

The perceptual similarity of orb-spider prey lures and flower colours

Thomas E. White¹ · Rhiannon L. Dalrymple^{1,2} ·
Marie E. Herberstein¹ · Darrell J. Kemp¹

Received: 3 May 2016 / Accepted: 15 November 2016
© Springer International Publishing Switzerland 2016

Abstract Receiver biases offer opportunities for the evolution of deception in signalling systems. Many spiders use conspicuous body colouration to lure prey, yet the perceptual basis of such deception remains largely unknown. Here we use knowledge of visual perception in key pollinator groups (bees and flies) to test whether colour-based lures resemble floral signals. We addressed this question at two levels: first according to the spectral reflectance of Australian orb-web spiders and flowers across a broad continental range, and second in reference to polymorphic variation in the species *Gasteracantha fornicata*. Analysis at the community level supported the hypotheses for broad-scale convergence among spider and flower signals. Moreover, data for *G. fornicata* indicate that each lure morph presents a signal biased towards the colouration of sympatric flowers. This analysis identified fly- and/or bee-pollinated plants whose flowers are likely to be indistinguishable from each *G. fornicata* colour morph. Our findings support the hypothesis that deceptive colour-based lures exploit prey preferences for floral resources. Further, the evidence implies a greater role for specific model/mimic relationships over generalised resemblance to flower-like stimuli as a driver of lure colouration and diversity.

Keywords Deception · Communication · Signal · Predation · Flower · Spider · Mimicry

Electronic supplementary material The online version of this article (doi:10.1007/s10682-016-9876-x) contains supplementary material, which is available to authorized users.

✉ Thomas E. White
thomas.white@mq.edu.au

¹ Department of Biological Science, Macquarie University, Sydney, NSW 2109, Australia

² Evolution and Ecology Research Centre, School of Biological, Earth, and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

Introduction

Animals receive and process information using sensory and perceptual systems that have evolved in response to a suite of often competing demands, such as speed versus accuracy (Skorupski et al. 2006; Warrant 2008; Chittka et al. 2009), and energetic cost versus performance (Ames 2000; Niven et al. 2007; Moran et al. 2015). These constraints inevitably produce biases, which have fundamentally shaped the evolution of communication systems (Christy 1995; Endler and Basolo 1998; Ryan and Cummings 2013). Our understanding of the relationship between sensory biases and signal evolution is particularly well developed with respect to visual sexual signals, in which innate colour preferences and receptor tuning to environments, for example, are known to have driven the evolution of male sexual signals towards colours that best stimulate female visual systems (e.g. Burley and Symanski 1998; Cummings 2007). Coevolution between signal designs and receiver sensory systems has also driven signal diversification, including polymorphism, though this too has been largely studied in the context of sexual communication (Fuller 2002; Leal and Fleishman 2002; Stuart-Fox et al. 2007).

Biases in sensory perception offer evolutionary opportunities for deception. Cryptic prey species may exploit the edge detection mechanisms of predators by using bold internal colour patterns, thereby creating ‘false’ edges that inhibit the formation of effective search images (Stevens et al. 2006). Similarly, predators may induce maladaptive responses in prey using signals that exploit innate sensory preferences (Heiling and Herberstein 2004; Herberstein et al. 2009), or by mimicking otherwise rewarding stimuli (Gaskett et al. 2008; Gaskett and Herberstein 2010; O’Hanlon et al. 2014a, b). Sit-and-wait predators, particularly orb-web spiders, are an exemplar group of deceptive signalling animals that often use conspicuous colouration to visually attract prey (Herberstein et al. 2000; White and Kemp 2015). Such ‘lures’ typically adorn the webs or bodies of predators, and actively increase the rate at which they capture visually-guided taxa (e.g. Diptera and Hymenoptera) above background levels (Hauber 2002; Tso et al. 2002; Bush et al. 2008; Peng et al. 2013; Rao et al. 2015). Although the attractant function of these signals is well documented, the ultimate basis of their attractiveness, that is, the sensory and/or perceptual pathways they have evolved to exploit in receivers, remain unclear.

