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Prey and predators perceive orb-web spider conspicuousness differently: evaluating alternative hypotheses for color polymorphism evolution

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Abstract

Color polymorphisms have been traditionally attributed to apostatic selection. The perception of color depends on the visual system of the observer. Theoretical models predict that differently perceived degrees of conspicuousness by two predator and prey species may cause the evolution of polymorphisms in the presence of anti-apostatic and apostatic selection. The spider *Gasteracantha cancriformis* (Araneidae) possesses several conspicuous color morphs. In orb-web spiders, the prey attraction hypothesis states that conspicuous colors are prey lures that increase spider foraging success via flower mimicry. Therefore, polymorphism could be maintained if each morph attracted a different prey species (multiple prey hypothesis) and each spider mimicked a different flower color (flower mimicry hypothesis). Conspicuous colors could be a warning signal to predators because of the spider's hard abdomen and spines. Multiple predators could perceive morphs differently and exert different degrees of selective pressures (multiple predator hypothesis). We explored these 3 hypotheses using reflectance data and color vision modeling to estimate the chromatic and achromatic contrast of *G. cancriformis* morphs as perceived by several potential prey and predator taxa. Our results revealed that individual taxa perceive the conspicuousness of morphs differently. Therefore, the multiple prey hypothesis and, in part, the multiple predator hypothesis may explain the evolution of color polymorphism in *G. cancriformis*, even in the presence of anti-apostatic selection. The flower mimicry hypothesis received support by color metrics, but not by color vision models. Other parameters not evaluated by color vision models could also affect the perception of morphs and influence morph survival and polymorphism stability.

Key words: aposematism, Araneidae, Gasteracantha cancriformis, luring, prey attraction, visual communication

The evolution and maintenance of color polymorphisms have traditionally been attributed to apostatic selection (Clarke 1979). Assuming that predators form a search image (Tinbergen 1960), the advantage of rarity promotes the coexistence of multiple prey types and stabilizes polymorphisms (Bond 2007). Nonetheless, other adaptive and nonadaptive explanations for the evolution and maintenance of color polymorphisms have been proposed (Grey and McKinnon 2007). For instance, gene flow between populations with distinct phenotypes that are favored by natural selection could maintain polymorphism within populations (Grey and McKinnon 2007; Farkas et al. 2013).

In the context of visual signaling, the distinct visual systems of prey and predators may play a role in the evolution and maintenance of color polymorphisms (Ruxton et al. 2004; White and Kemp 2015). Animal communication involves the generation, transmission, and processing of the signal by a receiver, in which an appropriate response is elicited (Endler 1993). Any factors that affect these steps can influence signal efficiency and, as a result, affect the direction of communication evolution (Endler 1993). Thus, the diversity of signals is likely influenced by variation in the sensory systems of receivers.

Considering that the same "color" may be perceived as cryptic or conspicuous by different species (Endler and Mappes 2004), each color morph of a polymorphic population may represent an adaptation to particular visual systems of prey or predator species (Endler 1992; Ruxton et al. 2004; White and Kemp 2015). The role of multiple predators on the evolution of prey coloration has been approached by theoretical models (Endler 1988; Endler and Mappes 2004). Endler's model (1988), for instance, indicated that a stable polymorphism might evolve in the presence of anti-apostatic selection (positive frequency-dependent) and apostatic selection (negative frequency-dependent) from different predators. Additionally, polymorphism might be stable in the presence of anti-apostatic selection from different predators, given that predators perceive prey conspicuousness differently and there is a covariance between the relative degree of crypsis and the degree of frequency-dependent selection by each predator (Endler 1988). Although Endler's model has been developed to predators' perception of prey, it could be applied to selection forces arising from other observers (e.g., variation in perception by prey).

Many orb-web spiders exhibit conspicuous coloration. Although sexual selection is a common explanation for bright coloration in other taxa such as birds (Ryan 1990), this scenario is less likely to happen in orb-web spiders, because they may lack color vision (Yamashita and Tateda 1978; Yamashita 1985). *Argiope argentata* (Araneidae), for instance, seems to possess only 1 photoreceptor (Tiedemann et al. 1986). The prey attraction hypothesis states that the bright coloration of some spiders is used to lure insects, possibly by mimicking flower coloration (e.g., Craig and Ebert 1994; Hauber 2002). The hypothesis has been empirically tested several times, and most studies have found support for it. The polymorphic spider *Nephila pilipes* (Araneidae) presents a melanic and a bright colored morph (Tso et al. 2004). The bright color patterns of this species are thought to resemble symmetric flower patterns that may attract bees, owing to the innate preference of bees for symmetry (Chiao et al. 2009). Moreover, yellow patches on the spider's body may be perceived as food resources by flower visitors (Tso et al. 2004). Besides being attractive to pollinators, the yellow patches also seems to attract hymenopteran predators. Therefore, it is possible that there is a trade-off between foraging success and predation risk in polymorphic populations in which some morphs are more cryptic than others (Fan et al. 2009).

The predators of orb-web spiders possess very distinct visual systems. Birds, for example, are tetrachromats, whose photoreceptors are most sensitive to ultraviolet/violet, blue, green, and red (Hart 2001), whereas spider-hunting wasps, such as members of the family Sphecidae, are trichromats, whose photoreceptors are most sensitive to ultraviolet, blue, and green (Peitsch et al. 1992; Briscoe and Chittka 2001). Similarly, the insect prey of orb-web spiders also vary in their types of color vision. For example, bees are trichromats with spectral sensitivities similar to those of sphecid wasps (Briscoe and Chittka 2001), whereas some lepidopterans are tetrachromats (Briscoe and Chittka 2001; Koshitaka et al. 2008; Arikawa 2017), and some dipterans possess photoreceptors with 5

different sensitivity peaks (Schnaitmann and Garbers 2013). Therefore, the maintenance of spider color polymorphism may result not only from a trade-off between prey attraction and predation risk, but also from selective pressure from multiple receivers (Endler 1992; Ruxton et al. 2004; White and Kemp 2015).

The orb-web spider *Gasteracantha cancriformis* (Araneidae) constructs large webs and rests in the web hub during the day (Levi 1978). Females of the species possess a hard abdomen with 3 pairs of spines, and vary in color, with some morphs quite conspicuous to human observers (Levi 1978; Gawryszewski and Motta 2012). The ventral side of females is mostly black, sometimes with small bright spots. In one studied population, the dorsal side of females possessed black or reddish spines and 4 distinct color patterns: yellow, white (without UV reflectance), red, and a combination of black and white (white patches reflects UV; Gawryszewski 2007; Gawryszewski and Motta 2012). The prey attraction hypothesis does not seem to explain the coloration of *G. cancriformis* because both naturally bright morphs and yellow-painted individuals failed to capture more prey than either naturally cryptic morphs or black-painted individuals (Gawryszewski and Motta 2012). Nonetheless, it remains possible that each color morph attracts preferentially specific types of prey. Although evidence is still needed, Edmunds and Edmunds (1983) suggested that the conspicuous body coloration of *Gasteracantha* spiders might serve as a warning signal to predators. Therefore, *G. cancriformis* color morphs may be an adaptation to warn predators that perceive color differently.

