



Original Article

Captivating color: evidence for optimal stimulus design in a polymorphic prey lure

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Many species – humans included – employ color as an instrument of deception. One intriguing example of this resides in the conspicuous abstract color patterns displayed on the bodies of female orb weaving spiders. These displays increase prey interception rates and thereby function at least as visual lures. Their chromatic properties however vary extensively, both across and within species, with discrete forms often co-existing in the manner of a stable polymorphism. Variation is principally expressed in terms of signal hue (color *per se*), but it is unclear how attractiveness scales with this property and if extant morphs are maximally attractive relative to a graded range of potential alternatives. We examined these questions by assessing catch rates among color-manipulated females of the dimorphic jeweled spider *Gasteracantha fornicata* in their natural webs. The manipulation altered dorsal appearance in a manner akin to adding six new variants of their existing white/yellow phenotypes. This magnified the natural variation in stimulus hue independently of chroma (saturation) across a range spanning most of the color spectrum. Catch rate varied across treatments in simple accordance with how greatly stimulus hue deviated from either of the two extant spider phenotypes. Predictions based on fly-perceived chromatic and achromatic background contrast were clearly unsupported despite dipterans constituting ~60 % of identifiable prey. This study supports the importance of signal coloration *per se* in *G. fornicata* and suggests that extant lure phenotypes reside in a broadly optimal spectral range for stimulating their aggregate prey community.

Key words: *Gasteracantha*, predation, sensory drive, signal design, spider, visual ecology.

INTRODUCTION

Animal coloration serves commonly as an instrument to deceive, deflect attention, and distort perception. The fundamental mechanisms of visual deception include various forms of crypsis (Stevens and Merilaita 2009) and mimicry (Turner 1987) that result in dupes failing to detect or misclassifying objects that they would otherwise pursue (if predators) or avoid (if prey). Deception in these cases, therefore, proceeds by circumventing behavioral responses in dupes. Alternative mechanisms involve stimuli designed to actively elicit maladaptive responses. So-called “aggressive” mimics for example manipulate their targets via a close resemblance to resources such as food (e.g., orchid mantids; O’Hanlon et al. 2014), mates (e.g., sexual deception; Jersakova et al. 2006), and offspring (e.g., brood parasitism; Brooke and Davies 1988). Human recreational anglers in a sense exemplify this strategy via their use of artificially colored flies and lures to attract fish (Moraga et al. 2015). A further class of deceptive signal resides among predators that seek to lure prey via striking displays of color which have no obvious analogs in the natural environment. Such signals are seen overwhelmingly in

the orb-weaving group of spiders (i.e., Family Araneidae; Hauber 2002; Bush et al. 2008), where they occur in the form of banded, spotted and variegated color patterns adorning the spiders themselves. These are displayed prominently by the foraging female spider, most typically from a characteristic station at the hub of their large orb-shaped capture web. An accumulation of evidence clearly supports the role of these abstract color signals in attracting arthropod prey (refer to recent reviews by White and Kemp 2015 and Ximenes et al. 2020; also see below). Much however remains to be learned about precisely *how* this is achieved; that is, the proximate psychosensory basis of prey attraction in such systems.

Aside from their characteristically abstract appearance, orb-weavers present lures that are curious for their degree of phenotypic variation. Among the genera known popularly as jewel spiders, which includes *Gasteracantha* and allied groups, such variation is evident among species as well as intraspecifically in the form of discrete polymorphism (Levi 1978; Gawryszewski and Motta 2012; Rao et al. 2015; White and Kemp 2015; Tan et al. 2019). Most often these sources of variation concern the spectral quality (i.e., color or hue) of the spider’s principal lure coloration. In the well-studied neotropical species *Gasteracantha cancriformis*, for example, individuals present a dorsal display dominated by either

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white (\pm ultraviolet), yellow, orange, or red (Muma 1971; Levi 1978, 1996). It is not unusual for differently colored orb-weaver morphs or species to co-exist across a common geographic range (or parts thereof), or even to be seen in close proximity within the same habitats (e.g., Kemp et al. 2013; Gawryszewski and Motta 2012). This implies multiple potential routes to achieving fitness via lure coloration (i.e., that multiple morphs represent alternative evolutionarily stable foraging strategies), which is curious because most other studied visual lures tend to converge on a single characteristic appearance (e.g., Vignolini et al. 2012). Although this could be taken to suggest that alternate orb-weaver morphs furnish equal capture success, it could arise more generally if capture benefits are balanced equally against the potential costs of displaying each particular color morph. Different color schemes may vary in their costliness to produce or bear, in the latter case because orb-weavers have their own visually-hunting predators (Edmunds and Edmunds 1986; Fan et al. 2009; Ximenes and Gawryszewski 2019; Ximenes et al. 2020; see further below).

As with the study of visual deception more generally, orb-weaver lures have increasingly been used to address the principles of sensory drive, a body of theory that considers the broader physical and perceptual contexts under which signaling systems evolve (Endler 1992). Key tenets of this theory include the visual significance of (1) ambient (habitat) light, and; (2) color sensitivity among relevant viewers (i.e., prey and predators). The first of these features refers to variation in the intensity or spectral quality of illumination across signaling microhabitats and/or throughout the day. This could influence how particular lure colors (and/or color combinations) contrast against natural viewing backgrounds (Endler 1992; Endler and Théry 1996). Notably, because spiders necessarily “declare” their signaling microsite via the positioning of their web, ambient signaling environments have proved readily quantifiable, yet ultimately insufficient to explain the presence of polymorphism (see, e.g., White et al. 2015). The second feature – receiver sensitivity – deals with variation in spectral sensitivity among relevant spider predators and prey species. Efforts on this front have sought to inform the potential for predator-prey interactions according to how lure colors stimulate known visual systems (such as the conserved avian model and the generalized honeybee model; e.g., Fan et al. 2009; Chiao et al. 2009; Ximenes and Gawryszewski 2019). The utility of this approach is however contingent in the first instance on the capacity to nominate appropriate viewers. This is particularly problematic for orb-weavers because – unlike specialist sit-and-wait predators such as crab spiders (Heiling et al. 2003) – they are opportunistic generalist predators of winged arthropods. Their prey compliments are reported to span at least 5–6 insect orders (Craig and Ebert 1994; White and Kemp 2016). Further, whereas smaller prey items make an important regular contribution to orb-weaver maintenance requirements, evidence suggests that captures of rare large items are ultimately vital for reproduction (Venner and Casas 2005). The rarity of such captures makes it difficult to predict prey identity, and most often there is little to no information on how key visual parameters vary among the species involved.

