



# Which side are you on? Spider web positioning affects prey capture more than body colour

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## Abstract

Colour has been hypothesized to play a crucial role in prey capture for sit-and-wait predators that rely on visual cues to deceive their prey. Prey capture success has been directly linked to colouration in spiders; however, evidence so far focuses mostly on dorsal colouration, excluding ventral patterns that are visible to prey and may be relevant for prey attraction. Here, we explored whether the dorsal and ventral colouration of a colour polymorphic spider is associated with light environment and prey capture success. We quantified the number of prey captured across three dorsal (black, white, and yellow) and two ventral (black and a mosaic yellow/orange pattern) morphs of *Gasteracantha cancriformis*, considering light intensity on dorsal and ventral sides. We found that spiders capture more prey in low light environments, and that individuals often expose their dorsal colouration towards low light levels. We did not find significant differences in prey capture rate between morphs dorsally or ventrally. These results indicate that how and where spiders position their web can be more important for prey capture than colouration. Alternative hypotheses such as aposematism, camouflage and thermoregulation deserve more attention in future studies that aim to understand the role of colouration in spiders and the factors causing spider colour polymorphisms.

**Keywords** Colour polymorphism · Light environment · Araneae · Web position · *Gasteracantha*

## Introduction

Colouration promotes survival and reproductive success in numerous ways, serving as warning signal, sexual attribute or providing physiological benefits (Ducrest et al. 2008; Cuthill et al. 2017; Caro and Ruxton 2019; Delhey 2019). The role of colouration varies from clade to clade, and multiple colours may be associated with distinct functions,

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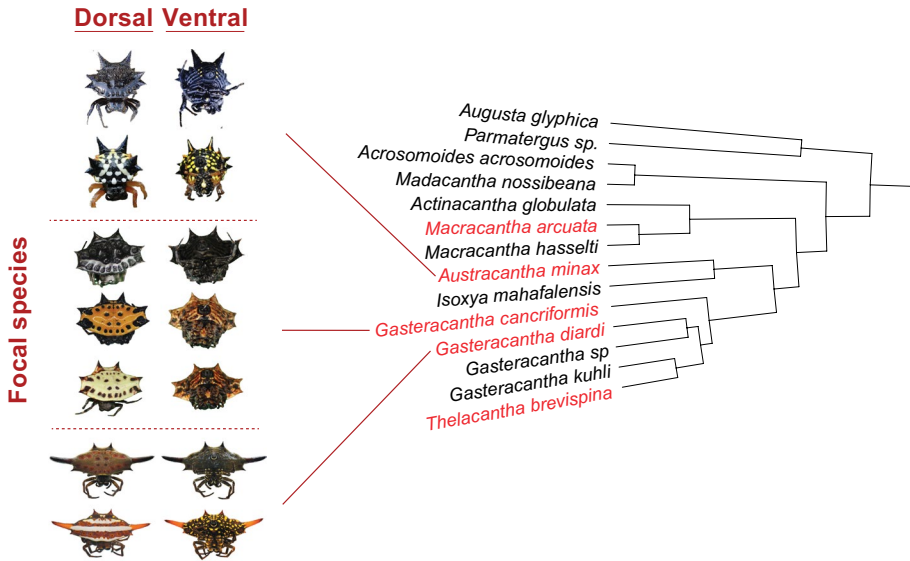
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which can lead to the presence of discrete colour variants within a single population (i.e., Colour polymorphism; Gray and McKinnon 2007; Mclean and Stuart-Fox 2014; Jamie and Meier 2020). For instance, phenotypic variation in the butterfly *Heliconius numata* is promoted by positive selection imposed by predators, coupled with selection associated with female mate preference (Chouteau et al. 2017). Likewise, colour polymorphism in *Timema* walking sticks is maintained by multineche polymorphism, where different colour morphs occupy different ecological niches provided by the host plant (e.g. stem and leaves) reducing predation (Nosil et al. 2018). Even though multiple studies have identified the drivers of colour variation, we still have limited understanding of the role of colouration in some common and abundant colour polymorphic lineages.

Sit and wait predators, like web-building spiders, can rely on colouration as an anti-predator defence (aposematism, Ximenes and Gawryszewski 2020), for thermoregulation (Rao and Mendoza-Cuenca 2016) and even prey attraction (Hauber 2002). The latter is widely acknowledged as a common function of colouration in the literature (Craig and Ebert 1994; Bush et al. 2008; White and Kemp 2015; Liao et al. 2019; Peng et al. 2020; Ximenes et al. 2020; Kemp et al. 2022), suggesting that individuals with conspicuous and bright colours capture more prey than individuals with dark coloration (Tso et al. 2002; Liao et al. 2019). This foraging advantage could be caused by deception, since brightly coloured patches could, in the eyes of prey, resemble mates or food items (e.g., flowers; White and Kemp 2015). However, several experiments have challenged this hypothesis, finding that prey capture rate can also be similar between different colour morphs of the same species (Tso et al. 2007; Gawryszewski and Motta 2012), and in some cases, inconspicuous individuals might even attract more prey (Nakata and Shigemiyama 2015). One key aspect, however, is that most studies exploring the effect of colouration on prey capture have considered only dorsal patterns (Gawryszewski and Motta 2012; White et al. 2017; Ximenes et al. 2020). This overlooks the role that ventral colours may have in prey capture (Craig and Ebert 1994; Tso et al. 2006, 2007; Peng et al. 2020) and that multiple lineages vary in their dorsal and ventral colourations (e.g. *Gasteracanthines* spiders; Fig. 1).

Differences between dorsal and ventral colours have been reported in numerous lineages (Rowland 2009; Kamilar and Bradley 2011; Allen et al. 2012). One common explanation for this colour variation is that each side of an individual may be exposed to differential light environments and animals can position themselves to optimize the signal that is being transmitted (Penacchio et al. 2015; Cuthill et al. 2016; Donohue et al. 2020). However, while this hypothesis has been widely explored from a predator perspective, the effect of dorsal and ventral colours on prey capture remains unexplored. Therefore, considering that the light environment might influence prey capture (Nakata 2021), it is possible that colour morphs of polymorphic spiders differ in how they position themselves on the web to attract prey.