In this study, we aimed to explore old and new hypotheses that could potentially explain the maintenance of color polymorphisms. We investigated 3 hypotheses for the evolution and maintenance of color polymorphism, using *G. cancriformis* as a model. Two derivations from the prey attraction hypothesis include (1) the *multiple prey hypothesis*, which posits that each color morph is adapted to lure a specific type of prey; and (2) the *flower mimic hypothesis*, which posits that the spiders attract prey *via* aggressive mimicry of flower colors, and that each color morph mimics a different flower color. In the first hypothesis, different prey would exert different degrees of anti-apostatic and apostatic selection depending on the degree of attractiveness for each type of prey. The second hypothesis is a proposed mechanism to explain why spider colors would be attractive to prey. In addition, (3) the *multiple predator hypothesis* posits that the conspicuous colors found in spiders could serve as warning signals to predators and that color polymorphism could evolve and be maintained if each color morph is adapted to the vision of a specific predator. Comparable to the multiple prey hypothesis, predators could exert apostatic and anti-apostatic selection on color morphs depending on the degree of conspicuousness and palatability for each predator type (see Endler 1988 model).

Materials and Methods

Color vision model

Color perception depends on both the signal reflectance and the visual system of the observer, as well as the background reflectance spectrum and ambient light intensity (Endler 1990). Physiological models of color vision include all these factors and have been effective for objectively studying animal coloration (i.e., independent of human subjective assessment; Renoult et al. 2015).

To estimate the perception of *G. cancriformis* color morphs by distinct predators and prey groups, we used the color vision model proposed by Chittka (1992). Although this model has been only

validated with behavioral experiments on bees, its general form allows us to apply it to other taxa (e.g., Théry and Casas 2002; Kemp et al. 2015). There are other models of color vision (Vorobyev and Osorio 1998; Endler and Mielke 2005), but when applied correctly, their results tend to be highly correlated (Gawryszewski 2018). In addition, receptor noise limited models (Vorobyev and Osorio 1998) are sensitive to accurate measurements of noise at photoreceptors (Lind and Kelber 2009; Olsson et al. 2017), which, for insects, is available only to the honeybee (see Olsson et al. 2017 for a recent review).

The Chittka (1992) model requires 4 inputs: (1) the irradiance reaching the observed object, (2) the observer photoreceptor excitation curves, (3) the background reflectance to which photoreceptors are adapted to, and (4) the reflectance curve of the observed object. First, the sensitivity factor R was determined for each photoreceptor as follows:

$$R = 1 / \int_{700}^{300} I_B(\lambda) S(\lambda) D(\lambda) d\lambda, \qquad (1)$$

where $I_B(\lambda)$ is the spectral reflectance function of the background, $S(\lambda)$ is the spectral sensitivity function of each photoreceptor, and $D(\lambda)$ is the illuminant irradiance spectrum. Secondly, the quantum flux P (relative amount of photon catch) is calculated as follows:

$$P = R \int_{700}^{300} I_S(\lambda) S(\lambda) D(\lambda) d\lambda, \qquad (2)$$

where $I_S(\lambda)$ is the spectral reflectance function of the stimulus. Assuming that the maximum excitation of a photoreceptor is 1, the phototransduction process is determined as follows:

$$E = P/(P+1). \qquad (3)$$

Stimulus spectra are projected into specific color spaces. The coordinates of each spectrum are calculated using photoreceptor excitations, as follows (Chittka et al. 1994):

$$X1 = \sin 60° \ (E_3 \ - \ E_1), \qquad (4)$$

$$X2 = E_2 - \ 0.5 \ (E_1 + E_3), \qquad (5)$$

and for tetrachromat organisms (Théry and Casas 2002), as follows:

$$X1 = \frac{2\sqrt{2}}{3} \cos 30° \ (E_3 - E_4), \qquad (6)$$

$$X2 = E_1 \ - \ \frac{1}{3} \ (E_2 + E_3 \ + E_4), \qquad (7)$$

$$X3 = \frac{2\sqrt{2}}{3} \ [\sin 30°(E_3 + E_4) \ - \ E_2]. \qquad (8)$$

Chromatic contrast between a color stimulus and background, or between 2 color stimuli, is calculated as the Euclidean distance (ΔS) between 2 points in color space, as follows:

$$\Delta S = \sqrt{\sum_{i=1}^{n} (X_{a_i} - X_{b_i})^2}, \qquad (9)$$

where Xi ($i = 1, 2, 3, \ldots, n$) represents the coordinate in the color space.

The color spaces are chromaticity diagrams and, thus, do not estimate the achromatic contrast between objects. Nonetheless, achromatic contrasts can be critical visual cues used by both prey and predators. In bees, achromatic contrast is more important than chromatic cues for objects that subtend a visual angle smaller than

$\sim$15 degrees, which means that bees must be close to flowers to use their color vision for discrimination tasks (Giurfa et al. 1997). Similarly, birds use achromatic contrast in the detection of small objects (Osorio et al. 1999). We estimated the achromatic contrast as the excitation (Equation (3)) of the photoreceptor responsible for achromatic discrimination in each organism (Chittka and Kevan 2005).

For our modeling, we used the reflectance data of *G. cancriformis* color morphs that were collected during a previous study (for reflectance curves, see Figure 1.8 in Gawryszewski 2007, and Figure 5 in Gawryszewski and Motta 2012). These data have already been used to estimate the visual contrast of the yellow, white, and black and white morphs from the perspective of *Apis mellifera* (Gawryszewski and Motta 2012). The spiders were collected from a Brazilian savanna physiognomy, namely Cerrado *sensu stricto*, which is characterized by shrubs and trees of 3–8 m tall that are contorted and possess thick, fire-resistant bark, a crown cover of >30%, and additional herbaceous vegetation (Oliveira-Filho and Ratter 2002). The background reflectance was estimated from the average reflectance of leaves, leaf litter, bark, and grasses that were collected from the same area as the spiders (see Figure 5 in Gawryszewski and Motta 2012). To avoid issues with negative values, we adjusted the reflectance data by subtracting the minimum value of each measurement from the reflectance values. For the illuminant spectrum, we used the International Commission on Illumination (CIE) standard illuminant of D65, which is comparable to open areas, such as the Brazilian savanna (Chittka 1996). Visual modeling calculations were conducted using the R package "colourvision" (Gawryszewski 2018).

