater exposure to predation as a function of the architecture of their webs and the presence or absence of a refuge tended to respond aggressively to a simulated predator attack, whereas those better protected tended to drop or flee once the defense of their web had been breached. These results are consistent with the expectation that antipredator adaptations are shaped by context-dependent trade-offs (Lima and Dill 1990, Mukherjee and Heithaus 2013). Spiders, like other animals, are subject to selective pressures to which they must respond with the goal of minimizing costs while maximizing benefits (Rayor and Uetz 1990, Scharf et al. 2013). In this case, the costs associated with investment in antipredator adaptations, such as refuges, spines, background contrasting, or background blending coloration, should pay off when spiders are otherwise poorly protected within the context of their webs.

Degree of Antipredator Coloration Investment

When considering that either background contrasting, background matching or spikes represent an investment in morphological antipredator protection, we found that orb-weaving spiders were more likely to invest in these strategies than either tangle or sheet-and-tangle builders (Table 2). Given the geometry of their webs (Blackledge et al. 2002) and the more open microhabitats they occupy (Blackledge et al. 2011, Haberkern et al. 2020), orb web-building spiders are likely at greater risk of falling victim to visual predators (Blackledge and Wenzel 2001, Pekár 2014). It would then follow that orb-weaving spiders adopted strategies that allow them to either blend into their surroundings to avoid detection, in particular against a refuge or equivalent, or invest in defensive adaptations along with coloration that warns potential predators that they are dangerous and thus should avoid eating them (i.e., aposematism) (Robledo-Ospina and Rao 2022).

Coloration and Spikiness

Whether orb-weaving spiders with apparent antipredator coloration tended to be background matching or background contrasting, in turn, was a function of the presence or absence of a refuge: species with a refuge appeared to be background matching, whereas those without a refuge tended to exhibit background contrasting colors or patterns (Fig. 4 and Table 2). Orb weavers in the genera *Cyclosa* (Araneidae; Fig. 2A and Table S1.b) and *Uloborus* (Uloboridae; Table S1.e), which build elaborate retreat-like structures on their orbs—a trashline, in the former, a bright white stabilimentum, in the latter—for instance, displayed a coloration that closely matched these structures. At the other end of the spectrum, spiders with the brightest/most color contrasting coloration tended to be orb weavers without a refuge, most notably, species in the araneid genera *Micrathena*, *Amazonepeira*, *Witica*, and *Alpaida* and the tetragnatid *Leucauge* (Supplementary Fig. S5).

The association between bright coloration and spikes (Fig. 4), as in *Micrathena* spp. (Fig. 2D) or *Gasteracantha* (Gawryszewski and Motta 2012, Magalhaes et al. 2023), is suggestive of aposematism, an adaptation prey used to advertise being distasteful or dangerous (Weldon 2013, Caro and Ruxton 2019). Speed and Ruxton (2005) point out the potential danger that spikes pose to predators, and thus, their association with bright coloration can be considered aposematic. For spiders such as *Micrathena* or *Gasteracantha*, the energetic investment of body armor and bright colors is likely to pay off by warding off visual predators such as birds and other relatively large diurnal predators, such as hunting wasps (Rypstra 1984, Gunnarsson 2007, Baird 2008, Pekár 2014, Crofts and Stankowich 2021). Furthermore, spikes would have an advantage over chemical defenses in being themselves a visual advertisement of danger (Speed and Ruxton 2005).

In contrast, an investment in spikiness would be unnecessary for 3D web builders, whose more secluded microhabitat and web geometry potentially leave them less exposed (Blackledge et al. 2002, Crofts and Stankowich 2021). Spikes could also interfere with movement and damage 3D webs, thus potentially being maladaptive in the context of this web geometry. We recorded intermediate levels of spikiness in some 3D builders, such as species in the Linyphiidae and in the web-building genera *Aglaoctenus* sp. (Lycosidae) and *Tapinillus* sp. (Oxyopidae) (Supplementary Fig. S5), consistent with these spiders having an intermediate level of exposure. Thus, despite their webs having a tangle portion above and/or below the sheet, some of these sheet-and-tangle spiders tend to sit on or below the horizontal sheet rather than within the tangle. Their webs also tend to be placed in more open microhabitats than those of tangle builders (Blackledge et al. 2011, Haberkern et al. 2020).