*Gasteracantha cancriformis* is a colour polymorphic web-building spider distributed in America, with at least 20 dorsal abdominal colour morphs across its distribution (Salgado-Roa et al. 2022). Previous work has discarded the prey capture hypothesis as possible explanation for the presence of multiple morphs within a single population, and has favoured instead the idea of an anti-predator role of colour (Gawryszewski and Motta 2012; Ximenes and Gawryszewski 2020). Nevertheless, these studies have not considered ventral variation in colour, which side is exposed towards prey, or the light environment where morphs are found. Moreover, given that the frequency and differences between colour morphs vary across the distribution of the species (Salgado-Roa et al. 2022), it is possible that previous findings cannot be generalized to all populations.



**Fig. 1** Ventral and dorsal colour variation of “Gasteracanthines” species. Species names in red are species with reported ventral and dorsal colour polymorphism. On the left side of the image there are three examples of polymorphic lineages, including the focal study species *Gasteracantha cancriformis*. The phylogeny was modified from Scharff et al. (2020). Photo credits: iNaturalist (iNaturalist.org), and Macharoenboon et al. (2021)

Here, we tested in the field whether there were differences in prey capture success across three different colour morphs of *G. cancriformis* when considering the relative position of the spider towards the prey and the light environment (illumination intensity). The studied population consisted of one colour morph completely dark on the dorsal and ventral sides, sympatric with two morphs that shared a mosaic yellow/orange ventral pattern but differ in their dorsal colouration (white and yellow; Fig. 1). We evaluated whether success in prey capture differs between dark and bright colour morphs depending on the light conditions, and thus whether these differences initially may facilitate the presence of multiple colour morphs in a single population.

## Methods

### Study site and data collection

We conducted field observations over 6 days in June of 2021 at a peripheral area of Ibagué-Colombia (4.37 N, -75.15 W; Supplementary Material Fig. S1.). The location is covered by a mixture of native shrubs, grass and planted *Tabebuia rosea* trees, its climatic conditions are similar to the ones found in a seasonally dry tropical forest with a mean temperature of 27 °C and precipitation that varies between 1200 and 1700 mm (Pizano and Garcia 2014). This site was chosen because it had an extremely high abundance of *G. cancriformis* (more than 100 individuals in a 1 km transect).

To evaluate the effect of coloration on prey capture success, we first randomly selected a minimum of 14 individuals per dorsal colour morph to perform repeated daily measures and observations on the same individuals when possible. We also considered a control observation group that consisted of a web without the spider. For this, we randomly removed every day 14 individuals from their webs. We surveyed spider webs during four daily checks at intervals of 1 h, from 7 to 11 AM (a total of 24 checks, visiting every individual four times per day), we stopped observations at this time because webs were in poor condition after this due to wind or prey captured. In every visit, the observer examined the web from a lateral view checking the surface of the web to determine which side the prey entered from, and recorded the following variables: (i) placement of the spider (dorsal/ventral side exposed towards open areas) (ii) number of prey on the web (iii) whether the prey entered from the ventral or dorsal side (iv) number of prey that remained on the web since last visit, (v) whether the spider captured any prey at the moment of the visit. We also used a digital illuminance meter (Model: LX1330B-Dr. meter; spectral sensitivity from 400 to 700 nm) to measure the light intensity (in lux) received by every individual on their dorsal and ventral sides. Although lux is a measure of light intensity to the human visual system, it is highly correlated with total light intensity (integral of irradiance; Johnsen 2012). Minor differences between lux and light intensity to different types of receivers are unlikely to affect our analyses because we converted to a binary variable (high and low luminosity) due to its bimodal distribution (Supplementary Material Fig. S2). To measure lux, we placed the equipment parallel to each individual side to measure the amount of light that was received by the spider on each side, while reducing effect of the angle where the spider was positioned. We took these measurements in situ during the last check of each day (11 AM). When possible, every prey item was classified down to the order level. Additionally, we measured the following variables to test whether other factors besides colouration could influence prey capture: (i) web capture area (following Herberstein and Tso 2000), (ii) opisthosoma width, (iii) web height off the ground and (iv) the presence of silk decorations. Three people recorded the data, focusing each on a maximum of 30 random individuals per day.

## Statistical analysis

We first tested whether there were differences in the opisthosoma width, web height and web area between colour morphs. To do this, we implemented linear models with dorsal colouration (white, black, yellow; and empty web when possible) as the independent variable and the web variables mentioned earlier as response, using base R (R Core Team 2021). We checked the fulfilment of the model assumption plotting the residual normality and heteroscedasticity.

## Positioning and light levels

To test whether there was a preference on which side spiders face towards open areas, we compared dorsal and ventral light measures of each individual, where the higher measure was considered as open space and the lower measure as vegetation. Hence, we implemented a generalized linear mixed model (GLMM) from a ‘binomial’ family and used side (dorsal or ventral) as fixed effect and orientation (towards open area or facing towards vegetation) as response variable. We also considered the identity of every individual spider as random effect because some individuals were observed more than

once. GLMM models were run using the R package *glmmTMB* (Brooks et al. 2017). The significance of the fixed effects was evaluated using type II Wald chi-square test in the R package *car* (Fox and Weisberg 2019).

Given that our data on light levels had a clear bimodal distribution (Supplementary Material Fig. S2), we treated this variable as binary (high/low) with values above 400 lx considered as ‘high’ luminosity and below that threshold as ‘low’ luminosity levels. This categorization is independent of how the spider positioned its body towards the open space or vegetation (Chi-square test of independence:  $X^2=2.11$ ,  $DF=1$ ,  $P=0.15$ ). This is because, although for any given individual open space had higher luminosity levels than vegetation, open space did not always fall within the high luminosity category (> 400 lx). Therefore, we also tested if individuals with different colour morphs preferred certain light conditions, and whether the side exposed to higher light levels was the same across morphs. To accomplish this, we used a GLMM from a ‘binomial’ family and used luminosity (high/low) as the response variable and colour morph and side (dorsal or ventral) as fixed effects, along with their interaction. We also considered the identity of every individual spider as random effect. We evaluated the significance of the fixed effects using type III Wald chi-square test implemented in the R package *car* (Fox and Weisberg 2019).