Multiple prey hypothesis

Using the model described above, we estimated the chromatic and achromatic conspicuousness of the *G. cancriformis* morphs (yellow, white, red, and the white patches of the black and white morph) to a suite of potential prey: *A. mellifera* (Hymenoptera, Apidae), *Drosophila melanogaster* (Diptera, Drosophilidae), and *Fabriciana adippe* (Lepidoptera, Nymphalidae). Those species are not necessarily sympatric with *G. cancriformis*, but orb-webs commonly intercept those orders in field experiments (Craig and Ebert 1994; Tso et al. 2002), and represent the diversity of visual systems among insects (Briscoe and Chittka 2001). The variation in maximum sensitivity is small in Hymenoptera; most species present 3 spectral curves (Briscoe and Chittka 2001). In Diptera, the number of photoreceptors is not so conserved among species (Briscoe and Chittka 2001; Lunau 2014). In Lepidoptera, the red receptor appears to have evolved several times independently (Briscoe and Chittka 2001). Furthermore, there are species with more than 4 photoreceptor spectral curves and with task-specific spectral curves (Briscoe and Chittka 2001). We decided to model *Fabriciana adippe* as a tetrachromat because circumstantial evidence and behavioral experiments support the tetrachromat color vision for at least some butterfly species (e.g., Koshitaka et al. 2008; Arikawa 2017). Blackiston et al. (2011), for instance, also consider a nymphalid butterfly as tetrachromat on color vision modeling.

For *A. mellifera* and *D. melanogaster*, we used photoreceptor sensitivity curves from the literature (Peitsch et al. 1992; Schnaitmann and Garbers 2013; Supplementary Figure S1). The graphical curves were extracted directly from the figures of relevant publications using DataThief III version 1.7 (Tummers 2006). For *F. adippe*, electrophysiological measurements of photoreceptor sensitivity peaks (λ_{max}; Eguchi et al. 1982) were used to estimate the 4
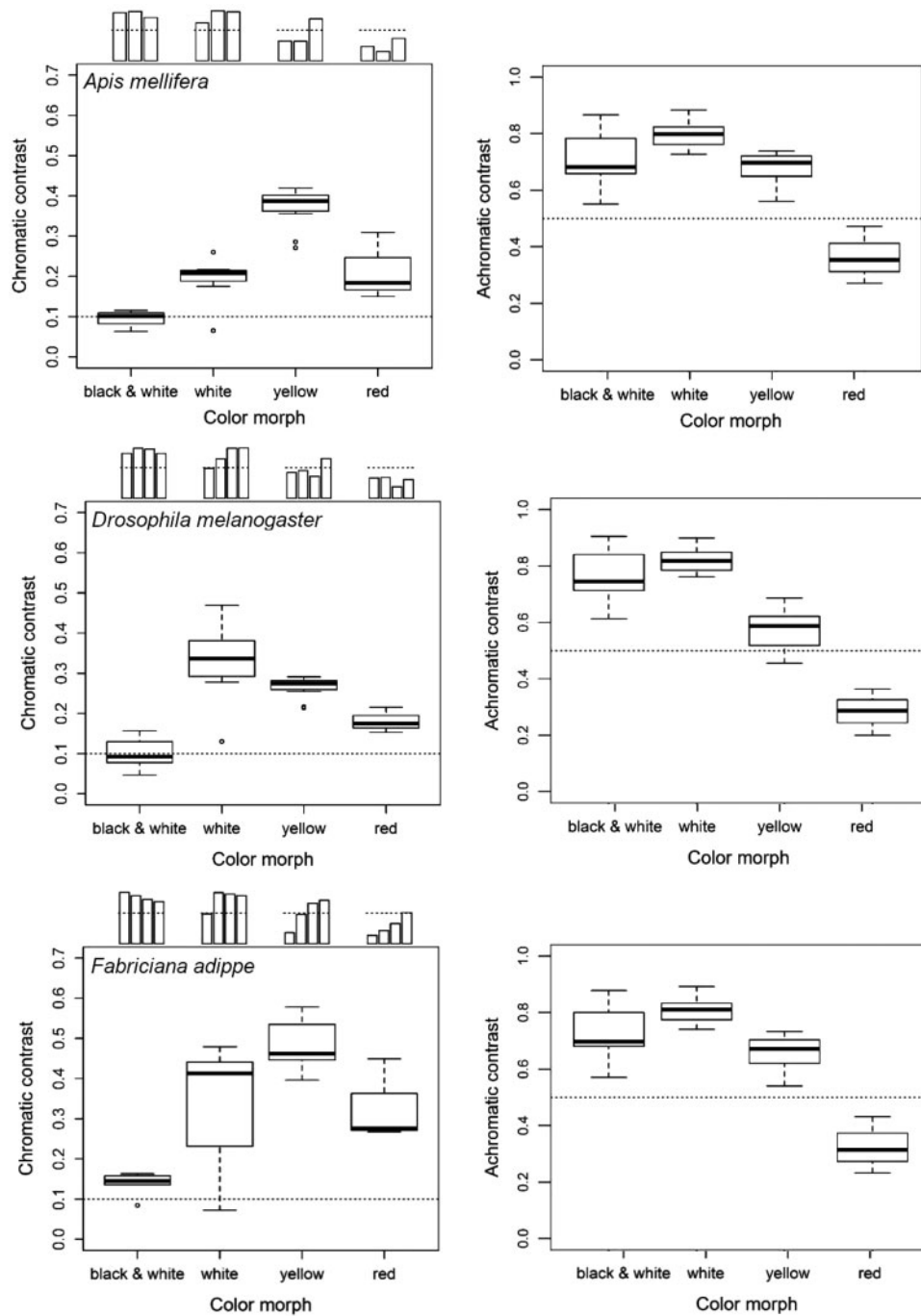
Figure 1. Chromatic (left) and achromatic (right) contrasts of 4 *Gasteracantha cancriformis* morphs (black and white, *N* = 6; white, *N* = 8; yellow, *N* = 12; and red, *N* = 3) when viewed against a Brazilian savanna background by prey with distinct visual systems: *Apis mellifera* (Hymenoptera), *Drosophila melanogaster* (Diptera), and *Fabriciana adippe* (Lepidoptera). Dotted vertical lines represent the discrimination thresholds for chromatic contrast (0.11) and photoreceptor excitation for the background in achromatic contrast (0.5). Upper bars are the excitation values of photoreceptors to each spider morph. Sets of 3 bars in *A. mellifera* indicate ultraviolet, blue, and green photoreceptors, respectively. Sets of 4 bars in *D. melanogaster* and *F. adippe* represents, respectively, ultraviolet, blue, green and red photoreceptors. The photoreceptors excitation for the background (0.5) is shown by the dotted lines.

photoreceptor curves (for details see Govardovskii et al. 2000), considering a beta-band (Supplementary Figure S1).

