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Prey colour biases of araneophagic mud-daubing wasps

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While foraging, it is critical for a predator to detect and recognize its prey quickly in order to optimize its energy investment. In response, prey can use low-cost energy strategies such as crypsis and immobility that operate early in the detection–attack sequence. Mesopredators, such as spiders, are themselves attacked by visually oriented predators such as mud-dauber wasps. However, it is not known which colour cues are used by wasps to detect and capture their spider prey or whether there are biases towards such cues. In this study, we evaluated the prey colour biases of two mud-dauber wasps (*Trypoxylon tridentatum* and *Trypoxylon bridwelli*) using full-spectrum digital photography and visual modelling. We compared the colour contrast of spiders that were preyed upon with that of the spiders in the surrounding habitat. We show that the spiders captured by the wasps had higher chromatic contrast with their typical backgrounds compared with other co-occurring spider species not found in *Trypoxylon* nests. Our results suggest that *Trypoxylon* wasps may exhibit colour biases and/or preferences when hunting their spider prey. Our study highlights the importance of considering the perceptual abilities and biases of predators when studying predator–prey interactions.

While foraging, it is critical for a predator to detect and recognize its prey quickly. To counter this, prey often use passive strategies such as crypsis that operate early in the detection–attack sequence, which reduce energy expenditure compared with secondary strategies such as escape or aggressiveness (Broom, Higginson, & Ruxton, 2010; Ruxton, Sherratt, & Speed, 2004). On the other hand, predators lose energy when a prey successfully avoids or hampers predator detection (Brown & Kotler, 2004; Jakob, Porter, & Uetz, 2001). Therefore, the predator is under selective pressure to overcome such prey strategies.

Predators may use different sensory modes when foraging in order to maximize the probability of detecting prey. For those that use visual cues, there are different visual mechanisms involved in different tasks, namely, spatial acuity (shape and detail recognition), temporal resolution (object tracking) and spectral sensitivity (colour and pattern recognition). Visually hunting predators use combinations of these mechanisms during predation (Cronin, Johnsen, Marshall, & Warrant, 2014). Among these, spectral sensitivity is an important mechanism that aids in target detection in different visual systems (Heiling, Herberstein, & Chittka, 2003; Hemmi, Marshall, Pix, Vorobyev, & Zeil, 2006; Taylor, Maier, Byrne, Amin, & Morehouse, 2014). Perception of different wavelength signals can be generally split into two main neural pathways, i.e. with achromatic and chromatic mechanisms. In a number of animals, achromatic vision is often associated with spatial vision, motion perception and detection of small objects (for example in Hymenoptera; Spaethe, Tautz, & Chittka, 2001), whereas colour vision is often involved in object discrimination at shorter ranges (Osorio & Vorobyev, 2005). Therefore, different mechanisms may be used in different stages of the prey detection and attack sequence.

Spider-hunting wasps are an excellent model to explore the issues related to the visual traits that can be crucial for a predator when foraging. In particular, mud-dauber wasps build nests with variable numbers of brood cells and provide them with one or multiple paralysed spiders to feed their offspring (Eberhard, 1970, 1973; Rayor, 1996). To locate their prey, spider-hunting sphecid

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wasps use either active or passive strategies such as locating contrasting spots, antennae tapping to detect cryptic spiders, web pulling and retreat tearing. These strategies can be highly variable across wasp species according to their food specialization (Coville, 1987).

Spider-hunting wasps are thought to hunt visually using a ‘search image’ (Cloudsley-Thompson, 1995). Vision in wasps is important not only for navigation and nest location using landmarks (Zeil, 1993), but also for approaching and landing near the spider web when foraging, since in some cases, they seem to orient themselves using the spider's contrast against the background (Eberhard, 1970). However, it has been suggested that wasps rely on both visual and chemotactile cues at different stages of prey location and recognition (Uma & Weiss, 2010). Accordingly, visual information may be involved in the searching/navigation behaviour subsequent to the chemical detection of the spider web, indicating that the visual information is important when the wasp tries to catch the spider in its final attack (Eberhard, 1970). Although Uma and Weiss (2010) evaluated the relative importance of visual signals against chemical cues, they did not consider prey selection from the perspective of the wasp visual system.

Because of the large variation in spider appearance (Hsiung, Shawekey, & Blackledge, 2019) and the difficulty in quantifying wasp hunting in nature, it has been logistically challenging to identify the prey traits that are important for spider-hunting wasps. However, by sampling the nests of mud-dauber wasps, it is possible to quantify the foraging outcomes of individual wasps in terms of prey characteristics, such as the sex, developmental state, size and other features of individual prey items (e.g. body coloration) even without observing prey capture directly (Patil & Arade, 2011; Powell & Taylor, 2017). This is because parasitized spiders are kept alive, albeit paralysed, in the wasp nests (Coville, 1987). Therefore, live prey allows for the evaluation of colour cues (i.e. spider body coloration) from the wasp perspective. Previous studies of *Trypoxylon* species have focused on prey diversity (Buschini, Borba, & Brescovit, 2008; Domínguez & Jiménez, 2008; Musicante & Salvo, 2010), prey preferences (Powell & Taylor, 2017) and some prey traits such as body size (Falcón-Brindis, Rodríguez-Estrella, & Jiménez, 2019).