### Prey capture success

For these analyses, we considered the total captured prey, which is the summatory of remaining prey on the web and direct observations of prey capture. We first explored if the presence of the different morphs on the web influences the capture of prey when compared to webs without any spider. We modelled the number of prey captured (per web per side) applying a type II negative binomial distribution. We selected this distribution because the variance in our count data was greater than the mean, which lead to a lack of uniformity of the residuals when applying a Poisson distribution ([https://fcsalgado.github.io/Gasteracantha\\_capturePrey/data\\_analyses.html](https://fcsalgado.github.io/Gasteracantha_capturePrey/data_analyses.html)). We used morph identity (including empty web), the square root of web area, the presence of web decorations and the observer (the person collecting data) as fixed effects. The interactions between the predictors were considered and then discarded because neither was statistically significant. The identity of every individual spider, the day and checking time were used as random effects. We computed these analyses with the R package *glmmTMB* (Brooks et al. 2017) and we checked the zero-inflation, under- or over-dispersion and the Q-Q plot of the residuals with functions from the R package *DHARMA* (Hartig 2021).

To explore in depth the differences in prey capture between colour morphs, we ran a model analysis excluding the empty web treatment from our analysis. We followed the above procedure but removing the presence of web decorations as a predictor (because of the clear absence of effect of this variable on prey capture). Instead, we included luminosity (high or low) and spider side (dorsal or ventral), the square root of web area and the observer (the person collecting data) as explanatory variables and the day, checking time and the identity of every individual as random effects. The significance of the fixed effects was evaluated using type II Wald chi-square test in the R package *car* (Fox and Weisberg 2019). We interpreted the results of all the statistical tests

considering the  $P$ -value as continuous measure of evidence rather than a reference to make binary conclusions (Muff et al. 2022).

## Results

We sampled a total of 129 individuals of the black ( $n=25$ ), yellow ( $n=41$ ) and white ( $n=63$ ) dorsal morphs and observed a total of 314 prey capture events. From these events, we identified 265 prey items to the order level and found that they belonged to seven orders (Diptera, Hemiptera, Coleoptera, Homoptera, Hymenoptera, Neuroptera and Lepidoptera), where dipterans were the most abundant prey (229 prey captured,  $\sim 86.4\%$  of the identified preys; Supplementary Material Fig. S3). We found that the three colour morphs have similar values of web area and web height, but differed in the opisthosoma width, with yellow morphs being slightly larger than black and white morphs (Table 1). We found no evidence of an association between opisthosoma width and prey capture ( $X^2=0.32$ ,  $DF=1$ ,  $P=0.73$ ), therefore we excluded opisthosoma width from subsequent analyses, to avoid multicollinearity issues with colouration. We also found very strong evidence that web height was related to web area (Estimate of  $F_{1272,85}=18.51$ ,  $P < 0.0001$ ), with larger spiderwebs being built higher up. Hence, we chose to only include web area in further models predicting prey capture, as this is a reliable indicator of foraging investment (Chacon and Eberhard 1980).

## Positioning and light levels

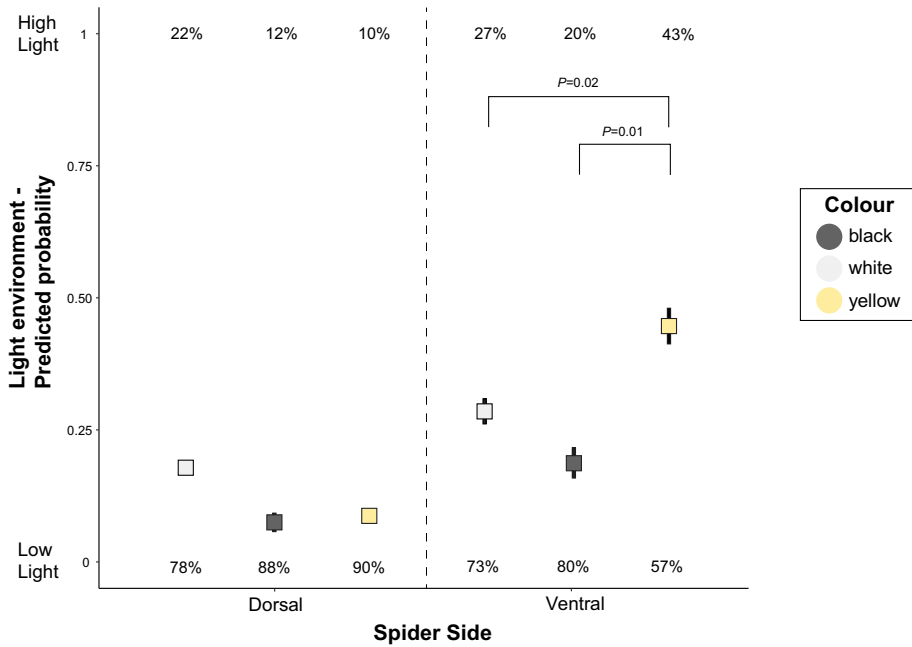
We found a higher frequency of individuals with ventral side oriented towards open areas ( $X^2=34.03$ ,  $DF=1$ ,  $P < 0.0001$ ) and high luminosity ( $X^2=104.95$ ,  $DF=1$ ,  $P < 0.0001$ ). Through the course of our observations, we did not notice any positional change at the hub. Morphs differed in exposure to high or low luminosity but only on the ventral side; yellow morphs exposed their ventral side to brighter light conditions than did black and white individuals ( $X^2=7.15$ ,  $DF=2$ ,  $P=0.02$ ; Fig. 2). We did not find luminosity differences between morphs for the dorsal side.