The most compelling evidence for prey attraction by orb-weaving spiders has come from experimental manipulations of body coloration *in-situ*; that is, as it is naturally presented in the wild (Hauber 2002; Bush et al. 2008; Chuang et al. 2008). This approach has shown unequivocally that the removal or camouflage of colorful markings results in a lower rate of prey interception (for a contrary report see Gawryszewski and Motta 2012). Notably, however, very few attempts have been made to manipulate the visual

characteristics of these stimuli in a graded manner, either within or (more importantly) outside the bounds of naturally occurring variation. Whereas we know that colorful lures attract prey, it remains unclear how attraction scales with variation away from the characteristics of extant stimuli. This encompasses uncharted possibilities such as whether novel attractant stimuli may occur along the color spectrum (yet remain possibly “out of reach” of spiders; *sensu* Burley and Symanski 1998) and whether supernormal stimulus variation (Gwynne and Rentz 1983) could actually elevate catch rates. More generally, the field lacks a quantitative statement relating spectral characteristics to prey attractiveness for any color-based lure system. This contrasts with how color signals are studied and interpreted in other contexts, such as mate choice, where preference functions have proven valuable for understanding signal evolution (Edward 2015).

In this study, we use the orb-weaving spider system to address how graded, broad-scale color variation influences the attractiveness of a polymorphic visual stimulus. Our study species is the northern jeweled spider *Gasteracantha formicata*, a small to medium sized orb-weaver found commonly throughout rainforest environments in tropical North Queensland, Australia. Females of this species possess a characteristically hardened plate-like abdomen bearing multiple distal spines and a striking light/dark banded dorsal color pattern. Visually, this banding generates internal pattern contrast (which may influence the orientation of prey at close range), and the light band coloration contrasts against natural viewing backgrounds (which may function for longer-range attraction; White and Kemp 2016). Experiments on naturally-occurring female *G. formicata* have implicated both the presence of dorsal banding *per-se* (Hauber 2002) and the orientation with which it is presented in the web (White 2017) as determinants of prey attraction. Although the banding pattern is essentially invariant, the overall signal is polymorphic for light band coloration (Kemp et al. 2013). Females occur in discrete phenotypes with bands that appear either human white or yellow (Figure 1) and which should each present alternate highly chromatic colors to ultraviolet-sensitive insect prey (White and Kemp 2016). These phenotypes coexist across a broad latitudinal range (albeit at varying frequencies; Kemp et al. 2013) where their signals are presented under common ambient light regimes and against the same envelope of visual backgrounds (White and Kemp 2016). Evidence suggests that their relative catch rates are equal overall (Kemp et al. 2013; White and Kemp 2016; White 2017), although each phenotype may be successful at different times under stochastically variable viewing conditions (White and Kemp 2016). Our goal here is not to address the *raison d'être* of polymorphism *per se*, instead we draw on its presence to inform an appropriate axis of signal variation for our experimental manipulation (see further below).

Signal manipulation, hypotheses, and predictions

We sought to manipulate the appearance of free-living *G. formicata* in a manner that expanded on the precise nature of spectral variation responsible for color polymorphism in this species. In spectral terms, the two *G. formicata* color morphs essentially arise from a near-identical “sigmoid” shaped reflectance function. Their principal difference stems simply from where along the wavelength scale this function is centered (i.e., white morph \approx 445 nm vs. yellow morph \approx 495 nm; Figure 1a). We drew from this to design treatment stimuli which reproduced the same sigmoid function in a greater breadth