In this paper, we evaluated the body coloration of the spiders captured by two *Trypoxylon* species (Hymenoptera: Crabronidae) as viewed through the hymenopteran visual system, by combining colour measurements of spider coloration and ecologically relevant backgrounds with visual modelling of wasp vision. The use of colour vision models is a useful tool to address the ecology and evolution of visual signals involved in the interactions between different organisms, allowing the estimation of the perception of focal stimuli by nonhuman visual systems (Kemp et al., 2015).

In this study, we asked the following questions. (1) Are there biases with respect to the species composition, abundance and appearance of spiders in the diet of *Trypoxylon* spp. wasps compared to the spiders in the surrounding habitat? (2) In terms of body coloration and contrast against the background, are captured spiders more conspicuous on average than other spiders in the habitat?

METHODS

We collected spiders found in the nests of two mud-daubing wasps from the *Trypoxylon* genus (Hymenoptera: Crabronidae): *Trypoxylon* (*Trypoxylon*) *bridwelli* Sandhouse, and *Trypoxylon* (*Trypargilum*) *tridentatum tridentatum* Packard (Fig. 1). These species nest in pre-existing cavities and accept artificial trap-nests (Falcón-Brindis et al., 2019). We collected nests during May–July 2019 in the Estación Biológica Dra. Laura Arriaga Cabrera (EBLAC), La Paz, Baja California Sur, Mexico (24°7'47.3''N, 110°26'8.6''W), a 215 ha reserve dominated by xeric scrublands, which is typical of the Sonoran desert (Wiggins, 1980).

Our study was divided into two main sections. First, we evaluated biases in the prey composition of wasps, comparing them to extant spider populations at La Paz (question 1). Second, we evaluated the chromatic and achromatic contrast of the prey from a visual ecology perspective (question 2).

We set up 90 artificial trap nests (Staab, Pufal, Tscharntke, & Klein, 2018; Fig. 1a–c) in groups of three traps along two transects and 15 m apart from each group. The trap design was identical to that used by Falcón-Brindis et al. (2019), which had five artificial cavities per trap for a total of 450 potential nests for *Trypoxylon tridentatum* and *Trypoxylon bridwelli*. The traps were monitored every 2 weeks, and spiders were removed for taxonomic determination and body colour measurements. These spiders were labelled as captured prey. We sampled the spider community in the same area by means of the beating tray technique and direct collection in order to estimate the potential wasp prey. This sampling was restricted to spiders measuring 1–10 mm in total body length, because previous studies with the same species (Falcón-Brindis et al., 2019) evaluated the correlation between wasp body size and prey size, highlighting that spider size is a crucial factor to the wasp when foraging. The sampling was done by three researchers collecting simultaneously in transects 10 m apart from the traps in six survey events.

Ethical Note

Our study was conducted on sampling spiders that had already been parasitized by wasps. We did not conduct behavioural experiments with live spiders or wasps. We did not need regulatory permits (as per Mexican regulations) for the sampling of spiders in the community. All spiders collected were deposited at the arachnological collection in the Laboratorio de Aracnología y Entomología (CARCIB), Centro de Investigaciones del Noroeste, where they will be used as a reference collection in future studies.

Prey Biases

To compare the wasp diet in terms of taxonomic composition, we conducted a nonmetric multidimensional scaling (NMDS) analysis paired with an analysis of similarities (ANOSIM) based on the Bray–Curtis distance. Then, we estimated the Levin index (B) and the Manly selectivity index (βi) to describe the niche width and the prey preferences of each wasp species, respectively. Statistical significance for Manly indexes was evaluated by comparing the observed and expected selectivity values using a χ^2 test, with P values Bonferroni corrected for multiple comparisons. Significant P values indicate positive or negative selectivity, while nonsignificant values indicate no selectivity (Manly, McDonald, Thomas, McDonald, & Erickson, 2002).

Spider Coloration and Visual Modelling

The colour properties of the spiders were measured by means of full-spectrum digital photography (Troscianko & Stevens, 2015). We generated a multispectral image of each spider with reflectance information in four channels: ultraviolet (UV), short-wavelength (SW), medium-wavelength (MW) and long-wavelength (LW). The photography set-up included a Canon 7D camera with the internal UV filter removed (LifePixel.com), attached to a UV-transmitting Nikkor EL 80 mm lens through a focusing helicoid. The aperture was fixed at f/5.6, but shutter speed varied in order to optimize exposure time. For the visible light photo, we used a UV/infrared