For achromatic contrast, bees only use the green photoreceptor (Giurfa et al. 1996), whereas flies only use the outer photoreceptors (R1-R6; Kelber and Henze 2013). For Lepidoptera, we assumed that they employ the green photoreceptor, considering that green receptors seem to be involved in motion perception in Papilionidae

(Horridge et al. 1984; Takemura et al. 2005; Takemura and Arikawa 2006). The color hexagon model assumes that photoreceptors respond to half their maximum for the background they are adapted to, so that the photoreceptor excitation for the background is equivalent to 0.5 units (Chittka 1992).

The multiple prey hypothesis predicts that different prey taxa perceive color morphs differently. To assess whether each spider morph

was perceived differently by prey species, we conducted 2 linear mixed models, 1 for chromatic contrast and 1 for achromatic contrast. Either the chromatic (ΔS) or achromatic contrast was used as the dependent variable, and spider morph and prey taxon were used as the independent variables (contrast = spider morph × observer). The spider morph was defined as yellow, white, red, or black and white, and the observers were defined as Hymenoptera, Diptera, or Lepidoptera. Individual spiders were used as random effects.

As a reference point, we used a color discrimination threshold of $\Delta S = 0.11$, which is the threshold value below which trained bees are unable to distinguish different flower colors (Chittka 1996). However, discrimination thresholds are variable, and can change depending on the study species, learning conditions, previous experience, background coloration, whether the task involves discrimination between colors or detection against the background, and whether objects are compared sequentially or simultaneously (Avarguès-Weber and Giurfa 2014). It should also be noted that threshold values were not behaviorally validated for other taxa.

Mimic model hypothesis

To test the multiple mimic models hypothesis, we compared how prey perceive flowers and spider morphs. We gathered all flower reflectance data available in the Floral Reflectance Database (FReD; Arnold et al. 2010), excluding reflectance data from lower flower parts, leaves, bracts, stamens, the inner parts of bell-shaped flowers, and unknown items, as well as spectra that did not cover 300–700 nm. Most species in the database only have 1 reflectance spectrum. For species with multiple reflectance spectra, we randomly selected a single spectrum. We did not average the reflectance of these species because there was no information available on whether these measurements referred to different individuals or different parts of single flowers. In total, we gathered reflectance data from 858 plant species. We grouped flowers visually according to the nine categories proposed by Chittka et al. (1994; see spectral curves in Supplementary Figure S2), which considers whether they reflect or absorb in 4 spectral ranges, UV (300–400 nm), blue (400–500 nm), green (500–600 nm), and red (600–700 nm). We deleted 3 spectral curves that did not seem to fit in any of these categories. Flowers classified as category 10 ($N = 16$) were not included in the analyses. A caveat of this analysis is that these flowers are not necessarily sympatric to *G. cancriformis*. However, the spectral curve variations in flowers are subtle, because there is a constraint on the blending of flower pigments (Chittka and Menzel 1992; Chittka et al. 1994). In addition, we computed reflectance curves from different countries available in the FReD database. A qualitative analysis strongly suggests that they all have similar shapes independent of the country of origin (Supplementary Figure S2).

The multiple mimic model hypothesis predicts that different color morphs mimic different flower colors. First, to evaluate the color regardless of the observer, we compared the hue (Equation (10)), saturation (Equation (11)), and brightness (Equation (12)) of flowers and spiders (Andersson and Prager 2006 and references therein):

$$H_3 = \lambda_{Rmid}, \tag{10}$$

where λ_{Rmid} is the wavelength at the middle point between the minimum and maximum reflectances;

$$S_8 = (R_{max} - R_{min})/B_2, \tag{11}$$

where R_{max} and R_{min} are the maximum and minimum reflectance points; and $B_2 = \sum_{\lambda 300}^{\lambda 700} R_i/n_w$, where R_i is the reflectance

corresponding to each wavelength point, and n_w is the total wavelength intervals;

$$B_3 = R_{max}, \tag{12}$$

where R_{max} is the maximum reflectance. In addition, the average color parameters of morphs in relation to individual flowers were illustrated in a histogram, where flowers collected in the Brazilian savanna ($N = 7$; same biome where the spiders were collected; see below) were treated individually.

Secondly, we computed the chromatic contrast (Euclidean distance) for spider morphs and flowers following the same steps as for the previous section, considering the visual systems of *A. mellifera*, *D. melanogaster*, and *F. adippe*. Then, we calculated a matrix of chromaticity distances between the average color loci of each spider color morph and each flower species and estimated the percentage of values below or equal to the theoretical detection threshold of 0.11. To evaluate if prey species perceived spider morph and flower similarly, we conducted a Wilcoxon test comparing each set of combinations between morph and flower category with the discrimination threshold of 0.11 (Student's t-test is conventionally used to compare the color contrast to a particular threshold, but our data were not normally distributed).

We computed the achromatic contrast by subtracting each value of photoreceptor excitation of flowers from values of excitation of morphs and finding the absolute value. Here, we also conducted a Wilcoxon test to assess which achromatic contrasts were lower than 0.11. We used the same threshold of chromatic discrimination because threshold values for achromatic discrimination are not available for those prey groups. For chromatic and achromatic analyses, we used a significance level of $P < 0.01$ in addition to the $P < 0.05$ convention to account for the increased risk of a type I error due to the multiple comparisons.

Multiple predator hypothesis

The methodology used to investigate the multiple predator hypothesis was similar to that used for the multiple prey hypothesis, except that we used predator species in our models. As predators, we considered the bird *Cyanistes caeruleus* (Paridae) and the wasp *Philanthus triangulum* (Sphecidae) because birds and wasps are the primary predators of orb-web spiders (Rayor 1996; Toft and Rees 1998; Blackledge et al. 2003; Gonzaga and Vasconcellos-Neto 2005; Gunnarsson 2007), they are visually guided hunters, and have distinct color vision systems. For *C. caeruleus*, we used photoreceptor sensitivity curves available in the literature (Hart 2001; Supplementary Figure S1), and for *P. triangulum*, we used photoreceptor sensitivity peaks to estimate photoreceptor sensitivity curves with a beta-band in the ultraviolet (data available in Briscoe and Chittka 2001; see Govardovskii et al. 2000 for an estimation of sensitivity curves from sensitivity peaks; Supplementary Figure S1). Again, those species are not sympatric with *G. cancriformis*, but we do not expect a significant variation in photoreceptors types within hymenopterans (Peitsch et al. 1992) nor Passeriformes (Hart 2001).

The multiple predator hypothesis predicts that different predator taxa perceive color morphs differently. To assess this prediction, we established 2 linear mixed models, 1 for chromatic contrast and 1 for achromatic contrast for each predator species. Either chromatic (ΔS) or achromatic contrast was used as the dependent variable, and spider morph and predator taxon were used as the independent variables (contrast = spider morph × observer). The spider morph was defined as yellow, white, red, or black and white. Individual spiders were used as random effects.