Finally, we show that body size is positively correlated with both spikiness and contrasting coloration, as larger spiders of all web types (e.g., Araneidae, Tetragnathidae, and Theridiidae) were more often covered in spikes and were more likely to contrast with their background (Fig. 4; Table 2). There are multiple reasons why this may be the case. Larger spiders may be more likely targets of large diurnal predators, such as birds, making spikiness a worthwhile investment compared to smaller spiders, which tend to be ignored by large predators (Mestre et al. 2013, Gawryszewski 2017). Larger spiders may also have more time to grow their spikes than smaller ones. Likewise, because of being more likely targets of diurnal predators, larger spiders may be more likely to contrast with their backgrounds, thus using tactics such as aposematic coloration (Askenmo et al. 1977). As we assessed coloration with the human eye, we acknowledge that we may have missed additional cases of contrasting coloration that are visible in a UV scale (see *Limitations* section).

Antipredator Behavior

In terms of the behavioral response of spiders to a mock predation event, spiders that were the least exposed in their webs (i.e., tangles and sheet-and-tangles, with or without a refuge) were more likely to respond defensively by fleeing or dropping from their webs rather than responding offensively with a threat display or bite (Table 2; Fig. 5). In addition to different levels of exposure, spiders with different web architectures may also be facing different types of predators and thus respond accordingly. Tangle web builders are often sheltered in the vegetation and within their webs, so they may be more at risk of predation by gleaning animals that hunt off the vegetation, such as ants or other spiders. There is evidence that some types of tangle web-building spiders may be feeding specialists on leaf-dwelling ants (Formicidae) (Liu et al. 2016, Líznarová and Pekár 2019, and pers. obs.). Because ants are also a common predator of spiders, it is feasible that their webs may be built to avoid ants in physical space by hanging from threads that are suspended above walking surfaces (Hölldobler 1970). Some sheet-and-tangle web builders, on the other hand, tend to lead a more cursorial lifestyle within their horizontal sheet, which may leave them more exposed to cursorial predators, such as ants and wandering spiders (Ctenidae) (Vieira and Höfer 1994, Finch 1997). These spiders may thus need adaptations that allow them to quickly retreat from predators rather than face them directly with an offensive strategy, consistent with personal observations in the field.

In terms of the spider's response to a simulated predator, we stress that our method involved mimicking a predation event by poking the spider. By doing this, we had already breached the 3D web as a first line of defense for 3D web builders, whereas for 2D web builders, the mock predator had not necessarily breached a defense. It is thus possible that the difference in the degree of offensive (2D weavers) vs. defensive (3D weavers) behaviors we observed may reflect this difference in treatment for spiders of these web types. Nakata (2009) avoided physical contact with the spider by exposing it to the vibrations emitted from a 440 Hz tuning fork. These vibrations are useful as a proxy for a spider's perceived predation risk because they are thought to mimic the approach of common aerial predators. Future studies that assess spider antipredatory responses may benefit from incorporating the technique outlined in Nakata (2009) into their methodology.

Significance

Our findings highlight the value of web-building spiders as a model system to examine the role of context dependence in the evolution of adaptations. The literature offers many examples of morphological and behavioral antipredator adaptations, from sticklebacks to guppies and beyond (Bell and Foster 1995, Valkonen et al. 2012), but limited treatment of extended phenotypes also being subject to, and feeding back on such pressures. Lessons from the spider system can illuminate the interplay of forces shaping animals and the structures they build. As with spider webs, birds' nests, for instance, can be thought of as extended phenotypes with traits likely subject to optimizing selection (Dawkins 2016). Bird nest architecture, microhabitat preference, color, and composition are all likely subject to trade-offs similar to those of spiders, where the risk of predation varies depending on context (Magnhagen 1991). Their design and microhabitat placement should thus feedback on the morphological and behavioral characteristics of many bird species (Mainwaring et al. 2014).