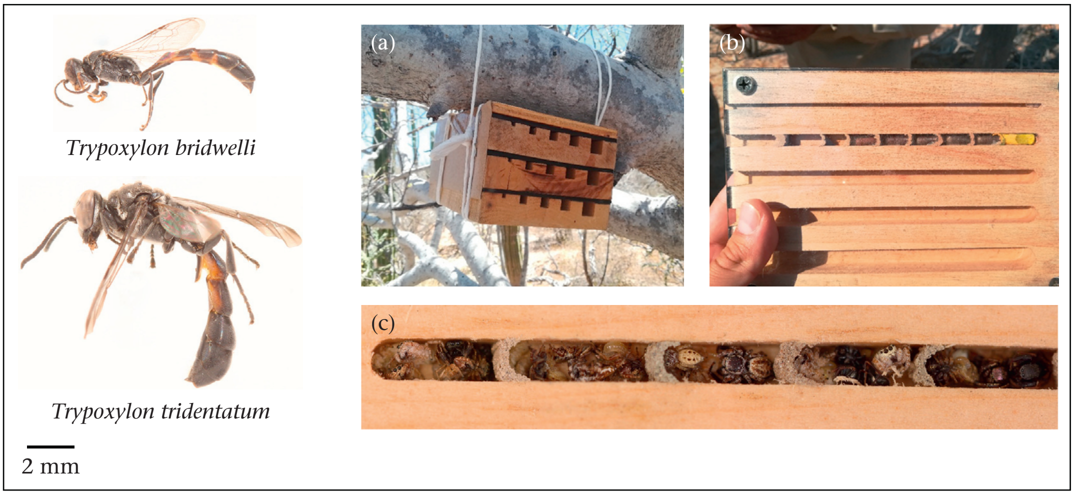

Figure 1. Nests of *Trypoxylon bridwelli* and *T. tridentatum* were used to evaluate the prey preferences of these wasps and chromatic/achromatic contrast of their spider prey against the background: (a) nest stations; (b) contents of a nest; (c) nest of *T. bridwelli* removed for taxonomical determination and multispectral photography.

(IR) blocking filter that transmits wavelengths of 400–700 nm (Baader UV/IR Cut filter), while UV photos were taken with a UV pass IR blocking filter that transmits at high efficiency between 300 and 400 nm (Baader U filter). We used natural sunlight as a light source, and all the images included a scale bar and two Zenith Sintered PTFE grey standards of 70% and 10% of reflectance, respectively.

Due to the lack of data for our focal species, especially with respect to their spectral sensitivity, we used the spectral sensitivity peaks published by Peitsch et al. (1992) for *Philanthus triangulum* (Hymenoptera, Sphecidae) (UV = 344 nm, SW = 444 nm, MW = 524 nm), the species most closely related to our focal species for which spectral sensitivity data are available. Then, using the nomogram from Govardovskii, Fyhrquist, Reuter, Kuzmin, and Donner (2000), we reconstructed the sensitivity spectrum of *P. triangulum*. We used formulas for A1 chromophores because this is the most commonly used chromophore in Hymenoptera (Briscoe & Chittka, 2001).

Once the sensitivity spectra for our focal species were calculated, and knowing the camera spectral sensitivities (with peaks at 372 nm, 465 nm, 557 nm and 624 nm in the UV, SW, MW and LW channels, respectively), we estimated the photoreceptor responses (quantum catch values) of the *P. triangulum* visual system using the MICA plugin (Troscianko & Stevens, 2015) with the standard D65 solar irradiance spectrum as our illuminant. We checked the validity of our conversion to the wasp visual system (photoreceptors UV, SW and MW for *P. triangulum*) using the 'cone mapping' option in MICA, and the polynomial model fitted well the model from the camera sensitivities peaks (R^2 between 0.988 and 0.999).

The quantum catch values for each spider colour were converted to colour loci (X and Y) applying the model proposed by Chittka (1992) for hymenopteran vision. These loci were projected into the colour hexagon space using the 'colourvision' package (Gawryszewski, 2018) in R (R Development Core Team, 2016). This colour hexagon space is a graphical representation of the perception of colour stimuli (Chittka & Brockmann, 2005). We estimated the area occupied by the polygon that contained all the points corresponding to the spiders from the nest of each wasp and from the community in the hymenopteran colour space. The area of those polygons was estimated through the R package 'geometry' (Habel, Grasman, Gramacy, Mozharovskyi, & Sterratt, 2019) in order to have a representation of colour diversity (Renoult, Kelber, & Schaefer, 2017) of the spiders found in the nests.

Using digital images, as above, we also estimated the quantum catch values of the backgrounds where the spiders were found. To do so, during habitat sampling for our survey of the extant spider community, we recorded the microhabitat (e.g. foliage, leaf litter and trunk) and background (plant species) for each spider collected. We then took multispectral photos of 10 samples of each background type (e.g. foliage of every plant species, tree trunks, bare soil) to model it in the wasp visual system. Using this data, we calculated the chromatic (ΔS; see Appendix, Equation A1) and achromatic or luminance contrast (L_{MW}; Equation A3) of the spider with their relevant background as a representation of conspicuousness through the receptor noise limited model (RNL) (Vorobyev & Osorio, 1998). For the achromatic (brightness) contrast, we used the values from the MW receptor, because there is evidence that bees use the green receptor for this task (Théry, Debut, Gomez, & Casas, 2005). We carried out all estimations using the Weber fraction ($w = 0.13$) and used the relative density for each receptor class (n_i) following Defrize, Théry, and Casas (2010) based on the values published for bees (1:0.471:4.412 ratios for the UV:SW:MW receptors, respectively). Finally, we compared the chromatic and achromatic distances between the spiders sampled from the community and those collected in the nests of both wasps by means of a Kolmogorov–Smirnov test.

RESULTS

We collected 405 individuals belonging to 48 spp. and 18 families from the habitat. From the artificial nests, we extracted 153 spiders preyed upon by *T. tridentatum* (14 spp., 4 families) and 99 spiders preyed upon by *T. bridwelli* (10 spp.; 6 families; Table 1). The two most common spiders in the community, *Hamataliwa* sp. ($N = 60$) and *Cyclosa walckenari* ($N = 26$), were not found in nests of either wasp species.