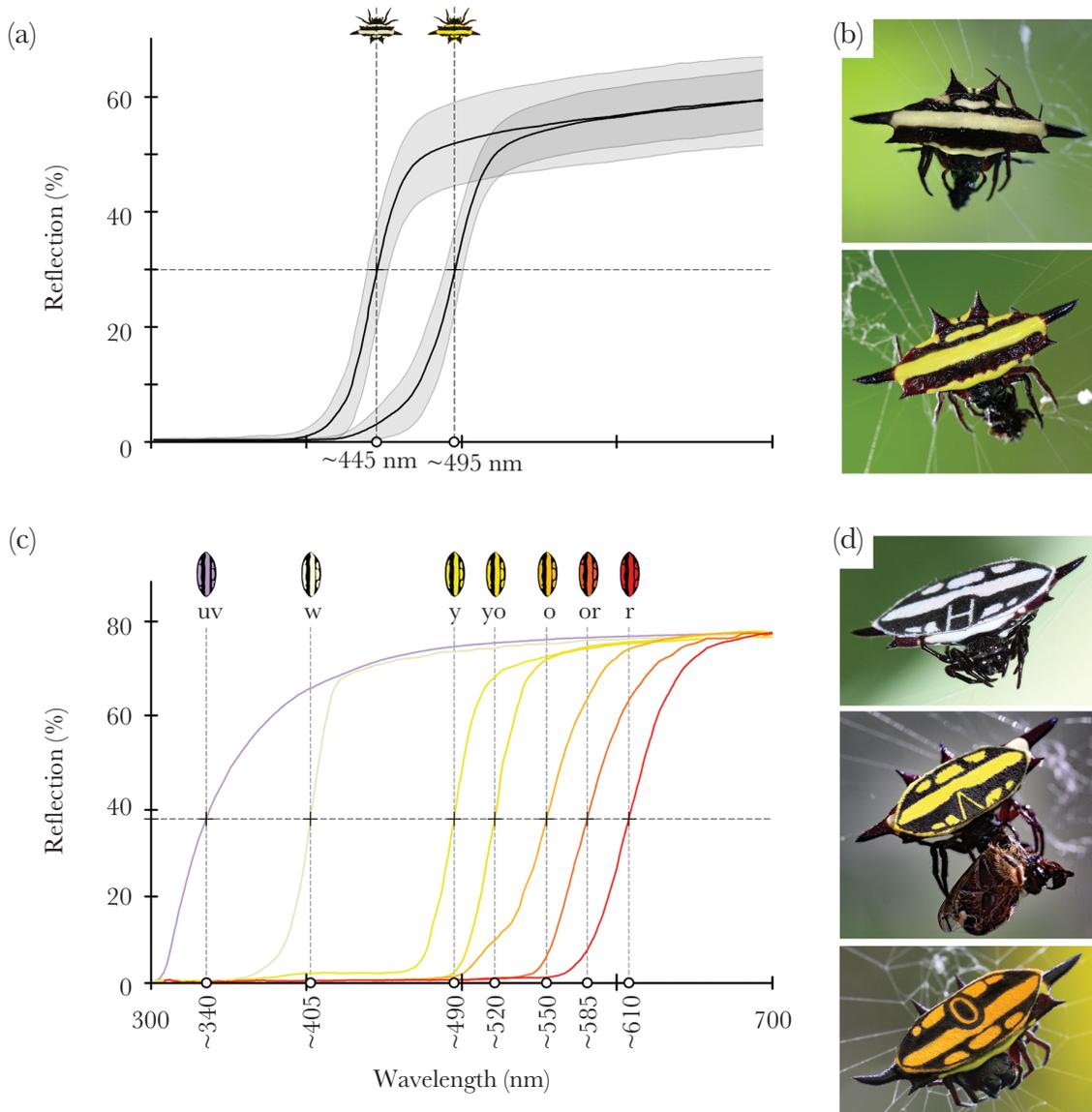


Figure 1

(a) Reflectance characteristics of the two naturally occurring female *G. formicata* phenotypes. The main traces represent averages of $n = 28$ (white) and $n = 20$ (yellow) spiders sampled from the experimental field site. Shaded areas span ± 1 standard deviation of each mean. Dashed vertical lines indicate the wavelength position of spectral inflection ($\lambda_{0.5}$) for each spider phenotype. This is the value of λ corresponding to half maximal reflectance intensity, which we use as a physical descriptor of stimulus hue; (b) Images of each color phenotype taken at the field site immediately before this experiment. A partially (extra-orally) digested prey item is visible in the chelicerae of each specimen. (c) Reflectance spectra of the seven color badges used to manipulate spider appearance. Each trace represents the average of scans taken from five different badges. Dashed vertical lines indicate values of stimulus $\lambda_{0.5}$ as described for panel a. Treatment abbreviations: uv = ultraviolet, w = white, y = yellow, yo = yellow-orange, o = orange, or = orange-red, r = red. (d) Manipulated spiders displaying white, yellow, and orange badges. Subject yellow “V” had recently caught and subdued a large prey item.

of positions across the light spectrum (Figure 1c). The justification for this approach is twofold. First, substantial color diversity in nature stems from variation to this generalized sigmoidal reflectance function (e.g., Hanley et al. 2017), and this includes *Gasteracantha* morphs across their full range of color variation (Gawryszewski and Motta 2012; White and Kemp 2015). Second, such variation is understood to arise from the spectral tuning of contributory pigment suites (Grether et al. 2004), and as such is generated by the adaptive modification of a pre-existing regulatory system. This implies the potential for high evolvability in this feature of the signal phenotype (sensu Grether et al. 2005).

Our experimental treatments equate to a manipulation of spectral inflection point (hereafter: $\lambda_{0.5}$; Figure 1d), which for most animals with three or more broadly-tuned receptor classes should be visible as variation in signal hue (and potentially in color category; sensu Caves et al. 2021). Notably, the treatments also vary systematically in overall reflectance intensity because shorter-wave positions of $\lambda_{0.5}$ allow incident light to reflect from across a greater total range of the visible spectrum. As can be seen from Figure 1c, our ultraviolet treatment would therefore reflect the greatest amount of light overall and our “red” treatment the least. This principle also holds for the natural *G. formicata* phenotypes in the sense that white

morphs (with their shorter-wave $\lambda_{0.5}$) will systematically reflect more overall light than yellow morphs. The repeated evidence for equivalent natural catch rates among the morphs (as described above) has therefore been used to argue against reflectance intensity *per se* as a fundamental driver of lure attraction (Kemp et al. 2013). We explore more nuanced possibilities regarding the relative causality of lure color and luminance in the discussion.