Table 1. ΔAIC and determination coefficients of linear mixed models of the chromatic and achromatic contrasts of prey and predators

	df	ΔAIC	Marginal R^2	Conditional R^2
Multiple prey hypothesis				
Chromatic dimension				
ΔS ~ morph * observer	**17**	**0**	**0.735**	**0.799**
ΔS ~ morph + observer	11	55.811	0.772	0.823
ΔS ~ morph	9	90.834	0.511	0.532
ΔS ~ observer	5	116.544	0.319	0.844
ΔS ~ 1	6	135.038	0	0.599
Achromatic dimension				
Excitation ~ morph * observer	**17**	**0**	**0.813**	**0.990**
Excitation ~ morph	9	120.658	0.609	0.700
Excitation ~ morph + observer	11	145.370	0.801	0.956
Excitation ~ 1	6	168.803	0	0.771
Excitation ~ observer	8	190.843	0.050	0.961
Multiple predators hypothesis				
Chromatic dimension				
ΔS ~ morph * observer	**13**	**0**	**0.824**	**0.952**
ΔS ~ morph + observer	10	23.489	0.814	0.922
ΔS ~ observer	7	57.926	0.306	0.932
ΔS ~ morph	9	76.386	0.402	0.402
ΔS ~ 1	6	111.434	0	0.494
Achromatic dimension				
Excitation ~ morph * observer	**14**	**0**	**0.655**	**0.847**
Excitation ~ observer	7	52.660	0	0.034
Excitation ~ morph	9	60.637	0.331	0.413
Excitation ~ morph + observer	10	65.573	0.359	0.437
Excitation ~ 1	6	76.770	0	0.034

As in the multiple prey hypothesis, we used discrimination thresholds as reference points. For the chromatic contrast, we considered color discrimination thresholds of ΔS = 0.11 and ΔS = 0.06 for the wasp (Dyer and Chittka 2004) and bird (Théry et al. 2005), respectively. For the achromatic contrast, we considered double cones in birds (Hart 2001), and assumed green photoreceptors for wasps, as in bees, and compared values obtained to an excitation of 0.5.

For all analyses, linear mixed models were performed using the "nlme" (Pinheiro et al. 2016) or "lme4" packages (Bates et al. 2015). Normality and homogeneity were verified by visual inspection of quantile–quantile and residuals vs. fitted values plots. The variance was heteroscedastic; therefore, we included the variable "morph" into the variance structure. We computed all nested models and used the Akaike information criterion (AIC) to select the best model. Marginal and conditional R^2 were estimated using the package "piecewiseSEM" (Nakagawa and Schielzeth 2013). Reflectance graphs were plotted using the "pavo" package (Maia et al. 2013; R Core Team 2015).

Results

Multiple prey hypothesis

For chromatic contrast, the model that included interaction between both variables, spider morph and prey taxon, presented the lowest AIC value (Table 1). The yellow morph presented the highest ΔS value for *A. mellifera* and *F. adippe* vision, whereas the white spider presented the highest ΔS value for *D. melanogaster*, followed by the yellow morph (Figure 1). The white patch of the black and white

spiders presented a ΔS value that was close to the theoretical discrimination threshold for all prey species (Figure 1). The red spiders presented ΔS values near the theoretical discrimination threshold for *A. mellifera* and *D. melanogaster*, but not for *F. adippe* (Figure 1).

For prey achromatic contrast, the model that considered the interaction between both variables presented the lowest AIC value (Table 1). For *A. mellifera* and *F. adippe*, the white morph had the highest excitation value, followed by the black and white, yellow, and red morphs, respectively (Figure 1). In *D. melanogaster* vision, the yellow morph had the highest achromatic discrimination, followed by white, black and white, and red (Figure 1). The model coefficients are provided in the supplementary material (Supplementary Tables S1 and S2).

Mimic model hypothesis

We found 3 peaks of hue for the flowers, around 400, 500, and 600 nm, which are similar to the average hue of spider morphs (Figure 2A). The saturation metric had only 1 peak for flowers, to which black and white, white, and yellow spider morphs were close (Figure 2B). The brightness of flowers also only presented a single peak. White, red and yellow spider morphs had an average brightness around this peak (Figure 2C).

For all 3 prey species, only the white patch of the black and white morph had a high percentage of values near the chromatic theoretical discrimination threshold of 0.11 when compared with all flower reflectance spectra: 43.86% for *A. mellifera*, 29.12% for *D. melanogaster*, and 35.65% for *F. adippe*. For the other spider morphs, only a small proportion of the Euclidean distances between flowers and morphs presented values <0.11. For *A. mellifera*, only 1.47% of yellow morphs, 8.13% of white morphs, and 4.88% of red morphs presented values lower than 0.11. For *D. melanogaster* only 1.29% of yellow morphs, 4.52% of white spiders, and 7.62% of red morphs had values lower than 0.11. For *F. adippe*, these values were 0.40%, 6.98%, and 0.31%, respectively.

For *A. mellifera*, only the black and white morph compared with the flower categories "3" (human white), "4" (human reddish blue or purple), and "8" (human white) had values significantly lower than 0.11 (Figure 3, Supplementary Table S3). For *D. melanogaster*, values lower than 0.11 only included the comparison between black and white morphs and category "8" of flowers (Figure 3, Supplementary Table S3). For *F. adippe*, only categories "4" and "8" compared with black and white morphs were lower than 0.11 (Figure 3, Supplementary Table S3). All other comparisons between spider and flowers colorations were higher than 0.11 (Figure 3, Supplementary Table S3). For achromatic contrast, almost one-third of the comparisons between flower categories and spider morphs had excitation values between 0 and 0.11 (Figure 3, Supplementary Table S3).