By examining the complex interaction between context-dependent antipredator adaptations and extended phenotypes in different groups of organisms, it can be elegantly demonstrated how natural selection balances different components of the phenotype to produce effective strategies depending on context. Previous studies on spider webs have largely focused either on orb web-building spiders (Eberhard 1990, 2020) or, collectively, on spiders with 3D webs (Blackledge et al. 2002), without differentiating between tangle and sheet-and-tangle webs. This leaves a wide-open field for future studies to explore the broad eco-evolutionary feedback shaping these organisms and the structures they build as context-dependent evolutionary adaptations.

Specimen collection statement

The authors attest that all legal and regulatory requirements, including export and mobilization and transportation permits, have been followed for the collection of specimens from source populations at any international, national, regional, or other geographic level for all relevant field specimens collected as part of this study.

Acknowledgments

We thank Jatun Sacha Biological Reserve, Universidad Amazónica IKIAM, Pontificia Universidad Católica del Ecuador, and the Ministerio del Ambiente of Ecuador for research permits (N°011-018-IC-FLO-DPAN/MA, N°017-19-IC-FAU-DNB/MA). Thank you, S. Straus, M. Ankenman, I. L. Olesen, K. Robinson, E. Berger, E. Calvache, and Clos, for your help in the field. We also thank T. Tasbihgou and H. Williams for helping with specimen preparation and with the design of figures, and C. Keller for the early edits to the manuscript. Thank you, J. Burini (primalshutter.com), T. Tasbihgou, N. Bay (Nickybay.com), and J. Rose for permission to use your photos. Thank you, S. Tomlinson, S. Rose, S. Longhorn, and other members of Facebook groups *Entomology* and *Spider/bug questions with thebuggirl* for identification help of photos of insects and spiders. Lastly, we thank the hundreds of Amazonian spiders that gave their lives so that we could conduct this study.

Author contributions

Andrea Haberkern (Conceptualization [lead], Data curation [equal], Investigation [lead], Methodology [equal], Visualization [equal], Writing—original draft [lead]), Jessica Schmidt (Data curation [equal], Investigation [supporting], Project administration [supporting], Visualization [equal], Writing—review & editing [equal]), Yi Lin Zhou (Data curation [equal], Investigation [supporting], Project administration [supporting], Visualization [supporting], Writing—review & editing [supporting]), Luis Camacho (Data curation [supporting], Formal analysis [lead], Software [lead], Validation [lead], Visualization [supporting]), Antonio Brescovit (Funding acquisition [supporting], Investigation [equal], Resources [supporting], Writing—review & editing [equal]), and Leticia Aviles (Conceptualization [equal], Formal analysis [supporting], Funding acquisition [lead], Methodology [equal], Project administration [lead], Supervision [lead], Writing—review & editing [lead])

Supplementary data

Supplementary data are available at *Insect Systematics and Diversity* online.

Funding

This research was funded by NSERC Canada Discovery grant (RGPIN-2019-06539) to L.A. A.D.B was funded by CNPq grant PQ 303903/2019-8.

Data availability

Data will be made available in the UBC Dataverse at Scholars Portal.

References

Askenmo C, von Brömssen A, Ekman J, et al. 1977. Impact of some wintering birds on spider abundance in spruce. Oikos 28(1):90. https://doi.org/10.2307/3543327

Baird TA. 2008. A growth cost of experimentally induced conspicuous coloration in first-year collared lizard males. Behav. Ecol. 19(3):589–593. https://doi.org/10.1093/beheco/arn014

Bell MA, Foster SA. 1995. The evolutionary biology of the threespine stickleback. J. Anim. Ecol. 64(3):418. https://doi.org/10.2307/5902