Prey Preferences of T. tridentatum *and* T. bridwelli

Diet differed significantly between the two co-occurring wasp species ($R = 0.61$, $P < 0.01$, stress = 0.057; Fig. 2). *Trypoxylon tridentatum* had a slightly wider niche ($B = 5.715$) than *T. bridwelli* ($B = 4.208$), and both wasp species exhibited prey preference for different spider species.

In the diet of *T. tridentatum* (Fig. 3a), the most abundant species were *Theridion* sp., *Eustala* sp., *Metepeira crassipes* and *Latrodectus*

Table 1
Relative abundance of spider species collected from nests of *Typoxylon tridentatum* and *T. bridwelli* and from the community (Comm.) in La Paz, Baja California Sur, Mexico

Family	Spider species	Source			Guild[a]
		Comm.	*T. tridentatum*	*T. bridwelli*	
Agelenidae	*Rothilena*	1			FW
Anyphaenidae	*Hibana* sp.	21			AH
	Lupettiana mordax	5		1	AH
	Wulfila sp.	6			AH
	N/A	18			
Araneidae	*Araneus* sp1.	2	3		OW
	Argiope argentata	2	2		OW
	Cyclosa caroli		2		OW
	Cyclosa walckenari	26			OW
	Cyclosa sp.	1	1		OW
	Eriophora edax	5	2		OW
	Eustala eleuthera		1		OW
	Eustala sp.	13	30	2	OW
	Gasteracantha cancriformis	16	5		OW
	Larinia sp.	1	3		OW
	Metepeira crassipes	2	2		OW
	Metepeira sp.		27		OW
	Gen. sp1	21	5		
Dyctinidae	*Mallos pallidus*	4		3	SWW
	Mallos pearcei			1	SWW
	N/A	5		2	
Diguetidae	*Diguetia canities*	4			SWW
Eutichuridae	*Cheiracanthium* sp.	1			S
Filistatidae	*Filistatoides* sp. nov.	1			BW
Hersiliidae	*Neoatma mexicana*	5			A
Mimetidae	*Mimetus hesperus*		2		WIS
Miturgidae	*Syspira tigrina*	1			GH
Oecobidae	*Oecobius annulipes*	4	3		SSW
Oxyopidae	*Hamataliwa* sp.	60			AA
	Oxyopes sp.	1			GA
	N/A	1			
Philodromidae	*Apollophanes* sp.	19			GA
	Philodromus sp.	2			GA
	Tibellus duttoni	5			GA
	Titanebo sp.	2			AA
Salticidae	*Colonus* sp.	9			JS
	Habronattus conjunctus	2			JS
	Metacyrba sp.	2			JS
	Paradamoetas sp.	1			JS
	Peckhamia picata	1		3	JS
	Phidippus californicus	1		1	JS
	Phidippus phoenix	15		10	JS
	Phidippus sp.	22		24	JS
	Salticus palpalis	1			JS
	Sassacus vitis	19		20	JS
	Sassacus sp.	3		1	JS
	N/A	2		1	JS
Scytodidae	*Scytodes* sp.	1			S
Sparassidae	Olios sp.	3			S
	N/A	2			
Theridiidae	*Anelosimus analyticus*	1			SWW
	Anelosimus sp.	1	1		SWW
	Euryopis sp.	2	2		SP
	Latrodectus hesperus	4	27		SWW
	Theridion submissum		3		SWW
	Theridion sp.		32	6	SWW
Thomisidae	*Mecaphesa dubia*	26		23	AA
	Timarus sp.	2			AA
	N/A	13		1	
Uloboridae	*Philoponella arizonica*	15			AA
N/A		2			
Total		**405**	**153**	**99**	

N/A: not available.

[a] Spider guilds modified from Cardoso, Pekár, Jocqué, and Coddington (2011). A: ambusher; AA: aerial ambusher; AH: aerial hunter; BW: burrow weaver; FW: funnel weaver; GA: ground ambusher; GH: ground hunter; JS: jumping spider; OW: orb weaver; S: stalker; SP: specialist; SSW: sensing sheet weaver; SWW: spacer web weaver; WIS: web-invading spider.

hesperus ($N = 32$, 31, 29 and 29, respectively). However, regarding prey selectivity, *Theridion* sp. ($\beta i = 0.458$), *M. crassipes* ($\beta i = 0.138$) and *L. hesperus* ($\beta i = 0.077$) were more commonly chosen by the wasps in comparison to their abundance in the general prey community. In contrast, in the diet of *T. bridwelli* (Fig. 3b), *Phidippus* sp., *Mecaphesa dubia* and *Sassacus vitis* were the most abundant species ($N = 34$, 23 and 21, respectively), and the highest preference was found with respect to *Theridion* sp. ($\beta i = 0.261$), *Peckhamia picata* ($\beta i = 0.074$) and *M. dubia* ($\beta i = 0.038$). *Trypoxylon tridentatum* preyed mostly on web-building spiders (orb weavers: $N = 83$; space webs: $N = 62$), and *T. bridwelli* captured mostly stalking ($N = 60$) and ambush ($N = 24$) spiders.

Prey Coloration from the Wasp's Perspective

Captured spiders showed low colour variation, as represented by the proximity of all points to the hymenopteran achromatic point in hexagonal visual space (Fig. 4a). However, when colour variation was evaluated in terms of the polygonal area occupied by the sampled spiders from the community or the nests (Fig. 4b), we found differences. The spiders in the community had higher colour diversity than those preyed upon by *T. tridentatum* and *T. bridwelli*. In addition, there was overlap between the polygons from the spiders selected by the different wasp species (area of overlap = 0.126).