We evaluated the consequence of variation in stimulus $\lambda_{0.5}$ for spider catch rates overall, and in relation to the hypothesis that extant *G. formicata* phenotypes are uniquely and/or optimally attractive to prey. In its most simplified and generalizable form, this “optimal phenotype” hypothesis predicts an orderly decline in prey attraction as stimuli deviate from the $\lambda_{0.5}$ values of extant phenotypes in either direction along the spectrum (i.e., as stimulus $\lambda_{0.5} \ll 445$ nm and $\gg 495$ nm; we do not address potential catch variation between these values). This is expected to produce some form of “bell”-shaped function for prey capture across the greater domain of $\lambda_{0.5}$, with maximal capture centered around 445–495 nm. Note that a decline in attraction as $\lambda_{0.5}$ exceeds ≈ 600 nm would otherwise be expected simply because many insect groups lack a long-wave class of photoreceptor (Briscoe and Chittka 2001). Aside from this, there are limited *a-priori* grounds for predicting the precise shape or symmetry of this function, and diversity in the spectral tuning of insect vision (Briscoe and Chittka 2001) implies that innumerable potential alternatives exist (including secondary or tertiary attractiveness peaks elsewhere along the spectrum). Given however that flies are a noted constituent of *G. formicata* prey (Hauber 2002; White and Kemp 2016), we also formally tested whether capture success is better explained by variation in signal conspicuousness to a standard dipteran viewer. For this we draw on published estimates for fly-specific chromatic and achromatic background contrast (White and Kemp 2016) that are directly equivalent to our experimental stimuli, and which were collected from the very same localities that we used to assay prey capture.

Finally, as mentioned earlier, lure coloration may also potentially influence the vulnerability of orb-weavers themselves to visually-hunting predators (Craig et al. 2001; Fan et al. 2009; Ximenes and Gawryszewski 2019). In the context of this experiment, an effect of this nature could determine differential survival among treatments and manifest subsequently as variation in post-marking tenure. We take the opportunity as presented for testing this effect, albeit cautiously given that the sampling design was conceived primarily for estimating prey capture success. Experimental subjects could also go missing for reasons unrelated to predation, such as dispersal, and so post-marking tenure presents an imperfect measure of predation risk.

MATERIAL AND METHODS

Color signal manipulation

We manipulated the appearance of free-living spiders using slim adhesive badges that overlaid their flat dorsal signaling surface (Figure 1d). The badges were constructed by coating sheets of filter paper with colorfast acrylic paint (see below) and using an inkjet printer to superimpose the black banded pattern. Alphanumeric symbols were embedded within the patterning to enable subject identification. Badges were affixed by means of double-sided adhesive tape (3M corporation, North Ryde, Australia), which afforded a swift and steadfast application. It generally took <40 s to pick a spider from her web, affix the badge, then encourage her back onto a primary radial thread.

Our color treatments drew from a search of available ink/paint products which yielded six variants of a closely matched reflectance function (Figure 1c). The chosen products were all acrylic paints (Table S1, Electronic Supplementary Material). Their color likely results from a single high-pass pigment that engenders the characteristic sigmoid-shaped reflectance function seen in *G. formicata*. Unpainted filter paper was used to create a seventh treatment with a spectral inflection point deep in the ultraviolet (i.e., $\lambda_{0.5} \approx 340$ nm). Peak reflectance amplitude – that is, the y-axis value corresponding to the long-wave sigmoidal “plateau” – varied little among the treatments (Figure 1c), but was systematically $\approx 19\%$ greater than the average measured for field-sampled spiders (i.e., 78 vs. 59%; compare panels a and c of Figure 1). Because stimulus intensity is scaled log-linearly in animal vision (Dowling 1987), this 19 % linear increment equates to a difference of 0.28 log units (i.e., 4.36 vs. 4.08 log%). We have no reason to expect that such a degree of departure from natural morph appearance would bias our present test in relation to signal chromaticity.

The design of this experiment posed a trade-off between the number of different treatments versus the statistical power for detecting treatment differences. We estimated an optimal treatment number of around six to seven using informal simulations that drew on known capture effect sizes (e.g., Hauber 2002; Kemp et al. 2013). This restricted number of treatments prompted us to explore a single relevant vector of stimulus variation ($\lambda_{0.5}$ for a sigmoid-shaped spectrum) even though much wilder colors might potentially be conceived for study.

Sampling protocol

Field sampling was conducted in and adjacent to the Cairns Botanical Gardens in North Queensland, Australia (16.90°S, 145.75°E). Two bouts were undertaken, the first spanning 21–29 November 2011, and the second spanning 19 September–5 October 2012. Precisely the same protocol was used each time, with female spiders assayed along a common ~ 1500 m transect (males were not relevant for study because they are considerably smaller, not colorful, and do not forage via spinning a web). The first day of each bout was given to surveying the transect, capturing mature individuals, and applying color badges. Individuals were assigned among treatments in repeating sequential order and haphazardly with respect to locality and microhabitat. On subsequent days we walked the transect hourly between 7 am and 3 pm (following Hauber 2002) to census individual presence/absence, record prey captures, and account web status. Mature females discovered in previously overlooked locations during these censuses were recruited into the experiment if they were accessible.

We defined prey capture as a large (> 5 mm diameter) item either bound to the web in silk or (most commonly) secured and fed on at the web hub (see Figure 1b). Such prey are critical for spider fitness (Venner and Casas 2005) and are processed swiftly via a process of envenomation, binding in silk, transport to the web hub, and ingestion (Muma 1971). We nevertheless endeavored to identify capture items where possible. Web status was recorded simply as either intact or disassembled, which was necessary because spiders occur at times without any appreciable spiral capture web. Data obtained online from the Australian Bureau of Meteorology (www.bom.gov.au) were used to classify the conditions during each transect as either clear or cloudy ($>25\%$ cloud cover).

We “badged” a total of 217 spiders. Of these, 18 were unsighted thereafter and were excluded from analysis. Most of these resulted

from one of us (DJK) bungling the procedure such that individuals lost contact with their web and fell to the ground. An additional 16 badged spiders were re-sighted but did not re-establish a functional orb-web; these were used only in the analysis of spider tenure. Data collected on the remaining 183 individuals were analyzed for capture success. This dataset amounted to 3606 observations across 30 transects in 2011 and 44 transects in 2012, which reduced to 3092 observations after the removal of cases where spiders occurred without a capture web.