Receiver-bias models have proven valuable for explaining the adaptive basis of signal design (Christy 1995; Christy and Backwell 1995; Endler and Basolo 1998). They emphasise the factors shaping the evolution of signal efficacy, as opposed to signal content. Such factors encompass biases that arise as emergent properties of sensory system construction (like the latent preference for white crests in Australian Grassfinches; Burley and Symanski 1998), and neural biases that evolved adaptively in unrelated contexts (as in the sand hoods of male fiddler crabs; Christy et al. 2003a, b). Colour based lures, in a general sense, are thought to attract prey because they are mistaken for something they are not, such as a food source or simply an object of potential interest (White and Kemp 2015). The principles of such models thus offer a guiding framework for examining the basis of lure attractiveness, and a route to understanding the drivers of the considerable diversity in this class of signal, both at inter-specific (e.g. Hoese et al. 2006; Tso et al. 2006; Rao et al. 2015) and intra-specific levels (e.g. Levi 1978; Tso et al. 2002; Kemp et al. 2013; Rao et al. 2015). Recent work using the colour polymorphic orb-web spider *Gasteracantha fornicata* suggested that simple conspicuousness is key to lure attractiveness, and that morphs may be discretely tuned to maximise colour and luminance contrast in visually noisy environments (White and Kemp 2016). While the conspicuousness of colour-based lures is crucial, a non-

exclusive hypothesis is that they have evolved to exploit prey preferences for floral colour signals. Under this hypothesis, diversity in lure colours may be driven, in part, by the spatial and/or temporal matching of multiple flower ‘models’ (Christy 1995; White and Kemp 2015). Although generally acknowledged, (Tso et al. 2004, 2006; Chiao et al. 2009), this hypothesis remains to be directly examined (reviewed in White and Kemp 2015).

Here we explored the basis of lure attractiveness by testing whether, and to what degree, colour based lures resemble sympatric flowers from the perspective of relevant receivers. Using data on inter- and intra-specific colour variation in Australian orb spiders, and an extensive floral reflectance dataset, we pursued two specific aims:

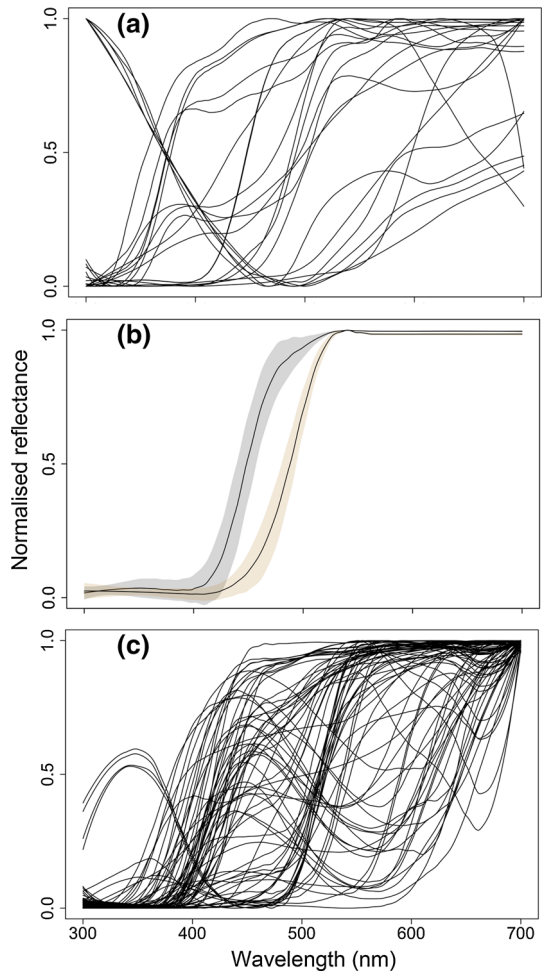
- (i) At the most general level, we aimed to test whether colour-based lures resemble sympatric flowers to relevant receivers. If the attractiveness of these signals is attributable, in part, to their resemblance to flowers, then the colour signals of predators and sympatric flowers should broadly overlap in the perceptual space of receivers (though this may also result from independent convergence upon a common signal structure; see discussion). If, in contrast, the attractiveness of lures is unrelated to their similarity to flowers and are targeting more general biases, such as simple detectability (White and Kemp 2016), then we expect no structured relationship—that is, minimal correspondence in colour space—between the signals of predators and flowers per se (Christy 1995; White and Kemp 2015).
- (ii) Following the results of (i), we aimed to distinguish between two further, alternate hypotheses. The first is that colour-based signals of predators may benefit from only a generalised resemblance to flowers. Common pollinators such as honeybees, for example, are known to prioritise colour cues when foraging, and to generalise learned colour information (depending on individual experience and viewing context; Dyer and Chittka 2004a, b; Avarguès-Weber et al. 2010). This may offer a suitably broad perceptual target such that lures are effective when presenting only an approximately similar signal. An alternative possibility is that the signals of predators have evolved to mimic one or more particular floral species. This would predict that the signals of a given lure and its putative floral model(s) should target the same receivers, and should be essentially indistinguishable to the intended viewers. We outline our specific predictions in greater detail below.