## Prey capture success

We found very strong evidence that the presence of spiders on the web decreased the number of prey captured ( $X^2=36.9$ ,  $DF=3$ ,  $P < 0.0001$ ; Fig. 3). Additionally, there was moderate evidence that individuals with bigger webs capture more prey ( $X^2=3.73$ ,  $DF=1$ ,

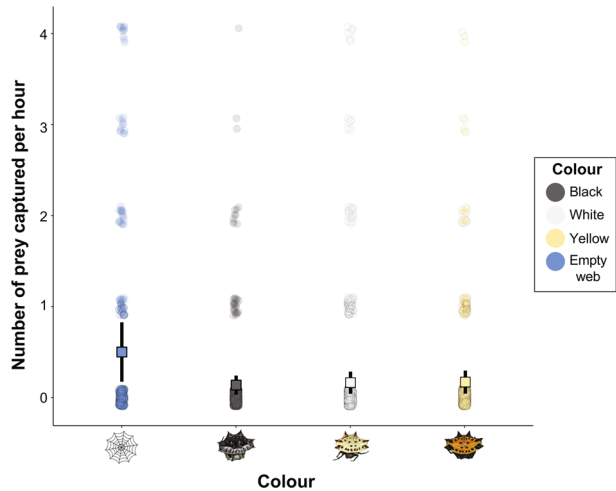
**Table 1** Web and abdomen parameters for the three dorsal colour morphs and ANOVA test results. Parameters values are presented as mean  $\pm$  standard error

Measure	White	Yellow	Black	Empty web	ANOVA
Web area (cm <sup>2</sup> )	360.56 $\pm$ 22.2	390.76 $\pm$ 23.6	372.07 $\pm$ 22.1	376 $\pm$ 34.7	$F_3=0.46$ ; $P=0.70$
Web height (cm)	126.2 $\pm$ 5.45	129.2 $\pm$ 5.15	130.6 $\pm$ 9.33	116.05 $\pm$ 9.49	$F_3=0.58$ ; $P=0.62$
Opisthosoma width (mm)	10.21 $\pm$ 0.17	10.52 $\pm$ 0.2	9.62 $\pm$ 0.33	NA	$F_2=3.43$ ; $P=0.03$

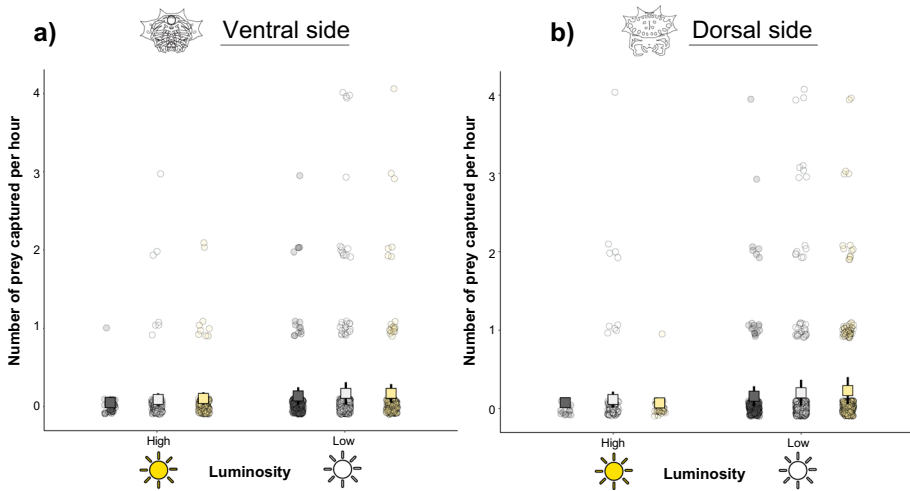


**Fig. 2** Side exposure to high or low light conditions. Squares and bars represent the mean  $\pm$  standard error of the predicted values from the GLMM model that tested the association of luminosity (high/low) with the interaction of colour morph and spider side (dorsal and ventral). Percentages show the proportion of individuals observed under high or low luminosity in each category. The *P*-values highlight that there are differences in exposure to light conditions between morphs on the ventral side

**Fig. 3** Total prey capture results for all the colour morphs and the empty web treatment. The squares and bars illustrate the mean  $\pm$  standard deviation of the predicted values obtained from the GLMM model that explored the association between the number of captured prey with colour morph identity. Small dots show the raw observations in the field. Colours are coded as in Fig. 2 and the blue symbols correspond to the empty web treatment



$P=0.053$ ). We also discarded any effect of the presence of web decorations on the number of insects captured ( $X^2=0.41$ ,  $DF=1$ ,  $P=0.51$ ). When we explored in depth associations between colour morph and prey capture, the model showed that colour morphs do not differ in their prey capture success ( $X^2=0.61$ ,  $DF=2$ ,  $P=0.73$ ; Fig. 4). However, spiders caught



**Fig. 4** Prey capture results per side and colour morph under high and low light conditions. The squares and bars illustrate the mean  $\pm$  standard deviation of the predicted values obtained from the GLMM model that explored the association between the number of captured prey with colour morph. Small dots show the observations in the field. Colours are coded as in Fig. 2. **a** Results for the dorsal side. **b** Results for the ventral side

a higher number of insects under dim light ( $X^2 = 10.85$ ,  $DF = 1$ ,  $P = 9E-4$ ; Supplementary Material Fig. S4), approximately 70% more prey than the ones under high luminosity.

## Discussion

We did not observe significant differences in prey capture success between either dorsal or ventral colour morphs of *G. cancriformis*, even when considering the light environment. Instead, we found that light environment strongly affects prey capture success independently of the colour morph, since webs in dim light capture 70% more prey than those in high luminosity conditions. We also observed that the yellow morph is exposed to higher luminosity ventrally than black or white morphs, but this habitat preference did not appear to correspond to reduced prey capture success. Thus, our data do not support an association of colour variation with differences in prey capture, but instead suggest that colour morphs of *G. cancriformis* may differ in their microhabitat preferences.

Our data shows that the presence of spiders at the hub reduces the capture of insects on the web. Because the population where we performed the observations consisted of both bright and dark abdominal colours, we hypothesize that the insects are using achromatic cues to avoid being captured. In fact, it has been suggested that bees can detect spiders on the web (Rao et al. 2008), and when they are at long distances they use achromatic cues (Heiling et al. 2005). Studies of other populations of *G. cancriformis* located in different and distant habitats show mixed support for the effect of spider presence on prey capture. Results of our study are consistent with observations and experiments in another dry tropical forest (i.e. the Brazilian Cerrado), where there was a negative effect of spider presence on prey capture success (Ximenes and Gawryszewski 2020). By contrast, in a population occupying humid Brazilian Atlantic forest, webs with spiders captured more



prey than empty webs (Messas et al. 2021). These mixed results might be associated with the particular abiotic characteristics of each ecosystem or the different prey communities present in each environment, factors that have been linked to foraging success in other lineages (Tate et al. 2016; Tate and Amar 2017; Nokelainen et al. 2022).