Multiple predator hypothesis

For the chromatic contrast, the model with interaction between variables presented the lowest AIC value (Table 1). The black and white morph presented the lowest ΔS value for both predators (Figure 4; Supplementary Table S4). The white morph was the one with the highest ΔS value for *C. caeruleus*, though yellow and red morphs presented similar values (Figure 4). For *P. triangulum*, the white spider morph presented the highest ΔS value, followed by the yellow and red morphs. The latter was near the theoretical discrimination threshold of 0.11 (Figure 4).
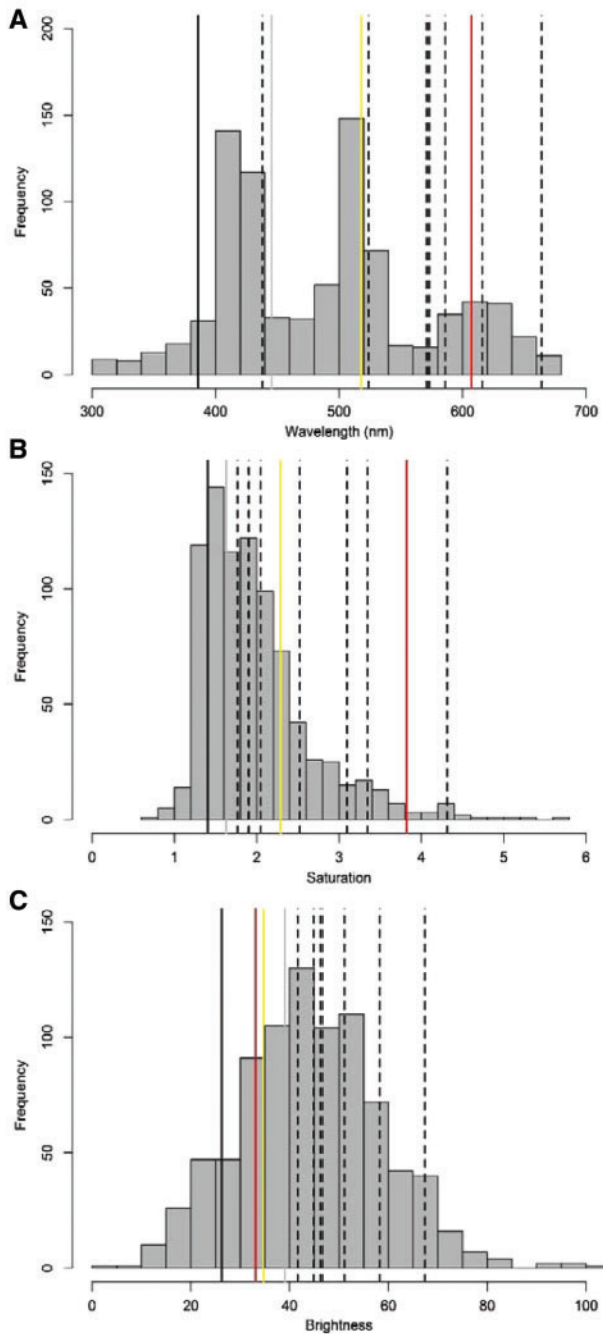
Figure 2. Frequency of color properties of flowers ($N = 858$): (A) hue, (B) saturation, (C) brightness. Average values of each *Gasteracantha cancriformis* morph are represented by solid colored lines: black and white morph (black line; $N = 6$), white morph (gray line, $N = 8$), yellow morph (yellow line, $N = 12$), and red morph (red line, $N = 3$). Flowers from the Brazilian savanna ($N = 7$) are represented by dotted lines.

For the achromatic contrast, the model that included the interaction between variables presented the lowest AIC value (Table 1), even though the values of the 2 predator species were similar. For *C. caeruleus*, the white morph had the highest excitation value, followed by the yellow, black and white, and red morphs (Figure 4). The yellow morph had the highest excitation value for *P. triangulum*, followed by white, black and white, and red morphs (Figure 4).

The model coefficients are provided in the supplementary material (Supplementary Tables S4 and S5).

Discussion

Most studies focus on a single signal receiver; however, we could better understand signal evolution considering multiple receivers (Endler and Mappes 2004; Schaefer et al. 2004). The multiple receiver hypothesis has been evaluated in intersexual and intrasexual relationships (Guindre-Parker et al. 2012), signaler interaction with prey and predators (Endler 1983), and interaction with pollinators and herbivores (Irwin et al. 2003). Here, we provide an exploratory perspective on how multiple receivers may influence color polymorphism evolution in orb-web spiders.

Multiple prey hypothesis

In *G. cancriformis*, spider morph conspicuousness is likely to be perceived differently by prey species, which provides support for the multiple prey hypothesis. The yellow and white morphs are the most contrasting for all 3 species, but chromatic data suggested that the former is more contrasting from the background for honeybee color vision, and the latter for flies. This scenario may lead to the evolution of polymorphism in the presence of anti-apostatic selection only (Endler 1988). Besides, the red morph showed a marked difference between prey observers. The inspection of photoreceptor values shows that for *A. mellifera* and *D. melanogaster*, the red morph does not present much chromatic information (i.e., low photoreceptor outputs and small differences between photoreceptor outputs; Figure 4), but does present chromatic information for *F. adippe* because of the long-wavelength photoreceptor sensitivity curve (Figure 4). This also means that the ΔS value for *A. mellifera* and *D. melanogaster* red morphs (Figure 4) should be considered carefully because the Chittka (1992) model may generate ΔS values higher than expected when all photoreceptor excitation values are low (i.e., a reflectance spectrum perceived as a black or dark gray; Vorobyev et al. 1999; Gawryszewski 2018). Translating into human color terms, our results suggest that *A. mellifera* and *D. melanogaster* would probably perceive the red morph as gray (achromatic), but *F. adippe* would perceive it as colorful.

Other studies evaluated the prey perceptual differences as a possible route to the evolution of color polymorphisms in orb-web spiders. Their results suggested that different morphs may exploit different visual channels in prey species (White and Kemp 2016; Ajuria-Ibarra et al. 2017). In *Verrucosa arenata* (Araneidae) and *G. fornicata* (Araneidae), the yellow morph had a higher chromatic contrast than the white morph, whereas in the achromatic dimension the white morph presented a higher contrast for prey taxa (White and Kemp 2016; Ajuria-Ibarra et al. 2017). Therefore, the yellow morphs would benefit from stimulating the chromatic channel, whereas white morphs would benefit from stimulating the achromatic channel. Similarly, our data suggest the maximum chromatic contrast for the yellow morph, but maximum achromatic contrast for the white morph from the perspectives of *D. melanogaster* and *F. adippe* (Figure 1).