Methods

Spider reflectance

In interspecific analyses, we used spectral reflectance data from 10 Australian spider species that are either known or are hypothesised to use colour as a deceptive visual signal. Some species have multiple colour elements and/or morphs, which we included separately in the analyses, totalling 15 average reflectance spectra. The data are a combination of spectra collected by the authors (using the procedure outlined below), and mean reflectance spectra extracted from published literature using the R package digitize (Fig. 1a; Poisot 2011). The species included are: *Gasteracantha fornicata*, *Gasteracantha quadrispinosa*, *Gasteracantha sacerdotalis*, *Micrathena gracilis*, *Argiope aetherea*, *Neoscona punctigera* (Chuang et al. 2008), *Nephila pilipes* (Tso et al. 2004), *Leucage magnifica* (Tso et al. 2006), *Cryptophora moluccensis* (Blamires et al. 2014), and *Argiope keyserlingi* (Hoese et al. 2006).

Fig. 1 **a** The mean reflectance of 15 colour patches from 10 Australian spider species whose colours are known or hypothesised to act as visual lures. Included are *Gasteracantha fornicata*, *G. quadrispinosa*, *G. sacerdotalis*, *Micrathena gracilis*, *Argiope aetherea*, *Neoscona punctigera*, *Nephila pilipes*, *Leucage magnifica*, *Cryptophora moluccensis*, and *Argiope keyserlingi*. **b** Aggregated reflectance spectra (mean \pm SD) of female *G. fornicata* ($n = 80$ ‘yellow’ yellow line, 44 ‘white’ grey line) collected in North Queensland, Australia. Reproduced in part from White and Kemp (2016). **c** The mean reflectance of 62 species of angiosperm collected from Cairns, Australia, whose distributions overlap *G. fornicata*. (Color figure online)



For our intraspecific analyses of the colour-polymorphic *Gasteracantha fornicata*, we used the reflectance spectra of 80 ‘yellow’ and 44 ‘white’ individuals (Fig. 1b, as described in White and Kemp 2016). Briefly, we measured reflectance using a JAZ EL-200 portable spectrometer (integration time = 100 ms, boxcar width = 10, averaged scans = 10) via OceanOptics SpectraSuite software (ver. 1.6.0_11), coupled with a PX-2 pulsed xenon light source and 500 μ m optical probes (with the light source and probe set at 90° and 45°, respectively; White et al. 2015). We recorded and averaged reflectance from a 5 mm area either side of the spider’s central dorsal band (i.e. the largest coloured band running perpendicular to the spiders body axis; Fig. 6), and recalibrated the spectrometer between each individual using a 99% diffuse ‘spectralon’ reflectance standard (Labsphere, New Hampshire). We used live spiders, which we cooled in a refrigerator at $4^\circ \pm 1^\circ$ for approximately 5 min immediately prior to measurement. We binned all spectra at 1 nm wavelength intervals, and applied minor LOESS smoothing ($\alpha = 0.15$) to remove noise. All post-capture spectral processing and visual modelling (detailed below, and in the

supplementary methods) was done using R (ver. 3.2.1; R Core Team 2014), primarily with the R package ‘pavo’ (v1.0; Maia et al. 2013).

Flower reflectance

We drew on the floral reflectance data of Dalrymple et al. (2015), which consist of reflectance spectra from 339 species of native Australian flowering plants, spanning a latitudinal gradient from Cairns, Queensland to southern Tasmania (Fig. 1c). Reflectance was recorded from at least three flowers on distinct individuals, in a process similar to that outlined above for *G. fornicata* (full details in Appendix 1 of Dalrymple et al. 2015). Flower sampling was designed to target the dominant colours of a given perianth, showy bract, or display stamen, and excluded endangered species or those with ontogenetic colour variation. The flowers of some species contain more than one dominant colour patch, which are included separately in our analyses (totaling 461 species-level spectra). As indicated below, for our interspecific, community-based analyses we averaged replicate floral reflectance spectra within species. For our intraspecific, individual-level analyses, we included all spectra from distinct individuals. We otherwise processed the flower data as outlined above.

Visual modelling

Previous work has shown that pollinating Diptera (particularly Tephritidae and Drosophilidae) and Hymenoptera are the dominant prey items of *G. fornicata* (Hauber 2002; White and Kemp 2016), and are a common target of luring spider species more broadly (Heiling and Herberstein 2004; Herberstein et al. 2009; Blamires et al. 2014). We therefore used a combination of visual models representative of dipteran and hymenopteran viewers.