We did not find evidence supporting differential prey capture rate between the sides of the spiders observed. These results differ from previous observations in a different colour morph of *G. cancriformis* from the Brazilian Atlantic Forest, where individuals captured more prey from their dorsal than ventral side (Messas et al. 2021). One explanation for this discrepancy is that in this population the species constructs the web with the dorsal body section directed towards open space (Messas et al. 2021), instead of towards the vegetation (as we found). This variation might be linked to local differences in light and wind direction, factors that can determine how spiders orient their body on the web (Robinson and Robinson 1978; Biere and Uetz 1981; Herberstein and Heiling 2001). In fact, the way spiders position their body on the hub varies among species (Nakata and Zschokke 2010; Rao et al. 2011; White et al. 2017) and may be related to prey attraction (Rao et al. 2015; Peng et al. 2020) or to other factors like thermoregulation (Biere and Uetz 1981; Herberstein and Heiling 2001; Rao and Mendoza-Cuenca 2016). Identifying the variables that determine *G. cancriformis* position preference on the web is still an open question and needs to be tested under controlled conditions.

Results from our study agree with previous experiments that rejected the role of dorsal bright colouration as a prey lure in populations where the dark morph is not present (Gawryszewski and Motta 2012; Ximenes and Gawryszewski 2020). Because of the time frame of our observations, it is possible that our results are able to capture only extreme effects, ignoring the total variation in prey capture rate. Nevertheless, we consider that, if this variation actually exists, it may not play a crucial role in the fitness of the colour morphs. The reason behind this idea is that in similar systems where bright colours are essential to attract insects, differential prey capture has been found when using a similar number of observations (Hauber 2002; Rao et al. 2015; Kemp et al. 2022). Alternative hypotheses such as aposematism, camouflage, and thermoregulation need to be investigated in the future to understand the function of spider colouration and maintenance of spider colour polymorphism. Based on indirect experimental evidence and observations (Edmunds and Edmunds 1986; Ximenes and Gawryszewski 2020), it is possible that conspicuous colouration may serve as an aposematic signal that reduces predation in *G. cancriformis*. Nevertheless, direct and control experiments are needed to support this hypothesis; in fact, the evidence for aposematism in spiders is still inconclusive and scarce (Robledo-Ospina and Rao 2022).

Our results highlight the importance of light environment for prey capture, since we observed that individuals in dim light capture significantly more prey than those under bright light. A possible explanation for this difference is that in conditions of high luminosity, web silk tends to be more visible in the eyes of the prey (Craig 1988), which can decrease the chance of flying into the web (Herberstein and Fleisch 2003). However, for some lineages the visibility of the web may be crucial to capture flying prey, especially if the web has decorations (Craig et al. 1996; da Silva et al. 2021). Another possibility is that our results reflect the abundance of prey in low luminosity, as it has been proposed that flying insects are more abundant in shaded areas rather than in sunny sites (Shelly 1988). In consequence, spiders in shaded environments would capture more prey in their web. In any case, these results suggest that colour variation should not have a large effect on prey capture, because most prey would enter the web under low luminosity, where differences

between colour morphs are probably less evident (Menzel 1981; Rose and Menzel 1981; Kelber et al. 2017).

The yellow morph's ventral side was more often facing towards high luminosity conditions, compared to the ventral side of the black and white morphs. This suggests it may be possible that the ventral colour variation of *G. cancriformis* is associated with microhabitat preferences. It is likely that the reason why we only observed differences in habitat light between morphs on the ventral side is because this side is frequently facing open areas (Hauber 2002; Rao et al. 2015), where there is room for larger variation in illumination (facilitating detection of differences across morphs). The presence of contrasting microhabitats in heterogenous environments has been hypothesized to promote phenotypic variation due to positive frequent dependent selection within each habitat (Bond 2007; Gordon et al. 2015). Microhabitat preference may be a consequence of background-matching behaviour to reduce predation (Fark et al. 2022; Heinze et al. 2022), an adaptation to maximise prey capture. Alternatively, it may be important for thermoregulation (Broennimann et al. 2014; Muri et al. 2015). However, we did not find that the yellow morph performed better in high luminosity conditions compared to the other morphs, in terms of prey capture. Moreover, because the yellow and white morphs share the same ventral colour and pattern, it is possible that other ecological factors are influencing colour morph frequency in certain light environments. Experimental evidence is needed to explore these hypotheses in detail. It is worth noting that our results are based on the measurement of the light intensity in units of lumens per meter squared (i.e. Lux). This unit has been criticised for representing the luminosity as perceived by the human eye, for its limited resolution (resolution of 1 lx), and for not providing spectral information (Marangoni et al. 2022; Aulsebrook et al. 2022). Despite these difficulties, we consider that our results are still valid because a large part of the daylight intensity is covered by the spectral sensitivity of the equipment used (Marangoni et al. 2022). In addition, we treated the light intensity as a binary variable, so the difference in their mean values (supplementary Fig. 2; low light = 42.42 lx, high light = 17,987 lx) was not affected by the limited resolution of the equipment. Another possible limitation of our study is that we measured light intensity only in a single period of the day, ignoring changes in the sun position and possible effect of passing of clouds or movement of foliage. Besides this obstacle, we think that the sun position did not affect our result because most of the spiders were facing their dorsal side towards the vegetation, as in other species (Hauber 2002; Rao et al. 2015). This means that at any time of the day, measurements of light exposure would be lower for the dorsal side when compared to the ventral side. Given that the time interval during which we collected data every day was short (4 h per day; 7–11 AM), we would not expect much variation in light measurements. In summary, we found no evidence that variation in dorsal and ventral colouration of *G. cancriformis* is associated with differences in prey capture. This reinforces the idea that we are still far from understanding the adaptive role of bright colours and the factors promoting dorsal and ventral colour polymorphism in this and other spider lineages. For instance, we still ignore what is causing the change in abundance of bright colours across the distribution of the species or the complete absence of white or yellow morphs in some locations (e.g., San Andrés-Colombia, Galapagos-Ecuador and Lima-Perú), and the ubiquity of dorsal and ventral dark morphs throughout the distribution of the species (Salgado-Roa et al. 2022). Our results also highlight that variables such as light environment and the position of the spider on the web can dramatically affect the number of insects caught and should be considered in future studies exploring prey capture.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10682-023-10244-6>.