Reflectance spectrometry

We measured the coloration of experimental color badges and of both unmanipulated and manipulated live spiders using an Ocean Optics USB-4000 spectrometer coupled with a PX-2 pulsed xenon light source (Ocean Optics, Dunedin, Florida, USA). We used the “beam method” of spectrometry (Endler 1992, Figure 6b), whereby a collimated beam of light illuminates the sample from directly overhead (i.e., the “zenith”) and reflectance is captured by a collector probe situated at 45 degrees. The collector was focused using an Ocean Optics UV-74 lens to sample an elliptical area of the specimen surface measuring approximately 1.2×0.8 mm. Measurements were taken in a photographic dark room, with the spectrometer programmed to average ten consecutive 100 ms scans per-sample. Calibration for black was achieved by blocking all light to the capture probe, and for white using an Ocean Optics Spectralon reflectance standard. Reflectance intensity is therefore expressed in % units relative to this widely-used standard. Each calibration was performed at ca. 5-min intervals throughout the period of measurement to control for drift in the intensity of PX-2 output. Further detail on the spectrometry protocol including an illustration of the measurement suite is provided by Kemp et al. (2013).

Visual modeling

In addition to simply comparing catch rate among treatments, we drew on published data (White and Kemp 2016) to investigate whether variation in catch rate was better predicted by visual background contrast as it should appear to flies. We were able to draw on this published dataset because White and Kemp (2016) calculated the fly-specific visual contrast for a set of hypothetical spider colors which included spectra essentially identical to our experimental stimuli (refer to the Figure 1B of said paper).

Fly-subjective visual contrast was estimated as the hypothetical mean chromatic and achromatic contrast presented by each experimental color stimulus against 1072 background radiance scans. These scans were collected throughout daylight hours from positions naturally occupied by 134 different spiders ($n = 67/77$ yellow/white morphs) within tropical garden-like habitats in Cairns and Townsville. Roughly half of these involved spiders situated within the bounds of our present sampling site. An Ocean Optics Jaz portable spectrometer was used to measure background radiance. Chromatic background contrast was estimated according to the position (i.e., Euclidean distance from the achromatic midpoint) of each morph spectrum in a tetrahedral color space (Endler and Mielke 2005) parameterized for the visual phenotype of *Drosophila melanogaster*. Chromatic contrasts were taken as the unweighted distance between spiders and their visual background based on the known involvement of the dipteran R7p, R7y, R8p, R8y receptors in chromatic processing (Salcedo et al. 1999; Morante and Desplan 2008). Values for achromatic contrast were taken as the Michelson

contrast (Michelson 1927) between spiders and their backgrounds calculated under the assumption that R1-6 receptor subtypes contribute primarily to luminance perception.

Statistical analysis

We analyzed capture success via a generalized linear mixed model (GLMM) approach using ASReml software (Gilmour et al. 2015). This allowed us to estimate and partition the random variance associated with individual spider identity. Such variance was anticipated because individuals are faithful to particular transect locations which may furnish differential prey intercept rates.

Our principal analysis was leveled at the probability of capture per-individual observation. The dependent variable was therefore binary (i.e., catch/no catch) and modeled according to a logistic distribution with a binomial response distribution and log-link function. We specified fixed effects of treatment (7 levels), “native” spider phenotype (white/yellow), cloud cover (sunny/cloudy), and time (morning/midday/afternoon). Spider identity was specified as a sole random effect comprising 183 levels. An initial model run revealed that additional random terms coding for day (19 levels) and year (2011/2012) were bounded at zero and so these terms were subsequently excluded. The full model (including intercept) was overparameterized to a degree equivalent to one level for each fixed effect. ASReml accounts for overparameterization by solving the generalized inverse equation wherein singular elements – arbitrarily assigned as the first level of each fixed term – are aliased and constrained to a baseline of zero. Hence, $k - 1$ levels are formally estimated. Fixed effects were tested for significance using conditional Wald F -tests, with denominator degrees of freedom adjusted as per Kenward and Roger (1997). We inspected plots of Pearson residuals versus model-predicted values to identify potential outliers as per Sarkar et al. (2011), and referred to the slope of Log(absolute residual) versus Log(predicted value) plots to confirm the absence of variance-mean dependency (Gilmour et al. 2015). We also referred to the so-called “variance deviation factor”, an index calculated by ASReml based on the deviance of the binomial portion of the equilibrium log-likelihood value (Gilmour et al. 2015), which indicated that dispersal was within the range as expected under a binomial distribution. Residual variance is expressed in the binomial logistic model on an underlying log-link scale, so we back-transformed this to the probability (0, 1) scale where necessary by multiplying by $\pi^2/3$.

We assessed predictions for how catch success should vary among treatments by regressing observed per-treatment catch success (dependent variable) on each relevant set of predicted values (independent variables). Predicted values for this analysis under the “optimal phenotype” hypothesis were estimated as the deviation in nanometers between the values of $\lambda_{0.5}$ for each treatment and its nearest extant *G. fornicata* phenotype (hereafter, “hue deviation”). Given that our simplest *a priori* expectation was for an inverted bell-shaped (i.e., parabolic or gaussian) relationship across the absolute wavelength range, we modeled the relationship between hue deviation and capture success as a sigmoid function. This was done using the non-linear least squares fitting (NLSF) procedure of Kemmer and Keller (2010) and as detailed in Electronic Supplementary Material. Predicted values for fly-subjective chromatic and achromatic background contrast were drawn directly from the estimates published in White and Kemp (2016; as explained earlier). Observed per-group catch success was estimated by averaging the Best Linear Unbiased Predictors (BLUPs) for capture success across