In terms of the chromatic contrast of the spiders against the background (Fig. 5a), there were differences between the spiders collected in the field and those preyed upon by the wasps. We found that the spiders in the community on average contrasted less with common backgrounds than did the spiders in the nests of *T. tridentatum* ($D = 0.180$, $P < 0.005$) and *T. bridwelli* ($D = 0.240$, $P < 0.005$). However, when comparing the spiders preyed upon by the wasps, we found that the chromatic contrast of prey items against the background was similar between the two wasp species ($D = 0.109$, $P = 0.46$). Similarly, we found no differences in average achromatic contrast of prey when comparing between wasp species ($D = 0.091$, $P = 0.698$; Fig. 5b). We also found no difference in achromatic contrast of spiders found in the broader spider community and those found in the nests of *T. tridentatum* ($D = 0.084$, $P = 0.438$) or *T. bridwelli* ($D = 0.092$, $P = 0.523$).

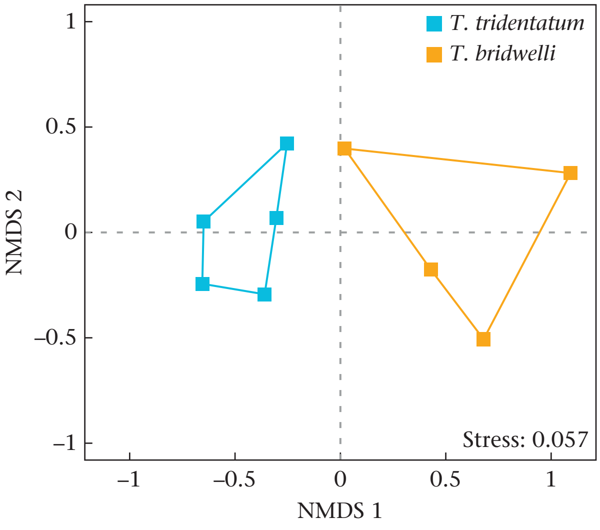

Figure 2. Nonmetric multidimensional scaling (NMDS) of the diet composition of the araneophagic wasps *Trypoxylon bridwelli* and *T. tridentatum* compared using an analysis of similarity (ANOSIM).