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**Author contributions** F.C.S.-R., I.M and D.S.-F. conceived and designed the study and analytical approaches. F.C.S.-R, E.C and M.S.T.-O. collected the data. F.C.S.-R. analysed the data and drafted the manuscript. F.C.S.-R., I.M and D.S.-F. edited the manuscript. All the authors approved the final version of the manuscript.

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**Data availability** Code and model results are available on [https://fcsalgado.github.io/Gasteracantha\\_capturePrey/data\\_analyses.html](https://fcsalgado.github.io/Gasteracantha_capturePrey/data_analyses.html). Input and code files are available on [https://github.com/fcsalgado/Gasteracantha\\_capturePrey](https://github.com/fcsalgado/Gasteracantha_capturePrey).

## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

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## References

- Allen WL, Baddeley R, Cuthill IC, Scott-Samuel NE (2012) A quantitative test of the predicted relationship between countershading and lighting environment. *Am Nat* 180(6):762–776. <https://doi.org/10.1086/668011>
- Aulsebrook AE, Jechow A, Krop-Benesch A, Kyba CCM, Longcore T, Perkin EK, van Grunsven RH A (2022) Nocturnal lighting in animal research should be replicable and reflect relevant ecological conditions. *Biol Lett* 18(3):20220035. <https://doi.org/10.1098/rsbl.2022.0035>
- Biere JM, Uetz GW (1981) Web orientation in the spider *micrathena gracilis* (Araneae: Araneidae). *Ecology* 62(2):336–344. <https://doi.org/10.2307/1936708>
- Bond AB (2007) The evolution of color polymorphism: crypticity, searching images, and apostatic selection. *Annu Rev Ecol Evol Syst* 38(1):489–514. <https://doi.org/10.1146/annurev.ecolsys.38.091206.095728>
- Broennimann O, Ursenbacher S, Meyer A, Gölz P, Monney JC, Schmocker H, Guisan A, Dübey S (2014) Influence of climate on the presence of colour polymorphism in two montane reptile species. *Biol Lett*. <https://doi.org/10.1098/rsbl.2014.0638>
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Machler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:400. <https://doi.org/10.3929/ethz-b-000240890>
- Bush AA, Yu DW, Herberstein ME (2008) Function of bright coloration in the wasp spider *Argiope brunemichi* (Araneae: Araneidae). *Proc R Soc B-Biol Sci* 275(1640):1337–1342. <https://doi.org/10.1098/rspb.2008.0062>

- 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>
- Chacon P, Eberhard WG (1980) Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. In *Bulletin - British Arachnological Society*. 5:29–38
- Chouteau M, Llaurens V, Piron-Prunier F, Joron M (2017) Polymorphism at a mimicry supergene maintained by opposing frequency-dependent selection pressures. *Proc Natl Acad Sci* 114(31):8325–8329. <https://doi.org/10.1073/pnas.1702482114>
- Craig CL (1988) Insect perception of Spider Orb Webs in three light habitats. *Funct Ecol* 2(3):277–282. <https://doi.org/10.2307/2389398>
- Craig CL, Ebert K (1994) Colour and Pattern in predator–prey interactions: the Bright body colours and patterns of a tropical orb-spinning spider attract flower-seeking prey. *Funct Ecol* 8(5):616–620. <https://doi.org/10.2307/2389923>
- Craig CL, Weber RS, Bernard GD (1996) Evolution of predator-prey systems: spider foraging plasticity in response to the visual ecology of prey. *Am Nat* 147(2):205–229. <https://doi.org/10.1086/285847>
- Cuthill IC, Allen WL, Arbuckle K, Caspers B, Chaplin G, Hauber ME, Hill GE, Jablonski NG, Jiggins CD, Kelber A, Mappes J, Marshall J, Merrill R, Osorio D, Prum R, Roberts NW, Roulin A, Rowland HM, Sherratt TN, Caro T (2017) The biology of color. *Science*. <https://doi.org/10.1126/science.aan0221>
- Cuthill IC, Sanghera NS, Penacchio O, Lovell PG, Ruxton GD, Harris JM (2016) Optimizing countershading camouflage. *Proc Natl Acad Sci* 113(46):13093–13097. <https://doi.org/10.1073/pnas.1611589113>
- Delhey K (2019) A review of Gloger’s rule, an ecogeographical rule of colour: definitions, interpretations and evidence. *Biol Rev* 94(4):1294–1316. <https://doi.org/10.1111/brv.12503>
- Donohue CG, Hemmi JM, Kelley JL (2020) Countershading enhances camouflage by reducing prey contrast. *Proc R Soc B Biol Sci* 287(1927):20200477. <https://doi.org/10.1098/rspb.2020.0477>
- Ducrest A-L, Keller L, Roulin A (2008) Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends Ecol Evol* 23(9):502–510. <https://doi.org/10.1016/j.tree.2008.06.001>
- Edmunds J, Edmunds M (1986) The defensive mechanisms of orb weavers (Araneae: Araneidae) in Ghana, West Africa (F. A. O. of the UN. (ed.)) Pub. for the Smith. Trop. Res. Inst.
- Fark SN, Gerber S, Alonzo SH, Kindsvater HK, Meier JI, Seehausen O (2022) Multispecies colour polymorphisms associated with contrasting microhabitats in two Mediterranean wrasse radiations. *J Evol Biol* 35(4):633–647. <https://doi.org/10.1111/jeb.13999>
- Fox J, Weisberg S (2019) An R companion to applied regression, Third. Sage, Newbury Park
- Gawryszewski FM, Motta PC (2012) Colouration of the orb-web spider *Gasteracantha cancriformis* does not increase its foraging success. *Ethol Ecol Evol* 24(1):23–38. <https://doi.org/10.1080/03949370.2011.582044>
- Gordon SP, Kokko H, Rojas B, Nokelainen O, Mappes J (2015) Colour polymorphism torn apart by opposing positive frequency-dependent selection, yet maintained in space. *J Anim Ecol* 84(6):1555–1564. <https://doi.org/10.1111/1365-2656.12416>
- Gray SM, McKinnon JS (2007) Linking color polymorphism maintenance and speciation. *Trend Ecol Evol* 22(2):71–79. <https://doi.org/10.1016/j.tree.2006.10.005>
- Hartig F (2021) DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. <https://cran.r-project.org/package=DHARMA>
- Hauber ME (2002) Conspicuous colouration attracts prey to a stationary predator. *Ecol Entomol* 27(6):686–691. <https://doi.org/10.1046/j.1365-2311.2002.00457.x>
- Heiling AM, Chittka L, Cheng K, Herberstein ME (2005) Colouration in crab spiders: substrate choice and prey attraction. *J Exp Biol* 208(10):1785–1792. <https://doi.org/10.1242/jeb.01585>
- Heinze P, Dieker P, Rowland HM, Schielzeth H (2022) Evidence for morph-specific substrate choice in a green-brown polymorphic grasshopper. *Behav Ecol* 33(1):17–26. <https://doi.org/10.1093/beheco/arab133>
- Herberstein ME, Fleisch AF (2003) Effect of abiotic factors on the foraging strategy of the orb-web spider *Argiope keyserlingi* (Araneae: Araneidae). *Austral Ecol* 28(6):622–628. <https://doi.org/10.1046/j.1442-9993.2003.t01-1-01319.x>
- Herberstein ME, Heiling AM (2001) Positioning at the hub: does it matter on which side of the web orb-weavers sit? *J Zool* 255(2):157–163. <https://doi.org/10.1017/S0952836901001224>
- Herberstein ME, Tso IM (2000) Evaluation of formulae to estimate the capture area and mesh height of orb webs (Araneidae, Araneae). *J Arachnol* 28(2):180–184. [https://doi.org/10.1636/0161-8202\(2000\)028\[0180:EOFTET\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2000)028[0180:EOFTET]2.0.CO;2)
- Jamie GA, Meier JI (2020) The persistence of polymorphisms across species radiations. *Trends Ecol Evol* 35(9):795–808. <https://doi.org/10.1016/j.tree.2020.04.007>
- Johnsen S (2012) The optics of life: a biologist’s guide to light in nature. Princeton University Press, Princeton