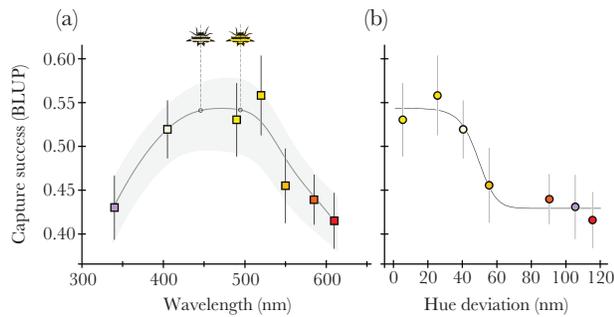


Figure 2

(a) Capture success as expressed by the mean \pm 1 s.e. of individual BLUPs (best linear unbiased predictors) for spiders in each treatment group (y-axis) plotted across the spectral range. The fitted line and shaded region are distance-weighted approximations of BLUP means and standard errors. Stylized spider images indicate the relative position of each naturally occurring phenotype along the wavelength axis. This axis is directly comparable to those in Figure 1a–b. (b) Observed capture success (y-axis; as described for panel a) plotted against hue deviation (x-axis), which represents the similarity of treatment stimuli to natural spider coloration. Hue deviation was calculated specifically as the absolute difference in nm between the $\lambda_{0.5}$ value of each stimulus and that of its nearest naturally occurring *G. formicata* phenotype. Values nearing zero indicate a closer match to either *G. formicata* morph and consequently a higher predicted catch rate under the optimal phenotype hypothesis. The data are accompanied by a best-fitting sigmoidal curve described by the equation:

the individuals within each treatment. These values were essentially identical to formal GLMM treatment estimates ($r = 0.997$) and were estimated for each group along with a measure of dispersion. We also estimated per-spider catch success using residuals from a least-squares regression of individual capture sum on number of transect observations. These estimates proved to correlate tightly with the BLUPs ($r = 0.984$) and yielded identical conclusions across all hypothesis tests; hence we limit our reporting to the latter.

Variation in the tenure of badged spiders was assessed using standard survival analysis techniques similar to those used previously for orb-weavers (Craig et al. 2001). Individuals that remained at the end of each experimental bout were accounted in this analysis as censored cases.

Means are accompanied by standard errors throughout unless otherwise specified.

RESULTS

Prey capture success

Experimental subjects caught 358 prey items at an overall rate of one capture every 11.6 web observations. Only 38 items proved identifiable and these were all insects. They consisted predominantly of dipterans (~68%) and hymenopterans (~21%), but at least 12 different insect families were represented overall (Table S3, Electronic Supplementary Material).

The GLMM indicated that our dorsal color manipulation had a significant effect on spider catch success ($F_{6,133.8} = 2.38$, $P < 0.05$; Figure 2a). There were however no effects due to native phenotype ($F_{1,136.7} = 0.100$, $P = 0.75$), time of day ($F_{2,3081} = 0.540$, $P = 0.58$) or cloud cover ($F_{1,3081} = 2.10$, $P = 0.15$), and the random “individual” term accounted for only ~4.0% of overall variance [component estimate = 0.138 ± 0.074 ; residual (scale) = $1.00 \times (\pi^2/3) = 3.29$; proportion of total = $0.138/(0.138 + 3.29) = 0.040$].

Table 1

Estimates of fly-subjective background contrast for each treatment stimulus as obtained from sensory modeling. Contrast estimates were modelled in arbitrary units and are presented here as values standardized to z-scores (i.e., $\mu = 0.0$, $\sigma = 1.0$). The “prey catch” column gives relative capture success for comparison, which was calculated by averaging the Best Linear Unbiased Predictor (BLUP) values across individuals within each treatment

Treatment	$\lambda_{0.5}$ (nm)	Fly-subjective visual contrast		
		Chromatic	Achromatic	Prey catch
Ultraviolet (uv)	340	-0.445	1.263	0.430
White (w)	405	-1.782	1.058	0.519
Yellow (y)	490	0.982	0.228	0.530
Yellow-Orange (yo)	520	0.862	-0.447	0.558
Orange (o)	550	0.771	-1.531	0.455
Orange-Red (or)	585	0.158	-0.798	0.439
Red (r)	610	-0.546	0.228	0.415

Catch variation across the full range of treatments yielded a surprisingly close fit to values predicted by the “optimal phenotype” hypothesis (least-squares sigmoidal fit: $F_{1,6} = 506.9$, $P < 0.001$, $R^2 = 0.964$; Figure 2b). Prey attraction, therefore, scaled according to how closely each stimulus resembled either of the two naturally-occurring *G. formicata* colors, and appeared categorically highest in the white, yellow, and yellow-orange treatment groups. Likewise, the data indicate a graded decline in catch rate across treatments ranging from yellow-orange to red (i.e., $yo > o > or > r$). This covaries inversely with their graded increase in $\lambda_{0.5}$ and hence their extent of visual deviation from *G. formicata*. The overall representation of catch success as a continuous function of $\lambda_{0.5}$ generated a “bell”-shaped profile of the nature anticipated for this scenario (Figure 2a).

Conversely, predictions based on fly-subjective background contrast (Table 1) proved not only as a less accurate fit for the observed data, but in fact explained negligible among-treatment variation (regressions of catch rate against fly-predicted chromatic contrast: $F_{1,5} = 0.28$, $P = 0.62$, $R^2 = 0.053$; achromatic contrast $F_{1,5} = 0.006$, $P = 0.94$, $R^2 = 0.001$). Tentative post-hoc exploration in light of this outcome revealed no fundamental improvement in a model comprising the linear combination of both chromatic and achromatic contrast ($F_{2,4} = 0.27$, $P = 0.76$, $R^2 = 0.12$). Variation in capture rate across the different treatments was therefore not readily explainable based on their (predicted) visual conspicuousness to flies.