Diptera

There is currently no well-established model of dipteran colour vision (in contrast, for example, to the Hymenoptera; Chittka 1992). We therefore used two models, both of which draw ultimately on knowledge gained from *Drosophila melanogaster* and the blowfly *Lucilia* sp. (though we use the photoreceptor sensitivities of *D. melanogaster* for all dipteran models; opsin λ_{\max} : R7p = 345 nm, R7y = 375 nm, R8p = 437 nm, R8y = 508 nm, where ‘p’ and ‘y’ indicate ‘pale’ and ‘yellow’ photoreceptors subtypes; Salcedo et al. 1999). First, we used the categorical colour vision model of Troje (1993). This model assumes the involvement of all four photoreceptor classes (Morante and Desplan 2008), and further posits that colour vision is based on two specific opponent mechanisms (R7p–R8p, and R7y–R8y). Based on behavioural data from *Lucilia* sp. (Troje 1993) the model predicts that colours are perceptually grouped into one of four colour categories, and that flies are unable to distinguish between colours that fall within the same category. To calculate the location of spider and flower colours in the categorical model, we first estimated photoreceptor quantum catch (Q) in receptor *i* as

$$Q_i = \int_{300}^{700} R(\lambda)I(\lambda)S_i(\lambda)d\lambda \quad (1)$$

where *R* is the spectral reflectance of an object, *I* is the illuminating spectrum, and *S_i* is the spectral sensitivity of photoreceptor *i*. Here, and throughout all models, the illuminating spectrum for spiders is taken to be the mean of 1072 illuminating irradiance spectra

recorded in the tropical forest habitats of *G. fornicata* in a previous study (White and Kemp 2016), whereas the illuminating spectrum for flowers is D65 daylight (sensu Chittka 1992). We then calculated the difference in relative stimulation between the ‘pale’ (R7p–R8p) and ‘yellow’ (R7y–R8y) photoreceptor pairs. The signs of these differences together define the four possible fly-colour categories (p+y+, p–y+, p+y–, p–y–; Troje 1993).

The categorical model is limited in that it has been independently verified only once (Fukushi 1994; with minimal consideration of alternative models; Lunau 2014), and subsequent behavioural studies have demonstrated that several fly species, including *D. melanogaster*, can apparently discriminate colours that fall within the categories of Troje’s model (e.g. Sutherland et al. 1999; Brembs and de Ibarra 2006; Yamaguchi et al. 2010). Importantly, for reasons detailed below, this model cannot account for the *degree* of difference between stimuli due to its grouping of stimuli into broad colour categories. We therefore also used a tetrahedral model of dipteran colour vision (sensu Brembs and de Ibarra 2006; Kelly and Gaskett 2014; Renoult et al. 2014; White and Kemp 2016). Such a model assumes that all four photoreceptor types are involved in drosophilid colour vision, as supported by physiological and behavioural evidence (Morante and Desplan 2008), and estimates the colour information available to dipteran viewers at the earliest stage of photoreception. The model makes minimal assumptions about subsequent neural processing of colour information, such as opponency mechanisms or colour categorization (Kemp et al. 2015). To calculate the location of spider and flower colours in the tetrahedron, we first estimated quantum catches as per Eq. (1), before log transforming them in accordance with the Weber-Fechner law (Vorobyev et al. 2001; Endler and Mielke 2005)

$$q_i = \log Q_i \quad (2)$$

We converted each set of catches to relative values, and calculated the location of each stimulus in a tetrahedral space (Endler and Mielke 2005) as

$$\begin{aligned} x &= \sqrt{\frac{3}{2}} \frac{1 - 2s - m - u}{2} \\ y &= \frac{-1 + 3m + u}{2\sqrt{2}} \\ z &= u - \frac{1}{4} \end{aligned} \quad (3)$$

where u , s , m , and l refer to the log-transformed quantum catch values for *D. melanogaster*’s R7p, R7y, R8p, and R8y photoreceptors, respectively.