- Kamilar JM, Bradley BJ (2011) Countershading is related to positional behavior in primates. *J Zool* 283(4):227–233. <https://doi.org/10.1111/j.1469-7998.2010.00765.x>
- Kelber A, Yovanovich C, Olsson P (2017) Thresholds and noise limitations of colour vision in dim light. *Philos Trans R Soc B Biol Sci* 372(1717):20160065. <https://doi.org/10.1098/rstb.2016.0065>
- Kemp DJ, Edwards W, White TE (2022) Captivating color: evidence for optimal stimulus design in a polymorphic prey lure. *Behav Ecol*. <https://doi.org/10.1093/beheco/arac034>
- Liao HC, Liao CP, Blamires SJ, Tso IM (2019) Multifunctionality of an arthropod predator's body coloration. *Funct Ecol* 33(6):1067–1075. <https://doi.org/10.1111/1365-2435.13326>
- Macharoenboon K, Siritwut W, Jeratthitikul E (2021) A review of the taxonomy of spiny-backed orb-weaving spiders of the subfamily gasteracanthinae (Araneae, araneidae) in thailand. *ZooKeys* 2021(1032):17–62. <https://doi.org/10.3897/zookeys.1032.62001>
- Marangoni LFB, Davies T, Smyth T, Rodríguez A, Hamann M, Duarte C, Pendoley K, Berge J, Maggi E, Levy O (2022) Impacts of artificial light at night in marine ecosystems—a review. *Glob Change Biol* 28(18):5346–5367. <https://doi.org/10.1111/gcb.16264>
- Mclean CA, Stuart-fox D (2014) Geographic variation in animal colour polymorphisms and its role in speciation. *Biol Rev* 89:860–873. <https://doi.org/10.1111/brv.12083>
- Menzel R (1981) Achromatic vision in the honeybee at low light intensities. *J Comp Physiol* 141(3):389–393. <https://doi.org/10.1007/BF00609941>
- Messas YF, Bergamo PJ, Villanueva-Bonilla GA, da Silva Souza H, Gonzaga MO, Vasconcellos-Neto J (2021) Deceptions of light and shadow: do the visual cues of *Gasteracantha cancriformis* (Araneae, Araneidae) improve prey interception by webs in the forest understory? *Zoologischer Anzeiger* 294:128–136. <https://doi.org/10.1016/j.jcz.2021.08.004>
- Muff S, Nilsen EB, O'Hara RB, Nater CR (2022) Rewriting results sections in the language of evidence. *Trends Ecol Evol* 37(3):203–210. <https://doi.org/10.1016/j.tree.2021.10.009>
- Muri D, Schuerch J, Trim N, Golay J, Baillifard A, El Taher A, Dubey S (2015) Thermoregulation and microhabitat choice in the polymorphic asp viper (*Vipera aspis*). *J Therm Biol* 53:107–112. <https://doi.org/10.1016/j.jtherbio.2015.06.009>
- Nakata K (2021) Relationship between body colour and microhabitat breadth in an orb-web spider. *Biol J Linn Soc* 134(3):679–684. <https://doi.org/10.1093/biolinnea/blab118>
- Nakata K, Shigemiyama Y (2015) Body-colour variation in an orb-web spider and its effect on predation success. *Biol J Linn Soc* 116(4):954–963. <https://doi.org/10.1111/bij.12640>
- Nakata K, Zschokke S (2010) Upside-down spiders build upside-down orb webs: web asymmetry, spider orientation and running speed in *Cyclosa*. *Proc R Soc B Biol Sci* 277(1696):3019–3025. <https://doi.org/10.1098/rspb.2010.0729>
- Nokelainen O, de Moraes Rezende F, Valkonen JK, Mappes J (2022) Context-dependent coloration of prey and predator decision making in contrasting light environments. *Behav Ecol* 33(1):77–86. <https://doi.org/10.1093/beheco/arab111>
- Nosil P, Villoutreix R, De Carvalho CF, Farkas TE, Soria-Carrasco V, Feder JL, Crespi BJ, Gompert Z (2018) Natural selection and the predictability of evolution in timema stick insects. *Science* 359(6377):765–770. <https://doi.org/10.1126/science.aap9125>
- Penacchio O, Cuthill IC, Lovell PG, Ruxton GD, Harris JM (2015) Orientation to the sun by animals and its interaction with crypsis. *Funct Ecol* 29(9):1165–1177. <https://doi.org/10.1111/1365-2435.12481>
- Peng P, Stuart-Fox D, Chen S-W, Tan EJ, Kuo G-L, Blamires SJ, Tso, I-Min, Elgar MA. (2020) High contrast yellow mosaic patterns are prey attractants for orb-weaving spiders. *Funct Ecol*. <https://doi.org/10.1111/1365-2435.13532>
- Pizano C, Garcia H (eds) (2014) *El Bosque Seco Tropical en Colombia*. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt (IAvH). Bogotá, D.C., Colombia. Available in: [http://repository.humboldt.org.co/bitstream/handle/20.500.11761/9333/BST\\_en\\_Colombia\\_FCF.pdf?sequence=1&isAllowed=y](http://repository.humboldt.org.co/bitstream/handle/20.500.11761/9333/BST_en_Colombia_FCF.pdf?sequence=1&isAllowed=y)
- R Core Team (2021) R: a language and environment for statistical computing. <https://www.r-project.org/>
- Rao D, Castañeda-Barbosa E, Nuñez-Beverido N, Díaz-Fleischer F (2015) Foraging benefits in a colour polymorphic neotropical orb web spider. *Ethology* 121(2):187–195. <https://doi.org/10.1111/eth.12330>
- Rao D, Cheng K, Herberstein ME (2008) Stingless bee response to spider webs is dependent on the context of encounter. *Behav Ecol Sociobiol* 63(2):209–216. <https://doi.org/10.1007/s00265-008-0651-z>
- Rao D, Fernandez OC, Castañeda-Barbosa E, Díaz-Fleischer F (2011) Reverse positional orientation in a neotropical orb-web spider, *Verrucosa arenata*. *Naturwissenschaften* 98(8):699–703. <https://doi.org/10.1007/s00114-011-0811-2>
- Rao D, Mendoza-Cuenca L (2016) The effect of colour polymorphism on thermoregulation in an orb web spider. *Sci Nat* 103:7–8. <https://doi.org/10.1007/s00114-016-1388-6>