Spider tenure

Badged spiders were re-sighted on between one and 47 census occasions at an average of 21.3 ± 0.96 subsequent sightings per individual. This equated in raw terms to an average tenure of 67.8 daylight hours (5.65 days), which is an underestimate because more than half of the test subjects ($n = 98$ of 194 total) remained present at the completion of sampling. Survival analysis found no tenure difference due to color treatment ($\chi^2_6 = 2.31$, $P = 0.889$) or native color phenotype (Gehan’s Wilcoxon $W = 0.669$, $P = 0.504$), and there was no difference among sampling years ($W = -0.998$, $P = 0.318$).

DISCUSSION

The colorful prey attractant markings of Araneid spiders present a fascinating and in many ways novel source of animal

color diversity. Tropical to subtropical members of the genera *Actinacantha*, *Gasteracantha*, and *Macracantha* (and their allies) are distinguished even within this group by their abstract dorsal patterns comprising highly saturated color displays that are often polymorphic (Levi 1978; White and Kemp 2015; Tan et al. 2019). These traits provide opportunities for testing theory at the interface of sensory ecology and polymorphic trait evolution (White and Kemp 2015). Empirical efforts to do so (e.g., Rao et al. 2015; White and Kemp 2016; Ximenes and Gawryszewski 2019, 2020) have however been ultimately challenged by the highly diverse nature of the viewing audience. In this study, we assess the prey attractant value of color variation directly and for the greater community of insects that spiders could potentially catch. The results provide, to our knowledge, the first conclusive demonstration that variation in spectral quality per-se is causally responsible for the attractiveness of an orb-weaver lure. Elegant prior experiments in this group (Craig and Ebert 1994; Hauber 2002; Bush et al. 2008) have established the importance of displaying a signal that includes color, but we demonstrate differential attractiveness among categorically equivalent stimuli that vary in a common feature of chromaticity (as well as luminance, as discussed below). In doing so, we also provide evidence that naturally occurring *G. formicata* phenotypes reside in an optimal spectral range for aggregate prey attraction. These findings are discussed along with inferences that arise for understanding prey lures and color signals more generally.

Our first and most elementary conclusion is that spectral property has a direct, causal influence on capture success. This is entirely consistent with Hauber's (2002) classic demonstration of prey-attractant function for the dorsal bands (or the banded pattern), which he established by studying a geographically distinct lowland rainforest population. It is likewise consistent with laboratory-based findings (White and Kemp 2017) for the attractiveness of each extant *G. formicata* phenotype to naïve dipteran viewers. An important point is that the present data describe the aggregate of species caught from across the prey community. Accordingly, whereas we demonstrate interception rate as a function of lure color, it need not follow that all captured species perceived this feature equivalently or were even necessarily attracted by it. Differential treatment attraction should be a function of all the ways that spider appearance stimulated prey vision and perception. This encompasses a potentially exclusive role for overall reflectance intensity (i.e., achromatic signal quality) in the attraction of some species. By the same token, this feature cannot by itself account for the observed catch profile across treatments. Stimulus intensity scales inversely with treatment $\lambda_{0.5}$; hence, if this were the critical determinant then we should expect a steady decline in catch across the spectral range (from ultraviolet to red), which was clearly not the case (Figure 2a). One caveat is that different animals perceive stimulus intensity in different ways depending largely on the spectral sensitivity of photoreceptors involved in their achromatic channel (Osorio and Vorobyev 2005). However, even species such as bees that rely exclusively on long-wave intensity reception should have perceived our short-wave stimuli as highly luminous (and theoretically equiluminant to yellow, orange, etc.). Flies on the other hand should have clearly perceived the ultraviolet stimulus as most luminous because they are thought to judge this using short visual fiber (SVF) receptors which are maximally sensitive between 300 and 400 nm (Hardie 1986). Color perception, therefore, stands as the most logically consistent explanation for differential treatment capture in these groups and indeed probably most insects attracted by the lure stimuli.

Further, in regard to flies, we found categorically nil support for predictions based on stimulus background contrast under a dipteran visual model. We tested for this because flies are expected to constitute most prey (Hauber 2002; White and Kemp 2016; White 2017), which was in fact borne out by the captures that we could identify. There are two potential explanations to consider. The first is simply that the visual model may not accurately represent how an aggregate diversity of dipteran prey perceive visual contrast or detect colorful stimuli (either overall, or under “visually noisy” field conditions). Relevant to this, modeling was based on putatively representative parameters derived in *Drosophila* (White and Kemp 2016), yet identifiable prey spanned five dipteran families and included a large contribution from the primitive families Tipulidae and Bibionidae. There is little direct information on vision (let alone perception) in these families (Lunau 2014). Modeling error may also arise from the use of generalized estimates/envelopes to approximate features of the visual environment (e.g., ambient illumination and background properties). Second, each stimulus may have appeared as predicted yet flies were simply not attracted by greater conspicuousness. There need not be an automatic relationship between conspicuousness and attraction because whereas the former deals with detectability, the latter relies on motivation to visit or inspect a stimulus more closely. Pollinators are for example motivated to seek floral rewards, in which case background contrast would prove beneficial for lures that operate by mimicking the appearance of flowers. The same could apply if lures stimulate an innate phototactic response, but it is unclear how either source of motivation is represented among the dipteran prey of *G. formicata*. Greater color conspicuousness would otherwise simply mean that spiders are more easily detected but ignored. It could even lower catch rates by allowing individuals to more readily classify lures as non-profitable or hazardous (Bush et al. 2008). Regardless of explanation, the lack of explanatory power based on fly vision raises questions about if and when visual modeling is appropriate for stimuli that are viewed by an aggregate audience (see further below).