Two caveats arise from analyses using color vision models, including our study. First, the relationship between supra-threshold values and behavioral discrimination tasks is not yet completely elucidated, but is likely to be nonlinear and varied between species (Garcia et al. 2017). Second, showing that one morph is more conspicuous than another does not necessarily translate into prey preference, because this preference may arise from other factors, such as previous experience (Dyer 2012). Furthermore, the color vision of butterflies is variable,
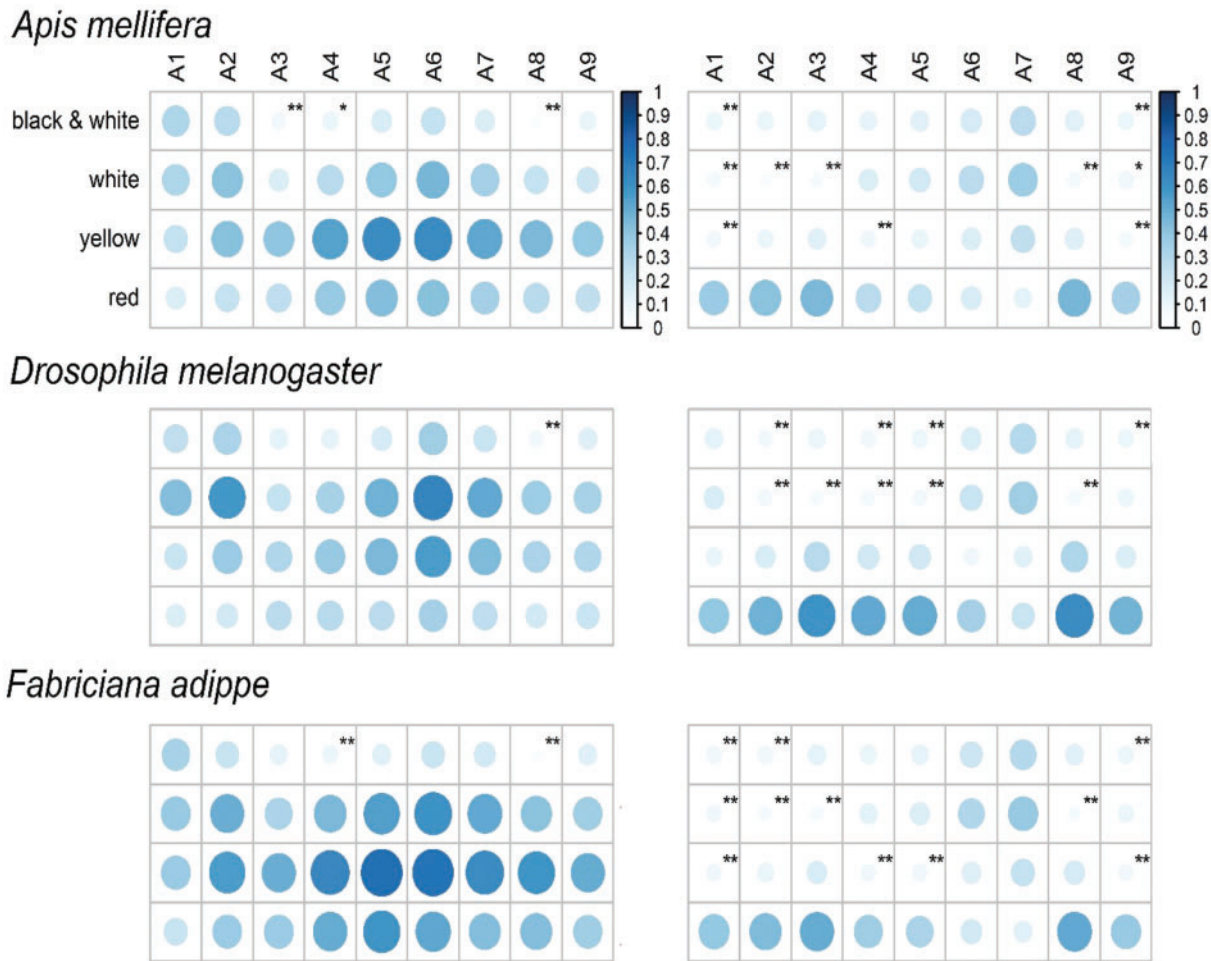
Figure 3. Correlation plot of chromatic (left) and achromatic (right) contrasts of 4 *Gasteracantha cancriformis* morphs (black and white, $N = 6$; white, $N = 8$; yellow, $N = 12$; and red, $N = 3$) when compared with 9 flower categories (Chittka et al. 1994) indicated by numbers. Low values are represented by smaller and lighter circles. These categories are based on reflectance curve shapes and can be translated into human colors as follows: type 1 ($N = 93$), yellow; type 2 ($N = 96$), yellow; type 3 ($N = 240$), white; type 4 ($N = 186$), reddish blue, purple or pink; type 5 ($N = 107$), violet; type 6 ($N = 19$), red; type 7 ($N = 34$), red; type 8 ($N = 12$), white; and type 9 ($N = 52$), pale yellow. These values were computed considering the Brazilian savanna as the background and were based on 3 potential prey: *Apis mellifera* (Hymenoptera), *Drosophila melanogaster* (Diptera), and *Fabriciana adippe* (Lepidoptera). One asterisks represent values significantly lower than the discrimination thresholds for chromatic contrast (0.11) at the $P < 0.05$ level and 2 asterisks at the $P < 0.01$ level, according to Wilcoxon tests.

with some species with task specific spectral channels (Briscoe and Chittka 2001). Therefore, experimental studies are needed to corroborate predictions arising from the color vision model data.

Mimic model hypothesis

Our results provided mixed support for the multiple model hypothesis. Considering only color metrics, most *G. cancriformis* morphs indeed have similar colorations to flowers (Figure 2). However, when we modeled color perception to potential prey, only the black and white morphs were similar to the flower categories (white flowers, white flowers with UV reflectance, and purple flowers). For the achromatic dimension, black and white morphs and white morphs had similar contrasts from 2 to 5 flower categories, whereas yellow morphs had similar contrasts to 3 flower categories for the honeybee, and 4 flower categories for the butterfly. In the Brazilian savanna, *G. cancriformis* is abundant during the beginning of the dry season, which overlaps partially with the flowering period of woody plants (Oliveira 2008; Gouveia and Felfili 1998), and pollinator occurrence (Oliveira 2008; Gouveia and Felfili 1998). Therefore, flower coloration mimicry may indeed be an advantageous foraging strategy for

spiders that are abundant during this period of the year. Despite that, a field experiment conducted with *G. cancriformis* showed that a bright coloration did not affect the foraging success of spiders (Gawryszewski and Motta 2012). It remains to be tested whether morphs attract specific types of prey, especially flower visitors.

Similar to our results, in *G. fornicata* the white morphs seem to be indistinguishable from sympatric flowers according to the results of bee color vision modeling, but yellow morphs and flowers were perceptually different (Maia and White 2017). Conversely, a study on various orb-web spider species that also used color vision models found that, as perceived by dipterans and hymenopterans, the colors of spiders are similar to those of flowers (White et al. 2016). Nonetheless, correlation does not mean causation. The similarity found between spider and flower color in White et al. (2016), and partially in our data, may only reflect the diversity of flower and spider colors.