Blackledge TA. 1999. Do stabilimenta in orb webs attract prey or defend spiders? Behav. Ecol. 10(4):372–376. https://doi.org/10.1093/beheco/10.4.372

Blackledge T, Wenzel J. 2001. Silk mediated defense by an orb web spider against predatory mud-dauber wasps. Behaviour 138(2):155–171. https://doi.org/10.1163/15685390151074357

Blackledge TA, Coddington JA, Gillespie RG. 2002. Are three-dimensional spider webs defensive adaptations? Ecol. Lett. 6(1):13–18. https://doi.org/10.1046/j.1461-0248.2003.00384.x

Blackledge TA, Kuntner M, Agnarsson I. 2011. The form and function of spider orb webs. Adv. Insect Physiol. 41:175–262. https://doi.org/10.1016/b978-0-12-415919-8.00004-5

Blamires SJ, Thompson MB, Hochuli DF. 2007. Habitat selection and web plasticity by the orb spider *Argiope keyserlingi* (Argiopidae): do they compromise foraging success for predator avoidance? Austral. Ecol. 32(5):551–563. https://doi.org/10.1111/j.1442-9993.2007.01727.x

Blamires SJ, Hou C, Chen L-F, et al. 2013. Three-dimensional barricading of a predatory trap reduces predation and enhances prey capture. Behav. Ecol. Sociobiol. 67(5):709–714. https://doi.org/10.1007/s00265-013-1493-x

Brescovit AD, Bonal AB, Bertani R, et al. 2002. Araneae. In: Adis J, editor. Amazonian Arachnida and Myriapoda: keys for the identification to classes, orders, families, some genera and lists of known species. Sofia, Bulgaria: Pensoft; p. 303–334.

Brooks ME, Kristensen K, Van Benthem KJ, et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R J. 9(2):378. https://doi.org/10.32614/rj-2017-066

Bruce MJ, Heiling AM, Herberstein ME. 2005. Spider signals: are web decorations visible to birds and bees? Biol. Lett. 1(3):299–302. https://doi.org/10.1098/rsbl.2005.0307

Cadier M, Andersen KH, Visser AW, et al. 2019. Competition–defense tradeoff increases the diversity of microbial plankton communities and dampens trophic cascades. Oikos 128(7):1027–1040. https://doi.org/10.1111/oik.06101

Caro T. Antipredator defenses in birds and mammals. Chicago (IL): University of Chicago Press; 2005.

Caro T, Ruxton G. 2019. Aposematism: unpacking the defences. Trends Ecol. Evol. 34(7):595–604. https://doi.org/10.1016/j.tree.2019.02.015

Caves EM, Johnsen S. 2018. Acuity view: an R package for portraying the effects of visual acuity on scenes observed by an animal. Methods Ecol. Evol. 9(3):793–797. https://doi.org/10.1111/2041-210x.12911

Caves EM, Nowicki S, Johnsen S. 2019. Von Uexküll revisited: addressing human biases in the study of animal perception. Integr. Comp. Biol. 59(6):1451–1462. https://doi.org/10.1093/icb/icz073

Clemente CJ, Mcmaster KA, Fox L, et al. 2005. Visual acuity of the sheet-web building spider *Badumna insignis* (Araneae, Desidae). J. Arachn. 33(3):726–734. https://doi.org/10.1636/s04-35.1

Clemente CJ, Mcmaster KA, Fox E, et al. 2010. The visual system of the Australian wolf spider *Lycosa leuckartii* (Araneae: Lycosidae): visual acuity and the functional role of the eyes. J. Arachn. 38(3):398–406. https://doi.org/10.1636/b09-96.1

Cloudsley-Thompson JL. 1995. A review of the anti-predator devices of spiders. Bull. Br. Arachnol. Soc. 10(3):81–96.