Our second principal conclusion is that natural *G. formicata* phenotypes exist in a region of the spectrum that is optimal for prey capture. We infer this from the statistical result (Figure 2b), but it can also be seen by the $\lambda_{0.5}$ position of each spider phenotype in relation to the spectral profile of catch success (Figure 2a). Obviously, this is not a basis for concluding optimality in relation to all potential alternatives. We however view the present inference reasonable and biologically relevant given that our approach to signal manipulation was inspired by the nature of extant signal variation in *G. formicata*. It is also the case that available spectral reflectance data for orb-weaver lures (Gawryszewski and Motta 2012) indicate strong conservatism of the sigmoidal-shaped function despite considerable spectral variation. This matches what should be expected if color variation arises from differences among suites of pigments situated on a highly reflective substrate, such as crystalline guanine (Oxford and Gillespie 1998). Pigment suites are known to be highly tunable within and across different animal species (e.g., Watt and Bowden 1966, Grether et al. 2005), which – as noted earlier – argues for evolutionary lability in this axis of color variation.

Following from this, we expressed catch success across the domain of $\lambda_{0.5}$ to generate a “prey attractiveness function” analogous to the preference functions used in mate choice studies (Edward 2015). The curve was approximated simply by a distance-weighted fit (\pm standard error) to sampled $\lambda_{0.5}$ points, and therefore involves a degree of extrapolation. The strongly autocorrelated nature of spectral data (Endler and Mielke 2005) offers some latitude

for this, but the margin for extrapolation error is nevertheless reduced where points are more closely spaced (for the present case: $\lambda_{0.5} > 490$ nm). Presently we consider the exercise largely heuristic in value. Such functions would however allow a more comprehensive account of prey attractiveness for different polymorphic phenotypes, populations, and species, or across different locations or time points (Craig and Ebert 1994). Were more data available, one may even be able to generate predictions for how hypothetical color variants or ranges of variation should influence catch success, which may have utility for interpreting polymorphism. For *G. formicata*, more intensive sampling of catch success at and around the spectral positions of each extant phenotype (i.e., $450 > \lambda_{0.5} < 500$ nm) should prove highly informative. Unique insight into the maintenance of these discrete alternatives could then come from testing if aggregate catch is equivalent among them and whether it may in fact decline across their intervening range.

Our data indicate a sharp decline in the prey attractiveness of “longer-wave” colors (i.e., deep oranges and reds) and the same for the “short-wave” ultraviolet stimulus (Figure 2). It is therefore curious to note that our entire range of manipulated hue variation is actually represented among the body colors of different extant orb-weaver species. Multiple colors within this range in fact often constitute the key feature of discrete polymorphisms in *Gasteracantha* and allied genera. This includes, for example, the alternatively red/orange/yellow forms reported for *Gasteracantha hasselli* and *Macracantha arcuate* (Tan et al. 2019), the white/yellow forms of *G. diardi* (Tan et al. 2019) (and many other species), and the full complement of forms spanning ultraviolet-white to white, yellow, orange and red in the neotropical species *G. cancriformis* (Muma 1971; Levi 1996; Gawryszewski and Motta 2012). Although such reports are expressed largely in terms of human-subjective hue, it seems likely that colors similar to our most “underperforming” *G. formicata* treatments (i.e., ultraviolet/orange/red) function as viable attractant stimuli elsewhere across the group. This is in fact verifiably true for *G. quadrispinosa*, a polymorphic species with dorsal orange and red lure phenotypes (White and Kemp 2015). Intriguingly, this species co-occurs with *G. formicata* in largely undisturbed rainforest habitats of North Queensland (albeit not at the study site used for this experiment). The existence of disparate hue variants across the broader group may echo common assertions (Craig and Ebert 1994) for how lure design should be adaptively tuned for local prey communities. In cases where highly divergent lure color schemes exist in the same localities and even the same habitats – as in *G. formicata/quadrispinosa* – the key to their co-existence may reside in fine-scale microhabitat partitioning and/or prey specialization. Such possibilities pose interesting avenues for future investigation. The present findings also add interest to the exploration of how attractiveness scales with finer-scale variation around and between the spectral position of each extant *G. formicata* color morph.

On a final note, we see value in underscoring one salient implication for the broader study of animal coloration. This relates to the stark discrepancy between expectation based on visual modeling and observation as given by real-world capture data. Our application of visual modeling incorporated logical and procedural assumptions of a nature typified by many applications of this approach across the literature. As we note earlier, these assumptions are that flies constitute most of the prey items captured by *G. formicata*, and that visual perception across this group are approximated by parameters derived from well-studied exemplar species (principally *Drosophila*; Salcedo et al. 1999; Morante and Desplan 2008). Similar assumptions are widespread, and may (should) be

stated explicitly, but they are also frequently implicit in the choice of a sole putatively “primary” viewer for which conclusions are subsequently generalized. We can point to examples from our own work on *G. formicata* in this regard (e.g., White and Kemp 2015, 2016). The present data however demonstrate a scenario whereby visual modeling yields a highly misleading view of the relationship between spectral variation and ecological outcomes in the wild. This was not entirely unexpected given the diverse and unpredictable prey complement of *G. formicata*. We nevertheless pose this finding as a cautionary tale for how sensory modeling may sometimes yield solutions akin to working hypotheses, and which stand for validation against the ultimate yardstick of real-world animal behavior.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at *Behavioral Ecology* online.

$$y = 0.427 + \frac{0.116}{1 + 10^{7.95*(\text{Log}_{10}(x) - \text{Log}_{10}(47.40))}}$$

Graphed points are color-coded for treatment identity in both panels and correspond to those indicated in Figure 1b.

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Data Availability: Analyses reported in this article can be reproduced using the data provided by Kemp et al. (2022).

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