Multiple predator hypothesis

Our results indicated partial support to the multiple predator hypothesis. The statistical results suggested an interaction between predator taxa and chromatic contrast. The red morph presented a
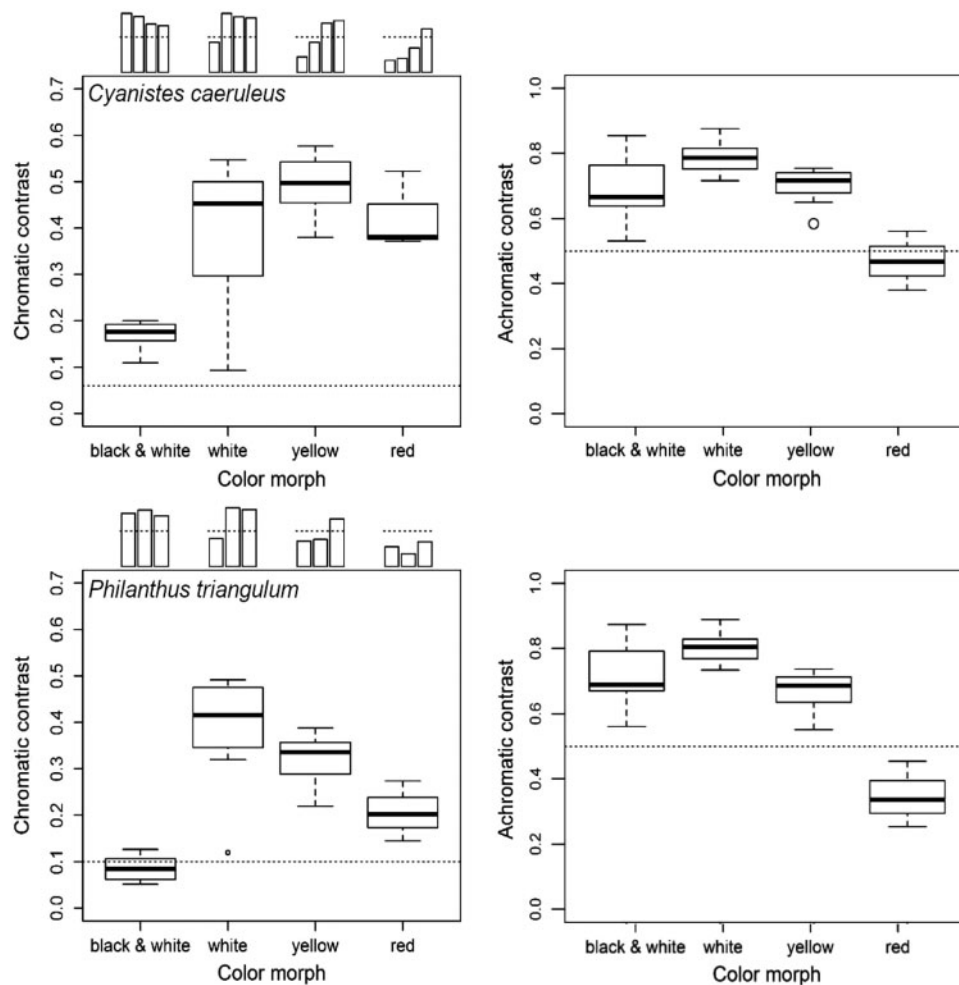
Figure 4. Chromatic (left) and achromatic (right) contrasts of 4 *Gasteracantha cancriformis* morphs (black and white, $N=6$; white, $N=8$; yellow, $N=12$; and red, $N=3$) when viewed against a Brazilian savanna background by predators with distinct visual systems: *Cyanistes caeruleus* (Passeriformes), and *Philanthus triangulum* (Hymenoptera). Dotted vertical lines represent the discrimination thresholds for chromatic contrast (0.06) and photoreceptor excitation for background in achromatic contrast (0.5). Upper bars are the excitation values of photoreceptors to each spider morph. For *C. caeruleus*, sets of 4 bars represent ultraviolet, blue, green, and red photoreceptors, respectively. For *P. triangulum*, sets of 3 bars indicate ultraviolet, blue, and green photoreceptors, respectively. The photoreceptor excitation for background (0.5) is represented by the dotted lines.

much higher chromatic contrast to a bird than to a wasp. Similar to the prey data, an inspection of photoreceptor excitation values suggest that the red morph is perceived as colorless by a wasp, but colorful to a bird (Figure 4). Nonetheless, the white and yellow morphs are highly detectable by birds and wasps in the chromatic and achromatic dimensions for both birds and wasps (Figure 4). Therefore, in the case of anti-apostatic selection from both wasps and birds, applying Endler's (1988) model to our results would likely suggest the evolution of monomorphism favoring either the white or the yellow morph, despite differences found in the red morph.

Alternatively, the interaction between apostatic and anti-apostatic selection forces from the predators of spiders could lead to the evolution of polymorphism in *G. cancriformis*. For instance, a scenario where a *Gasteracantha* sp. is avoided by birds but consumed by wasps could lead to the evolution of polymorphism, because selection from birds would favor the most conspicuous and abundant morph (yellow or white), but selection from wasps would favor the least conspicuous and least abundant morph (black and white or red). In *Nephila pilipes* (Araneidae), for instance, the yellow patches seem to attract wasp predators (Fan et al. 2009).

Nonetheless, it remains to be experimentally tested whether conspicuous colors in *Gasteracantha* spp. represent aposematic signals for either birds or wasps. Some circumstantial evidence supports at least that *Gasteracantha* spp. might be more defended than most other orb-web spiders; spiders of the genus *Gasteracantha* possess spines and a hard abdomen (Edmunds and Edmunds 1983), which may serve as a defense against wasps and/or birds, and the spider-hunting wasp *Sceliphron laetum* avoids provisioning initial instars with *Gasteracantha* spiders (Elgar and Jebb 1999).

Alternative hypotheses and conclusion

Variation in the perception of color by receivers may not be sufficient to explain color polymorphism in *G. cancriformis*. Gene flow, for instance, may act together on the maintenance of color variation (Grey and McKinnon 2007). Additionally, thermoregulation and the effect of illumination on the signaler detectability may also influence perception (Rojas et al. 2014; Rao and Mendoza-Cuenca 2016). Furthermore, color vision models do not include other mechanisms, such as cognition, color categorization, past experiences, or

memory imprecision (Renoult et al. 2015), even though these factors may affect detectability and, consequently, influence the survival rate of morphs differently (Théry and Gomez, 2010). Beyond color, other visual parameters, such as the geometry, shape, contour, size, angle, texture, and distance of visual detection (Troscianko et al. 2009) may influence the behavior of both prey and predators toward spiders (Théry and Gomez 2010). Additionally, nonadaptive explanations, such as overdominance and allele equilibrium, in the absence of selection, are often ignored when studying polymorphisms from an ecological perspective.

In conclusion, we presented a small step forward for the multiple receivers hypothesis on the evolution of color polymorphism in orb-web spiders. In short, in *G. cancriformis*, polymorphism may be possible even if prey exerts anti-apostatic selection only or when there is an interaction between apostatic and anti-apostatic selection from different predators. Flower mimicry is a possible explanation for the evolution of some of these spider morphs. Considering these scenarios, many combinations of complex trade-offs arising from multiple prey and predators are possible. Predation experiments, field experiments that evaluate prey taxa caught by the different spider morphs, and ecological data on the abundance and composition of prey and predator populations that occur sympatrically with *G. cancriformis* are paramount to validate and complement the findings of the present study.

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Author Contributions

N.G.X. and F.M.G. contributed to the design of the study. N.G.X. wrote the article and ran the statistical analyses. F.M.G. supervised the analyses and commented on the article.

Supplementary Material

Supplementary material can be found at https://academic.oup.com/cz.

Conflict of Interest

No competing interests declared.

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