Corcobado G, Herberstein ME, Pekár S. 2016. The role of ultraviolet colour in the assessment of mimetic accuracy between Batesian mimics and their models: a case study using ant-mimicking spiders. Die Naturwissenschaften 103(11–12):90. https://doi.org/10.1007/s00114-016-1410-z

Crofts SB, Stankowich T. 2021. Stabbing spines: a review of the biomechanics and evolution of defensive spines. Integr. Comp. Biol. 61(2):655–667. https://doi.org/10.1093/icb/icab099

Dawkins R. The extended genotype: the long reach of the gene. Oxford, England: Oxford University Press; 2016. p. 468.

Eberhard WG. 1990. Function and phylogeny of spider webs. Annu. Rev. Ecol. Syst. 21(1):341–372. https://doi.org/10.1146/annurev.es.21.110190.002013

Eberhard WG. 2019. Hunting behavior of the wasp *Polysphincta gutfreundi* and related polysphinctine wasps (Hymenoptera, Ichneumonidae). J. Kansas Entomol. Soc. 91(3):177. https://doi.org/10.2317/0022-8567-91.3.177

Eberhard WG. Spider webs: behavior, function, and evolution. Chicago (IL): The University of Chicago Press; 2020. p. 816.

Edwards SM, Auguie B, Jackman S, et al. 2020. Lemon: freshing up your 'ggplot2' Plots. CRAN. [accessed 2022 June 23] https://cran.r-project.org/package=lemon.

Endler JA. 1990. On the measurement and classification of colour in studies of animal colour patterns. Biol. J. Linn. Soc. 41(4):315–352. https://doi.org/10.1111/j.1095-8312.1990.tb00839.x

Finch O-D. 1997. Spider wasps (Hymenoptera, Pompilidae) as predators of a spider taxocoenosis. Paper Presented at: Proceedings of the 16th European Colloquium of Arachnology European Society of Arachnology; Siedlce, Poland; p. 83–89.

Fox J, Weisberg S. 2019. An R companion to applied regression. 3rd ed. Thousand Oaks (CA): SAGE Publications; p. 608.

Gawryszewski FM. 2017. Anti-predator strategies. In: Malheiros G, editors. Behaviour and ecology of spiders. New York: Springer Cham; p. 397–415.

Gawryszewski FM, Motta PC. 2012. Colouration of the orb-web spider *Gasteracantha cancriformisdoes* not increase its foraging success. Ethol. Ecol. Evol. 24(1):23–38. https://doi.org/10.1080/03949370.2011.582044

Gunnarsson B. 2007. Bird predation on spiders: ecological mechanisms and evolutionary consequences. J. Arachn. 35(3):509–529. https://doi.org/10.1636/rt07-64.1

Haberkern AM, Fernandez-Fournier P, Avilés L. 2020. Spinning in the rain: interactions between spider web morphology and microhabitat use. Biotropica 52(3):480–487. https://doi.org/10.1111/btp.12752

Higgins L. 1992. Developmental changes in barrier web structure under different levels of predation risk in *Nephila clavipes* (Araneae: Tetragnathidae). J. Insect Behav. 5(5):635–655. https://doi.org/10.1007/bf01048010

Hölldobler B. 1970. *Steatoda fulva* (Theridiidae), a spider that feeds on harvester ants. Psyche: J. Entomol. 77(2):202–208. https://doi.org/10.1155/1970/52793

Kassambara A. 2020. ggpubr: "ggplot2" based publication ready plots. CRAN. [accessed 2022 June 23] https://cran.r-project.org/package=ggpubr.

Kovoor J, Muñoz-Cuevas A, Ortega-Escobar J. 2008. Diel morphological changes in the photoreceptors of *Lycosa tarentula* (Araneae, Lycosidae). Biol. Rhythm. Res. 26(3):272–291. https://doi.org/10.1080/09291019509360342

Levi HW. 2002. Keys to the genera of Araneid Orbweavers (Araneae, Araneidae) of the Americas. J. Arachnol. 30(3):527–562. https://doi.org/10.1636/0161-8202(2002)030%5B0527:KTTGOA%5D2.0.CO;2

Levi HW, Levi LR. 1962. The genera of the spider family Theridiidae. Bull. Mus. Comp. Zool. Harv. 127(1):1–71.