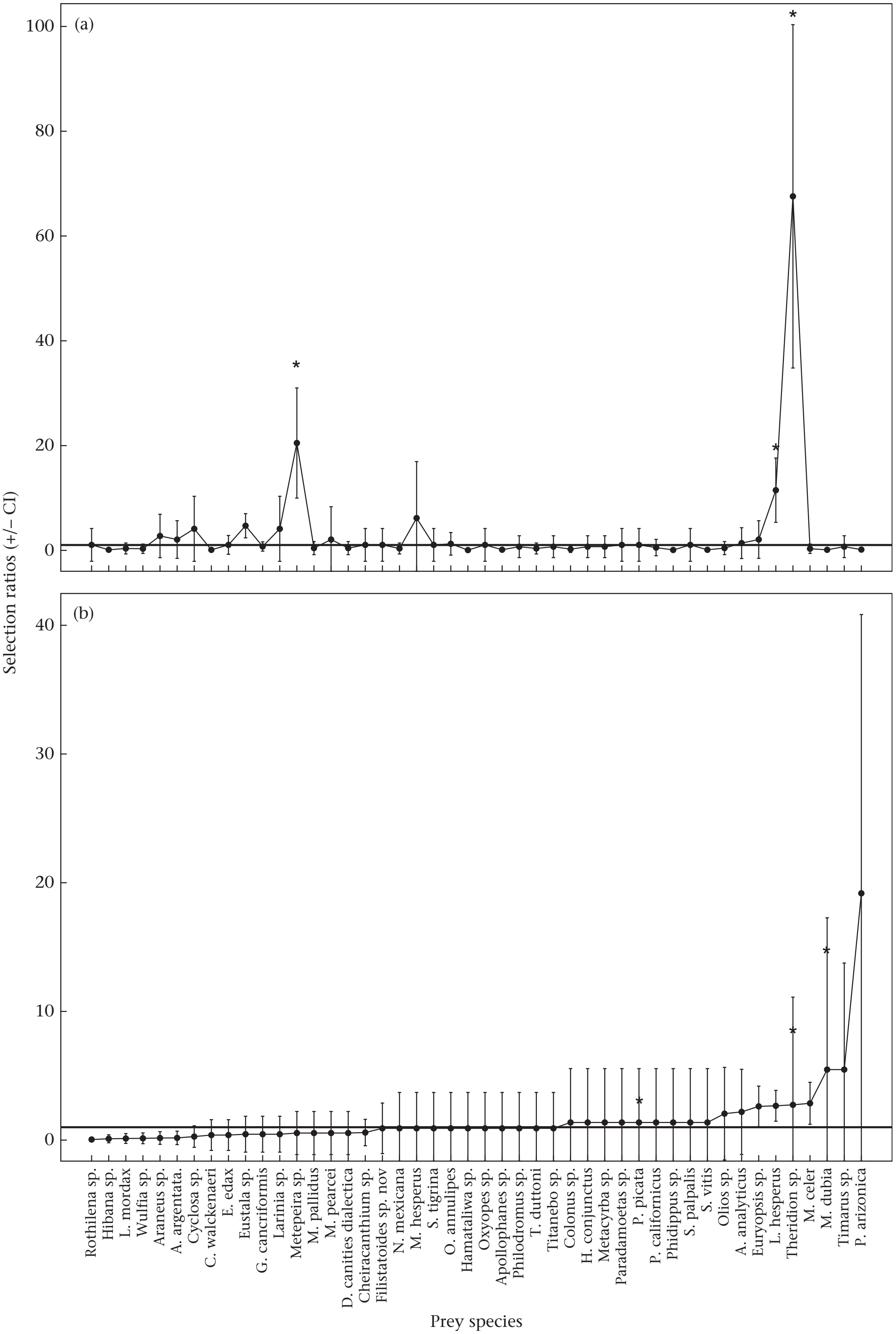

Figure 3. Manly selectivity measure of prey captured by (a) *Trypoxylon tridentatum* and (b) *T. bridwelli*. Values above the horizontal line indicate positive selection. Error bars indicate 95% confidence intervals. Asterisks indicate that a significantly higher proportion of prey were captured relative to their availability: *Theridion* sp. (βi = 0.458), *Metepeira crassipes* (βi = 0.138) and *Latrodectus hesperus* (βi = 0.077) for *T. tridentatum*; and *Theridion* sp. (βi = 0.261), *Peckhamia picata* (βi = 0.074) and *Mecaphesa dubia* (βi = 0.038) for *T. bridwelli.*

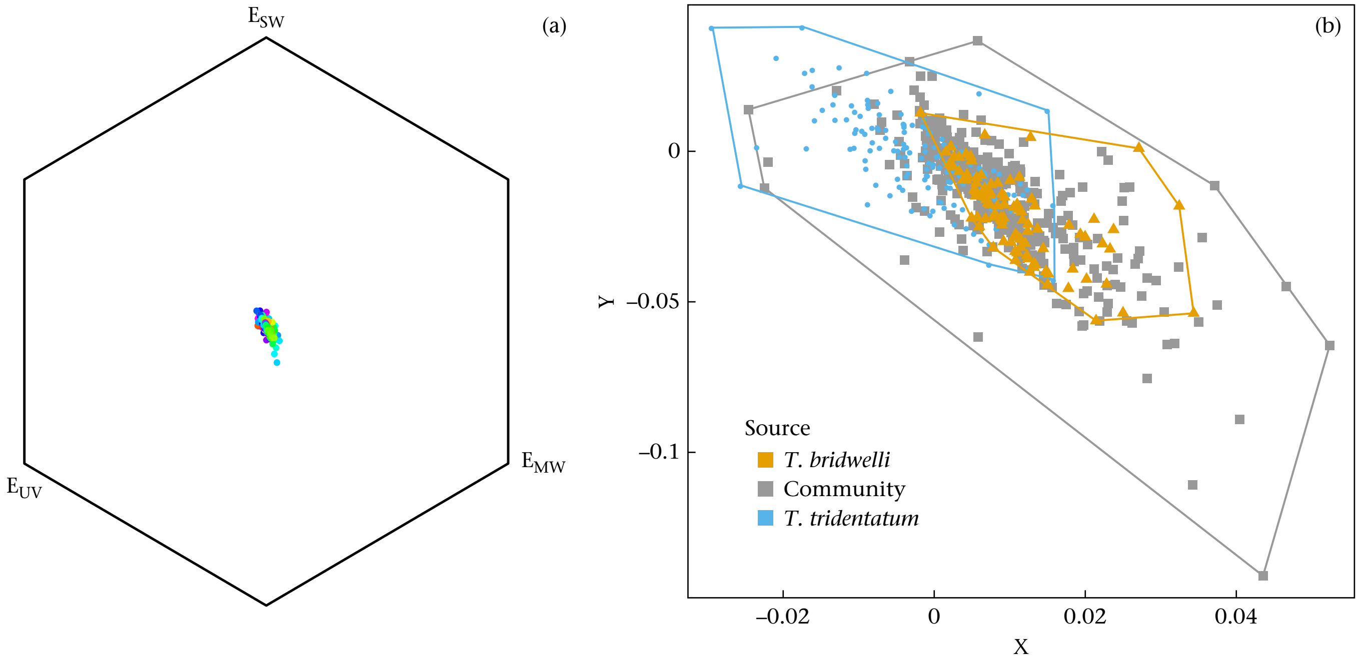

Figure 4. (a) Colour loci of the spiders distributed in the chromaticity diagram of hymenopterans; (b) enlarged area showing the polygons occupied by the spiders collected from the community (grey, area = 0.398) and preyed upon by *Trypoxylon tridentatum* (blue, area = 0.215) and *T. bridwelli* (yellow, area = 0.173).

DISCUSSION

Our main objective was to investigate how wasps perceive spider body coloration, and to evaluate whether spider coloration influences capture rate and/or active selection of spiders by foraging wasps. Our findings suggest that wasps may be selecting spiders with particular colour properties when compared with spiders in the community nearby. These colour properties may make prey spiders more conspicuous with respect to the wasp visual system, and this high chromatic saliency may make the spiders more vulnerable to detection.