We used the log-linear receptor-noise limited model (Vorobyev et al. 2001) to estimate the discriminability of individual spiders and flowers from the perspective of dipteran receivers (for reasons outlined in section ii, below). This model estimates the visual distance between colour stimuli in units of ‘just noticeable differences’ (JND’s). Quantum catches were modeled as per Eqs. (1)–(2), and the distances between stimuli in a tetrahedral space was estimated as

$$\Delta S = \sqrt{\frac{(e_1 e_2)^2 (\Delta f_4 - \Delta f_3)^2 + (e_1 e_3)^2 (\Delta f_4 - \Delta f_2)^2 + (e_1 e_4)^2 (\Delta f_3 - \Delta f_2)^2 + (e_2 e_3)^2 (\Delta f_4 - \Delta f_1)^2 + (e_2 e_4)^2 (\Delta f_3 - \Delta f_1)^2 + (e_3 e_4)^2 (\Delta f_2 - \Delta f_1)^2}{(e_1 e_2 e_3)^2 + (e_1 e_2 e_4)^2 + (e_1 e_3 e_4)^2 + (e_2 e_3 e_4)^2}} \quad (4)$$

where e_i is the ‘neural’ noise for receptor i assuming a Weber fraction of 0.1 (Brembs and de Ibarra 2006) and a relative photoreceptor density of 1:2.2, pale:yellow (Kirschfeld et al.

1978). Δf_i is the natural log ratio of the quantum catches for photoreceptor i when viewing spider and flower colours. Under ideal laboratory conditions the receptor noise model predicts that stimuli one JND apart may, on average, be reliably discriminated (Vorobyev and Osorio 1998; Vorobyev et al. 2001). We used a conservative range of 1–4 JND's as an indicative set of distances within which stimuli are predicted to be difficult to distinguish by dipteran viewers in natural settings (though this should be considered tentative).

Hymenoptera

We used the hexagon colour space (Chittka 1992) to explore the relationship between flower and spider colours considering a hymenopteran visual system. The colour hexagon is broadly applicable across hymenopteran species because the photopigments underlying trichromatic vision in Hymenoptera—including native Australian taxa—appear to be highly conserved (Chittka 1992; Briscoe and Chittka 2001). Importantly, distances across the hexagon have been validated against behaviour, and applied to address comparable questions about hymenopteran colour vision (Chittka 1992; Dyer et al. 2008; Avarguès-Weber et al. 2010; Morawetz et al. 2013; Spaethe et al. 2014). Extensive psychophysics work indicates that Euclidean distances within the hexagon model offer a reliable measure of perceptual distance (Chittka 1992; e.g. Dyer et al. 2008; Avarguès-Weber et al. 2010; Morawetz et al. 2013; Spaethe et al. 2014). In general, distances <0.04 fall below the discrimination threshold, those between 0.04 and 0.11 can only be discriminated following differential conditioning, and distances above 0.11 can be reliably discriminated with only absolute conditioning (Chittka et al. 2003; Dyer and Chittka 2004b; Dyer and Neumeyer 2005; Avarguès-Weber et al. 2010). We used the spectral sensitivity of *Apis mellifera* (opsin $\lambda_{\max} = 340, 440, 536$ nm; Briscoe and Chittka 2001) as modeled according to a vitamin A1 template (Govardovskii et al. 2000). In the hexagon space, the relative amount of radiation absorbed by each photoreceptor (i.e. quantum catch) is calculated as

$$P_i = K \int_{300}^{700} R(\lambda)I(\lambda)S_i(\lambda)d\lambda \quad (5)$$

where R is the spectral reflectance of an object, I is the illuminating spectrum, and S_i is the spectral sensitivity of photoreceptor i . K is an adaptation coefficient that models photoreceptor adaptation (i.e. von Kries adaptation) to the typical viewing background (taken to be a green foliage background) as per:

$$K = \frac{1}{\int_{300}^{700} R_{bkg}(\lambda)I(\lambda)S_i(\lambda)d\lambda} \quad (6)$$

We then converted photoreceptor stimulation values to neural excitations using the hyperbolic transform

$$E_i = \frac{P_i}{P_i + 1} \quad (7)$$

where P_i is the photon flux in receptor i , before calculating the location of stimuli in the hexagon as

$$x = \frac{\sqrt{3}}{2(E_g + E_{uv})} \quad (8)$$

$$y = E_b - 0.5(E_{uv} + E_g)$$

where E_{uv} , E_b , and E_g refer to the excitation values for *A. mellifera*'s 'ultraviolet', 'blue', and 'green' sensitive photoreceptors.

(i) Is there a link between lure and flower colour signals?

We tested for a link between spider lure (both inter- and intraspecific) and flower colour signals using analogous measures of sensory 'overlap' estimated according to the three models outlined above. In the categorical dipteran model, predicted perceptual overlap is characterised by the co-occurrence of points in the same colour category (Troje 1993). In the tetrahedral dipteran model, we calculated the exact volume of overlap between spider and flower colour loci, which has been shown to be a useful index of similarity in mimicry systems (Stoddard and Stevens 2011). Specifically, we divided the volume of the overlap between spiders and flowers by the volume of the smaller of the two, converted to a percentage. A value of 100 thus indicates that one set of points is entirely contained within the other, while a value of zero indicates that the sets of points do not intersect. Finally, in the hymenopteran colour hexagon, we calculated the frequency distribution of flower and lure colours across a radial grid of 108 sectors that dissect the hexagon (Chittka et al. 1994; Dyer et al. 2012). We then examined the distribution of stimuli across the five 'bee-hue' sectors (UV, UV-blue, blue, blue-green, green, and UV-green; Chittka et al. 1994).