- Robinson MH, Robinson BC (1978) Thermoregulation in orb-web spiders: new descriptions of thermoregulatory postures and experiments on the effects of posture and coloration. *Zool J Linn Soc* 64(2):87–102. <https://doi.org/10.1111/j.1096-3642.1978.tb01060.x>
- 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>
- Rose R, Menzel R (1981) Luminance dependence of pigment color discrimination in bees. *J Comp Physiol* 141(3):379–388. <https://doi.org/10.1007/BF00609940>
- Rowland HM (2009) From Abbott Thayer to the present day: what have we learned about the function of countershading? *Philos Trans R Soc B Biol Sci* 364(1516):519–527. <https://doi.org/10.1098/rstb.2008.0261>
- Salgado-Roa FC, Chamberland L, Pardo-Diaz C, Cisneros-Heredia DF, Lasso E, Salazar C (2022) Dissecting a Geographical Colourful Tapestry : Phylogeography of the Colour Polymorphic Spider *Gasteracantha cancriformis*. *J Zoologic Systematics Evol Res* vol. 2022, Article ID 8112945, 11 pages, 2022. <https://doi.org/10.1155/2022/8112945>
- Scharff N, Coddington JA, Blackledge TA, Agnarsson I, Framenau VW, Szűts T, Hayashi CY, Dimitrov D (2020) Phylogeny of the orb-weaving spider family Araneidae (Araneae: Araneoidea). *Cladistics* 36(1):1–21. <https://doi.org/10.1111/cla.12382>
- Shelly TE (1988) Relative abundance of day-flying insects in treefall gaps vs shaded understory in a neotropical forest. *Biotropica* 20(2):114–119. <https://doi.org/10.2307/2388183>
- da Silva FC, Moleta M, Dos Anjos CA, Schade GM, Staichak G, Tozetto L, Gonçalves F, Martins K, Farion I, Krug CK, Costa DA, Castilho L, Bessa E (2021) Testing traditional hypotheses about prey capture efficiency in orb-web spiders. *J Ethol* 39(1):3–8. <https://doi.org/10.1007/s10164-020-00663-1>
- Tate GJ, Amar A (2017) Morph specific foraging behavior by a polymorphic raptor under variable light conditions. *Sci Rep* 7(1):1–12. <https://doi.org/10.1038/s41598-017-07829-x>
- Tate GJ, Bishop JM, Amar A (2016) Differential foraging success across a light level spectrum explains the maintenance and spatial structure of colour morphs in a polymorphic bird. *Ecol Lett* 19(6):679–686. <https://doi.org/10.1111/ele.12606>
- Tso IM, Huang JP, Liao CP (2007) Nocturnal hunting of a brightly coloured sit-and-wait predator. *Anim Behav* 74(4):787–793. <https://doi.org/10.1016/j.anbehav.2006.09.023>
- Tso IM, Liao CP, Huang RP, Yang EC (2006) Function of being colorful in web spiders: attracting prey or camouflaging oneself? *Behav Ecol* 17(4):606–613. <https://doi.org/10.1093/beheco/ark010>
- Tso I-M, Tai P-L, Ku T-H, Kuo C-H, Yang E-C (2002) Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tetragnathidae). *Anim Behav* 63(1):175–182. <https://doi.org/10.1006/anbe.2001.1878>
- White TE, Dalrymple RL, Herberstein ME, Kemp DJ (2017) The perceptual similarity of orb-spider prey lures and flower colours. *Evol Ecol* 31(1):1–20. <https://doi.org/10.1007/s10682-016-9876-x>
- White TE, Kemp DJ (2015) Technicolour deceit: a sensory basis for the study of colour-based lures. *Anim Behav* 105:231–243. <https://doi.org/10.1016/j.anbehav.2015.04.025>
- Ximenes NG, Gawryszewski FM (2020) Conspicuous colours in a polymorphic orb-web spider: evidence of predator avoidance but not prey attraction. *Anim Behav* 169:35–43. <https://doi.org/10.1016/j.anbehav.2020.08.022>
- Ximenes NG, De Souza Moraes V, Ortega JCG, Gawryszewski FM (2020) Behavioral ecology color lures in orb-weaving spiders: a meta-analysis. *Behav Ecol*. <https://doi.org/10.1093/beheco/arz210>

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