Lima SL. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. Biol. Rev. Camb. Philos. Soc. 84(3):485–513. https://doi.org/10.1111/j.1469-185X.2009.00085.x

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. 68(4):619–640. https://doi.org/10.1139/z90-092

Liu J, May-Collado LJ, Pekár S, et al. 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). Mol. Phylogenet. Evol. 94(Pt B):658–675. https://doi.org/10.1016/j.ympev.2015.09.023

Líznarová E, Pekár S. 2019. Trophic niche and capture efficacy of an ant-eating spider, *Euryopis episinoides* (Araneae: Theridiidae). J. Arachnol. 47(1):45. https://doi.org/10.1636/0161-8202-47.1.45

Magalhaes ILF, Martins PH, Feleiro BT, et al. 2024. Complete phylogeny of Micrathena spiders suggests multiple dispersal events among Neotropical rainforests, islands, and landmasses, and indicates Andean orogeny promotes speciation. Cladistics. https://doi.org/10.1101/2023.11.01.565210

Magnhagen C. 1991. Predation risk as a cost of reproduction. Trends Ecol. Evol. 6(6):183–186. https://doi.org/10.1016/0169-5347(91)90210-O

Mainwaring MC, Hartley IR, Lambrechts MM, et al. 2014. The design and function of birds' nests. Ecol. Evol. 4(20):3909–3928. https://doi.org/10.1002/ece3.1054

Manicom C, Schwarzkopf L, Alford RA, et al. 2008. Self-made shelters protect spiders from predation. Proc. Natl. Acad. Sci. U.S.A. 105(39):14903–14907. https://doi.org/10.1073/pnas.0807107105

Mestre L, Garcia N, Barrientos JA, et al. 2013. Bird predation affects diurnal and nocturnal web-building spiders in a Mediterranean citrus grove. Acta Oecol. 47:74–80. https://doi.org/10.1016/j.actao.2013.01.001

Montgomerie RD, Weatherhead PJ. 1988. Risks and rewards of nest defence by parent birds. Q. Rev. Biol. 63(2):167–187. https://doi.org/10.1086/415838

Morehouse NI, Buschbeck EK, Zurek DB, et al. 2017. Molecular evolution of spider vision: new opportunities, familiar players. Biol. Bull. 233(1):21–38. https://doi.org/10.1086/693977

Mukherjee S, Heithaus MR. 2013. Dangerous prey and daring predators: a review. Biol. Rev. Camb. Philos. Soc. 88(3):550–563. https://doi.org/10.1111/brv.12014

Nakata K. 2009. To be or not to be conspicuous: the effects of prey availability and predator risk on spider's web decoration building. Anim. Behav. 78(5):1255–1260. https://doi.org/10.1016/j.anbehav.2009.08.012

Opell BD. 2017. Checklist of American Uloboridae (Arachnida: Araneae). Gt. Lakes Entomol. 16(2):61–66. https://doi.org/10.22543/0090-0222.1464

Peitsch D, Fietz A, Hertel H, et al. 1992. The spectral input systems of hymenopteran insects and their receptor-based colour vision. J. Comp. Physiol. A Sens. Neural Behav. Physiol. 170(1):23–40. https://doi.org/10.1007/BF00190398

Pekár S. 2014. Comparative analysis of passive defences in spiders (Araneae). J. Anim. Ecol. 83(4):779–790. https://doi.org/10.1111/1365-2656.12177

Pérez I De Lanuza G, Font E. 2014. Ultraviolet vision in lacertid lizards: evidence from retinal structure, eye transmittance, SWS1 visual pigment genes, and behaviour. J. Exp. Biol. 217(Pt 16):2899–2909. https://doi.org/10.1242/jeb.104281

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

Rayor LS, Uetz GW. 1990. Trade-offs in foraging success and predation risk with spatial position in colonial spiders. Behav. Ecol. Sociobiol. 27(2):77–85. https://doi.org/10.1007/bf00168449