If lures have evolved to resemble sympatric flower, we predict strong overlap between the two sets of points within the framework of each model. In the categorical space, lures and flowers should fall within the same colour category. In the tetrahedron, the convex hulls of lures and flowers should strongly overlap (ca. >80%). Finally, in the hexagon space, individuals should be similarly distributed, with co-incident peaks in the same bee-hue sector. If colour-based lures have not been selected to resemble flowers, and have—for example—been favoured for their detectional properties (White and Kemp 2016), then we do not expect these patterns of overlap *per se*. This follows from the fact that there are numerous, equivalent ways to maximise detectability and/or stimulate a given visual system (e.g. colours that fall near any one of the vertices of the hexagon are predicted to stimulate the honeybee visual systems roughly equally; Chittka 1992).

(ii) Do lures show a generalised or specific resemblance to flowers?

Following the results of (i) above, we examined the corollary question of whether lures may present either a generalised or specific resemblance to sympatric flowers. That is, the degree to which lures resembled sympatric flowers at an intraspecific level. Here we restricted our analyses to the finer-scale data from the colour polymorphic tropical species *G. fornicata*. We tested two predictions. First, if lures are mimicking particular flowers, we predicted that spiders should be equally or more similar to sympatric (far-north Queensland, Australia) as opposed to allopatric flowers. To test this, we used a randomisation procedure to estimate the similarity of spiders to sympatric versus allopatric flower communities, from the perspective of dipteran and hymenopteran viewers. For a given 'run', we randomly selected 40 reflectance spectra from both *G. fornicata* morphs, and 40 floral reflectance spectra from Australian angiosperms sampled in each of Cairns (where *G. fornicata* co-occur), Brisbane, Melbourne, and Tasmania, Australia. We then calculated the mean distance between every spider-flower pair within a location (in JND's in the tetrahedron for dipteran viewers, and Euclidean distances in the hexagon for hymenopteran viewers) and retained the minimum of these values. We retain the minimum of all values within a location because a mimicry hypothesis predicts that the lures of spiders

should be essentially indistinguishable from one, or very few, putative flower models (which presumably would fall closest to a given spider in the relevant colour space). This sampling process was repeated 5000 times (Adams and Anthony 1996) to ultimately derive a subjective measure of colour-similarity between *G. fornicata* morphs and sympatric versus allopatric floral communities (Fig. 4). We then statistically tested for differences in spider-flower distances between these two groups by calculating p-values as the proportion of distance values in the sympatric (Cairns) distribution that were equally or more extreme than the combined distribution of distances from allopatric (Brisbane, Melbourne, and Tasmania) floral communities, multiplied by two (for a two-tailed hypothesis test; Adams and Anthony 1996). We report Cohen's *d*—the distance between the means of each distribution, in units of pooled standard deviation—as a measure of effect size, for all tests.

Second, we tested the prediction that, if spiders are mimicking particular floral species, we should find one or more sympatric flowers that target the same receivers (i.e. pollinating Diptera and Hymenoptera), and that are essentially indistinguishable to their shared receivers. To achieve this, we estimated the degree of colour overlap between each *G. fornicata* morph and individual sympatric flower species, in the tetrahedral and hexagon models of dipteran and hymenopteran vision. As outlined above for species-level analyses, we calculated the exact volume of overlap (if any) between each morph and every flower species (comprised of spectral measurements from at least three independent individuals), and divided this by the volume of the smaller of the two, converted to a percentage. We tested the prediction of the floral mimicry hypothesis that potential 'model' flower species should show strong colour overlap with a given *G. fornicata* morph. We further explored whether putative flower models target the same receivers as spiders; that is, whether the most visually similar flowers are known as fly or bee pollinated (see supplementary information in White and Kemp (2016) for prey-composition data for *G. fornicata*).