Wasp Diet

In terms of diet composition, our results corroborate previous findings of the specialization of these wasp species on either web builders (Araújo & Gonzaga, 2007; Pitilin, Araújo, & Buschini, 2012) or ambush/stalkers (Musicante & Salvo, 2010). Prey selection is an adaptive response to the community source (Buschini et al., 2008), but prey choice is not a haphazard behaviour, since different species prey on spiders depending on different traits such as spider guild, chemical cues (Uma, Durkee, Herzner, & Weiss, 2013; Uma & Weiss, 2010), body size (Falcón-Brindis et al., 2019) and body coloration (this study).

Through the Predator's Eyes

By explicitly including information about the visual capabilities of these animals, our study represents a major advance in the investigation of these araneophagic wasps and their prey selection including modelling of the predator vision in this system, as has been done in other Hymenoptera–spider systems (Defrize et al., 2010). Although previous research has highlighted the importance of visual traits in wasp–spider interactions (Coville, 1987; Gonzaga & Vasconcellos-Neto, 2005), it has been based on behavioural data rather than on modelling the predator's visual perspective. Our approach reveals the relative importance of the chromatic and achromatic vision mechanisms in wasp foraging behaviour when visual cues are involved. Since we did not measure the spectral sensitivities of the wasp species used in this study, our interpretation should be considered as a cautious approximation of how the wasps may perceive prey in their habitat. Future work should incorporate these explicitly sensory approaches to augment behavioural characterization. Approaches that include multimodal investigations, as called for by Uma et al. (2013) will significantly improve our understanding of this predator–prey interaction from a broader sensory ecology perspective.

In terms of the sensory signals involved, Uma and Weiss (2010) proposed that the detection and attack sequence in the wasp–spider system might follow two possible scenarios: (1) the attack is initiated with chemical cues or (2) visual information is predominant, with both scenarios ending with prey recognition and capture. It is important to highlight that both sensory signals (visual and chemical) operate together and one may modulate the other.

However, in the hypothetical vision-first scenario, detection is driven by the visual contrast of the spider against the background (e.g. the filter paper on which the spider was presented in Uma and Weiss (2010)). Accordingly, our results show that wasps may use colour when foraging to help detect and/or identify their prey, and that the chromatic contrast between a spider and its background could be important in modulating predator behaviour in addition to olfaction.

To understand how colour might influence foraging decisions, it is important to know the way in which wasps and spiders interact. For example, when many web builders (common prey for *T. tridentatum*) perceive predator cues, they often drop to the ground and are subsequently chased by the wasps (Blackledge & Pickett, 2000). Other species remain motionless when they detect the presence of a predator (Gawryszewski, 2017). This is particularly common for stalkers like the jumping spiders (common prey for *T. bridwelli*) (Shamble et al., 2016). In both cases, detection of the spider by the wasp at close range may be driven by chromatic contrast (Osorio & Vorobyev, 2005), while detection of small targets at longer distances is often accomplished using achromatic vision (Spaethe et al., 2001). This discrimination is crucial for the