Robertson M, Avilés L. 2018. Rain, predators and vegetation lushness may structure web-building spider communities along precipitation gradients. Ecol. Entomol. 44(2):217–226. https://doi.org/10.1111/een.12699

Robledo-Ospina LE, Rao D. 2022. Dangerous visions: a review of visual antipredator strategies in spiders. Evol. Ecol. 36(2):163–180. https://doi.org/10.1007/s10682-022-10156-x

Rypstra AL. 1983. The importance of food and space in limiting web-spider densities; a test using field enclosures. Oecologia 59(2-3):312–316. https://doi.org/10.1007/BF00378855

Rypstra AL. 1984. A relative measure of predation on web-spiders in temperate and tropical forests. Oikos 43(2):129. https://doi.org/10.2307/3544758

Scharf I, Peter F, Martin OY. 2013. Reproductive trade-offs and direct costs for males in arthropods. Evol. Biol. 40(2):169–184. https://doi.org/10.1007/s11692-012-9213-4

Sih A. 1980. Optimal behavior: can foragers balance two conflicting demands? Science 210(4473):1041–1043. https://doi.org/10.1126/science.210.4473.1041

Speed MP, Ruxton GD. 2005. Warning displays in spiny animals: one (more) evolutionary route to aposematism. Evolution 59(12):2499–2508. https://doi.org/10.1111/j.0014-3820.2005.tb00963.x

Stanford CB. 2002. Avoiding predators: expectations and evidence in primate antipredator behavior. Int. J. Primatol. 23(4):741–757. https://doi.org/10.1023/a:1015572814388

Straus S, Gonzalez AF, Matthews P, et al. 2021. Economies of scale shape energetics of solitary and group-living spiders and their webs. J. Anim. Ecol. 91(1):255–265. https://doi.org/10.1111/1365-2656.13628

Su I, Buehler MJ. 2020. Mesomechanics of a three-dimensional spider web. J. Mech. Phys. Solids 144:104096. https://doi.org/10.1016/j.jmps.2020.104096

Tibbetts EA. 2002. Visual signals of individual identity in the wasp *Polistes fuscatus*. Proc. Biol. Sci. 269(1499):1423–1428. https://doi.org/10.1098/rspb.2002.2031

Tseng L, Tso I-M. 2009. A risky defence by a spider using conspicuous decoys resembling itself in appearance. Anim. Behav. 78(2):425–431. https://doi.org/10.1016/j.anbehav.2009.05.017

Valkonen JK, Nokelainen O, Niskanen M, et al. 2012. Variation in predator species abundance can cause variable selection pressure on warning signaling prey. Ecol. Evol. 2(8):1971–1976. https://doi.org/10.1002/ece3.315

Vieira RS, Höfer H. 1994. Prey spectrum of two army ant species on Central Amazonia, with special attention on the effect on spider populations. Andrias 13:189–198.

von Uexküll J. Cartas biológicas a una dama. Buenos Aires: CULCyT; 1920.

Wang B, Yu L, Ma N, et al. 2022. Conspicuous cruciform silk decorations deflect avian predator attacks. Integr. Zool. 17(5):689–703. https://doi.org/10.1111/1749-4877.12621

Weldon PJ. 2013. Chemical aposematism. Chemoecology 23(4):201–202. https://doi.org/10.1007/s00049-013-0140-3

Whiting MJ, Holland BS, Keogh JS, et al. 2022. Invasive chameleons released from predation display more conspicuous colors. Sci. Adv. 8(19):eabn2415. https://doi.org/10.1126/sciadv.abn2415

Wickham H. ggplot2: elegant graphics for data analysis. New York: Springer-Verlag; 2016. https://ggplot2.tidyverse.org.

Withgott J. 2000. Taking a bird's-eye view…in the UV. BioScience 50(10):854. https://doi.org/10.1641/0006-3568(2000)050%5B0854:tabsev%5D2.0.co;2