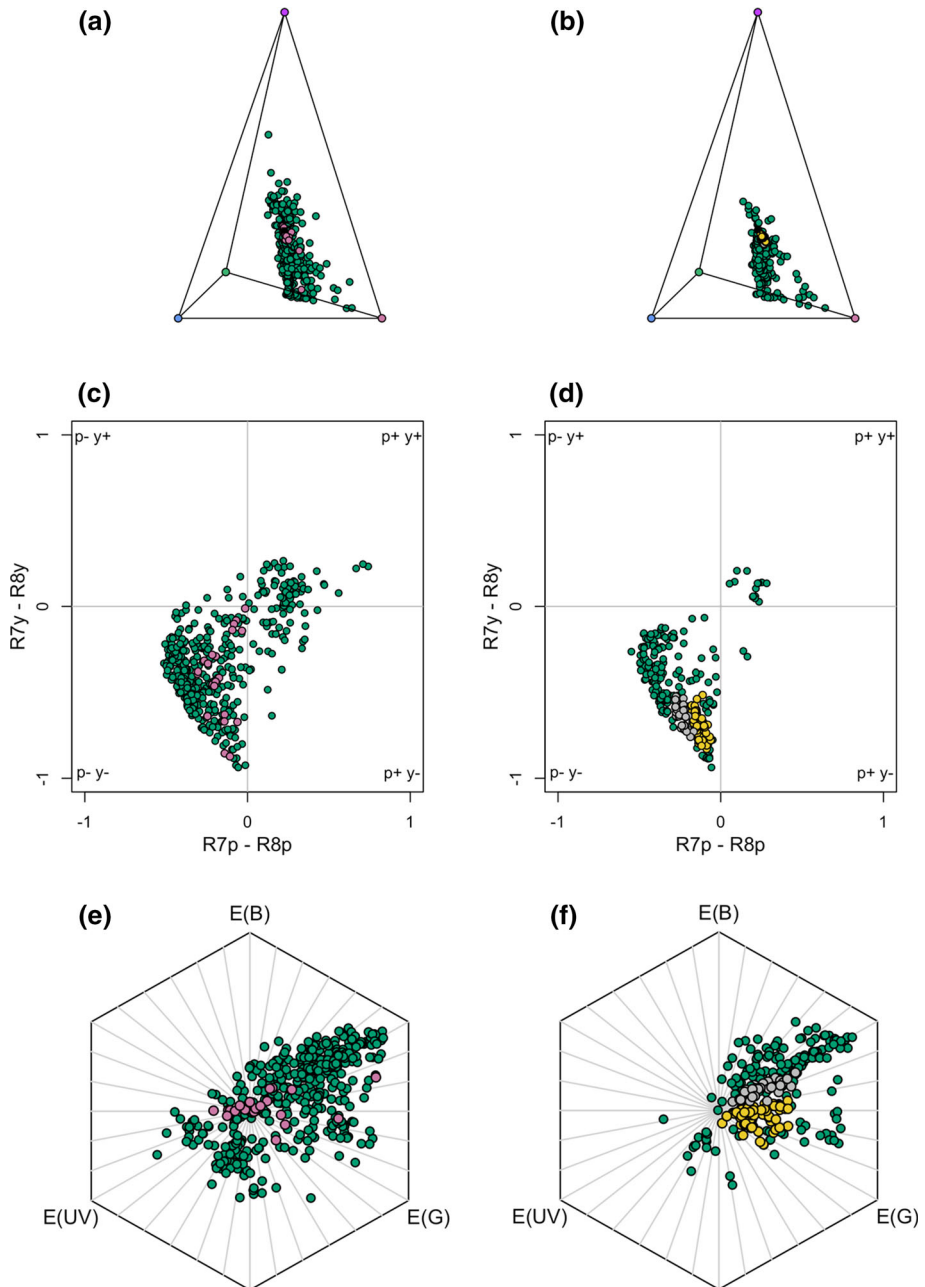
Results

Is there a link between colour-based lures and flower colour signals?

Perceptual models for both Diptera and Hymenoptera all predicted a similarly broad resemblance between flower and lure colour signals. The tetrahedral dipteran model predicted 100% overlap between flowers and lures, which held at both the inter-specific (Fig. 2a) and intraspecific level (Fig. 2a). Similarly, in the categorical dipteran model, all lures fell within the same colour category as one another, along with the majority of flowers (Fig. 2c, d). This held between (Fig. 2c) and within (Fig. 2d) species. The frequency distribution of lure and flower colour loci in the hexagon colour space showed strong similarity (Fig. 3), with most individuals of each group falling within the blue-green bee-hue sector. This also held between (Fig. 2e, and purple line in Fig. 3) and within (Fig. 2f, and white and yellow lines in Fig. 3) species, though there was a second primary-peak in the distribution of interspecific lure colours between the UV and UB-blue sectors.

Do colour-based lures show a generalised or specific resemblance to flowers?