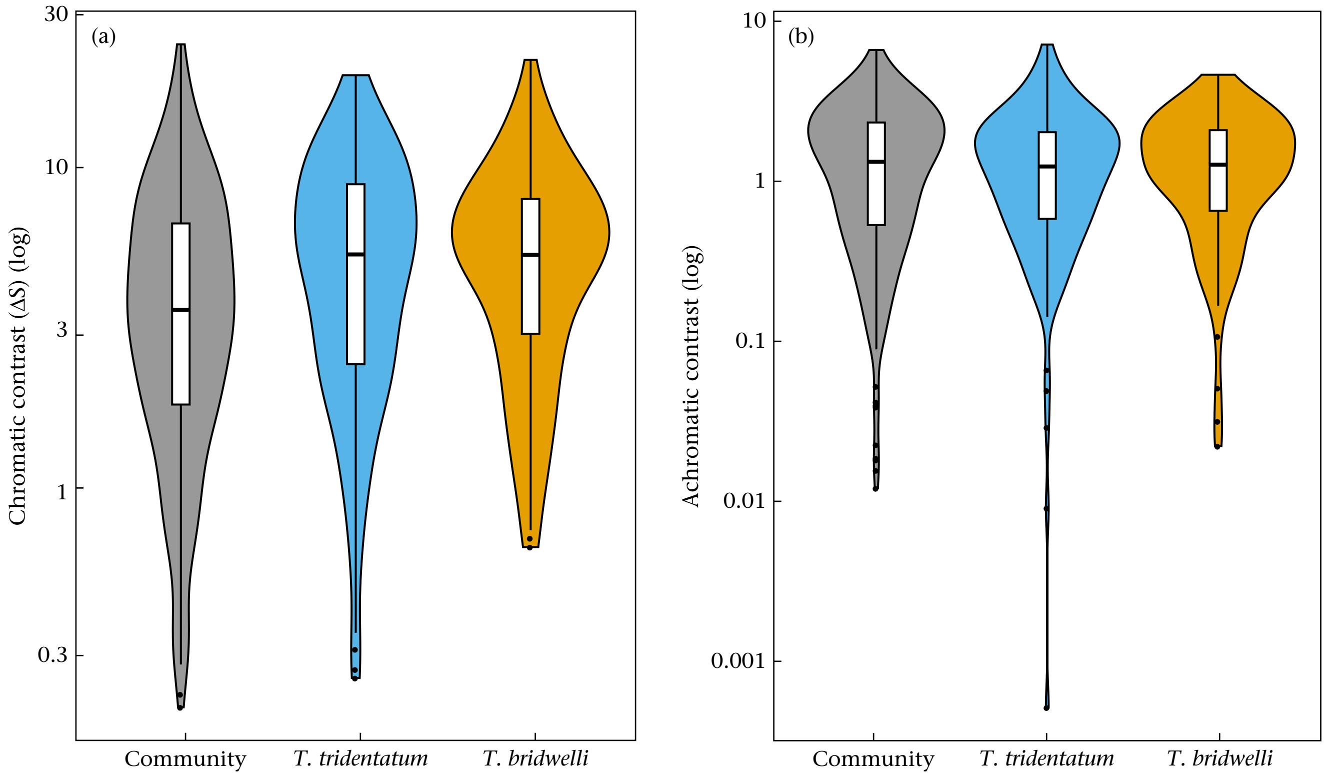

Figure 5. Distribution of the (a) chromatic and (b) achromatic contrast against the background of the spiders collected from the community and found in the nests of *Trypoxylon tridentatum* and *T. bridwelli*.

wasps to detect and recognize immobile prey, making spiders with higher contrast against the background more likely to be detected.

Some mud-dauber wasps within a population show intraspecific variation in their foraging preferences. While some individuals can act like generalists, others show specialist behaviour (Powell & Taylor, 2017). This variation in the prey preference may result from learning of search images (based on visual or chemical cues, or both cues). In our case, the relatively low diversity of body colours in spider prey found in wasp nests, as compared to the colour diversity of the broader spider community, suggests that these wasps prey on spiders with more conspicuous body colours. This may enhance search image formation, because in this case, the stimulus provided by the spider against its background is sufficiently salient to the wasp visual system that it ‘pops out’ of the visual scene (Itti & Koch, 2001).

Finally, in terms of taxonomic composition and body size of prey, niche segregation is an important mechanism favouring the coexistence of sympatric wasps (Falcón-Brindis et al., 2019). Our results showing that the body colours of the spiders occupied different polygons in hymenopteran visual space for each wasp species suggest that this niche segregation makes sense from a visual ecological perspective. However, the area of overlap in the polygons in the hymenopteran visual space is a topic of further research since this may be due to the use of one spectral sensitivity and visual model (*P. triangulum*) to evaluate the perception of two different wasp species. Sampling complete nests during longer reproductive periods may further our understanding of vision-mediated predator–prey interactions in this system.

Author Contributions

Conceptualization: L.R.-O., D.R., N.M., F.E.; formal analysis: L.R.-O.; funding acquisition: L.R.-O., D.R.; investigation: L.R.-O.; methodology: L.R.-O., D.R., F.E., A.F.-B., M.L.J.; project administration: L.R.-O., D.R., F.E.; resources: L.R.-O., D.R., F.E., M.L.J.; supervision: F.E., D.R.; visualization: L.R.-O.; writing – original draft: L.R.-O.; writing – review and editing: L.R.-O., D.R., F.E., N.M., A.F.-B., M.L.J.

Declaration of Interest

We have no conflicts of interest to declare.

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Appendix

Chromatic and Achromatic Contrast Distances Following the Receptor Noise Limited Model (RNL)

The chromatic and achromatic contrast of the spiders against their common background was estimated by means of the receptor noise limited model (RNL) (Vorobyev & Osorio, 1998) using the equations to calculate the chromatic (ΔS) for a trichromatic Hymenoptera visual system, and the achromatic (brightness) distance ($\mathrm{Achro}_{\mathrm{MW}}$) using the response values form the MW receptor, which is usually involved in this task (Théry et al., 2005):

$$\Delta S^2 = \frac{{e_1}^2(\Delta q_3 - \Delta q_2)^2 + {e_2}^2(\Delta q_3 - \Delta q_1)^2 + {e_3}^2(\Delta q_1 - \Delta q_2)^2}{(e_1 e_2)^2 + (e_1 e_3)^2 + (e_2 e_3)^2} \tag{A1}$$

where e_i is the standard deviation of noise in receptor channel i and is given by a Weber fraction (w) of 0.13; n_i represents the relative density for each receptor class estimated from the photoreceptor ratio published for bees (1:0.471:4.412 for UV:SW:MW; Defrize et al., 2010) and setting the least common photoreceptor type to

1, obtaining an n_i of 2.132:1:9.434 for the UV:SW:MW photoreceptors, respectively.

$$e_i = \frac{w}{\sqrt{n_i}} \tag{A2}$$

Δq_i corresponds to the difference or the chromatic distance in quantum catch for each photoreceptor i (UV, SW and MW for Hymenoptera) between the spider ($Q_{\mathrm{spider},i}$) and the background ($Q_{\mathrm{back},i}$).

$$\Delta q_i = \ln\left(\frac{Q_{\mathrm{spider},i}}{Q_{\mathrm{back},i}}\right) \tag{A3}$$

Finally the achromatic or luminance contrast (L_{MW}) was estimated as follows, using the quantum catch values and the receptor noise corresponding to the MW channel:

$$L_{\mathrm{MW}} = \left|\frac{\ln\left(\frac{Q_{\mathrm{spider},3}}{Q_{\mathrm{back.},3}}\right)}{e_3}\right| \tag{A4}$$