We found between-morph variation in the predicted resemblance of *G. fornicata*'s lures to sympatric versus allopatric flower communities, as modelled to dipteran and hymenopteran viewers. Consistent with a mimicry hypothesis, 'white' *G. fornicata* individuals were



predicted to be more similar to sympatric flower communities as viewed by both dipteran ($P < 0.001$, $d = 2.609$) and hymenopteran ($P = 0.011$, $d = 0.61$) viewers (Fig. 4). Yellow individuals, in contrast, were on average equally similar to sympatric and allopatric flower communities across dipteran ($P = 0.728$, $d = 0.105$) and hymenopteran ($P = 0.638$, $d = 0.201$) models (Fig. 4). In both models, yellow and white spider morphs

Fig. 2 The colours of flowers and spiders considering tetrahedral (a, b), and categorical (c, d) models of dipteran vision, based on the visual phenotype of *Drosophila melanogaster*, and the hexagon (e, f) model of honeybee (*Apis mellifera*) vision. Panels on the left denote the species-averaged reflectance of 461 floral colour patches from 339 species (green) plotted along with 15 colour patches from 10 species of Australian spider (purple) whose colours are known or hypothesised to act as visual lures. Panels on the right contain the reflectance of individual floral colour patches (green) from 62 species sampled in Cairns, Australia, along with yellow (yellow) and white (grey) individuals of the sympatric orb-web spider *Gasteracantha fornicata*. (Color figure online)

and floral communities typically fell within or below the range of values in which receivers are predicted to have difficulty reliably discriminating between stimuli under natural conditions (vertical dashed lines in Fig. 4, horizontal dashed lines in Fig. S1).

Also consistent with the hypothesis that lure colours show a specific, rather than general, resemblance to flowers, we found significant overlap between several sympatric flower species and each *G. fornicata* morph (Fig. 5; Table 1). For yellow *G. fornicata* in both models, we found the greatest overlap between *Hibbertia linearis* and *Hibbertia riparia* (Fig. 6), whose close relatives are pollinated by Coleoptera and/or Hymenoptera (Keighery 1975; Bernhardt 1984, 1986). For white individuals across both models, we found the largest overlap with *Zieria arborescens*, a species thought to be pollinated primarily by dipterans (Department of Primary Industries, Parks, Water and Environment, Tasmania 2012). In the hexagon space, we also found a considerable degree of overlap with the vine *Faradaya splendida*.

Discussion

Receiver-bias models have proven a useful framework for understanding the evolution of signal design (Christy 1995; Burley and Symanski 1998; Endler and Basolo 1998; Christy et al. 2003a). Our results support the application of the principles of such models to

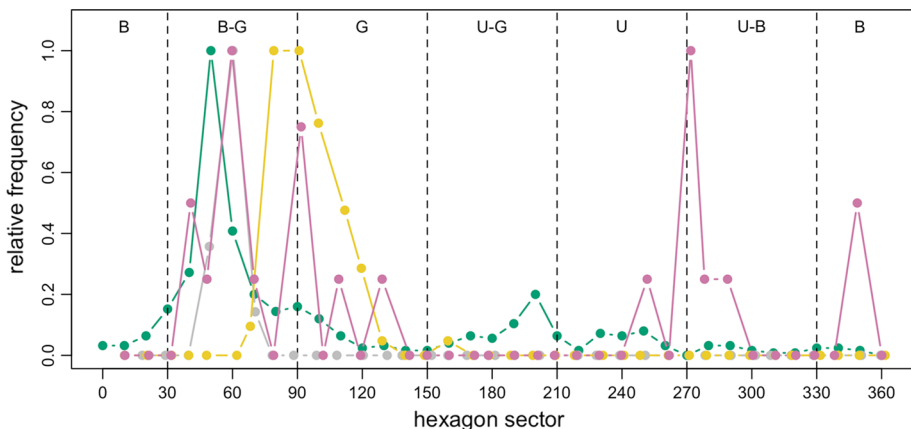


Fig. 3 The relative frequencies of floral colour patches sampled in Cairns (green), the colour-based lures of 10 Australian spiders (purple), and the white (grey) and yellow (yellow) morphs of *G. fornicata*. Data represent the frequency distributions of stimuli in 10° sectors around the colour hexagon (grey lines in Fig. 2c, d), with 0° at the 12:00 angle, increasing clockwise. Text and vertical lines indicate the five 45° ‘bee-hue’ categories: blue (B), blue-green (BG), green (G), ultraviolet-green (UV-G), ultraviolet (UV), ultraviolet-blue (UV-B). (Color figure online)

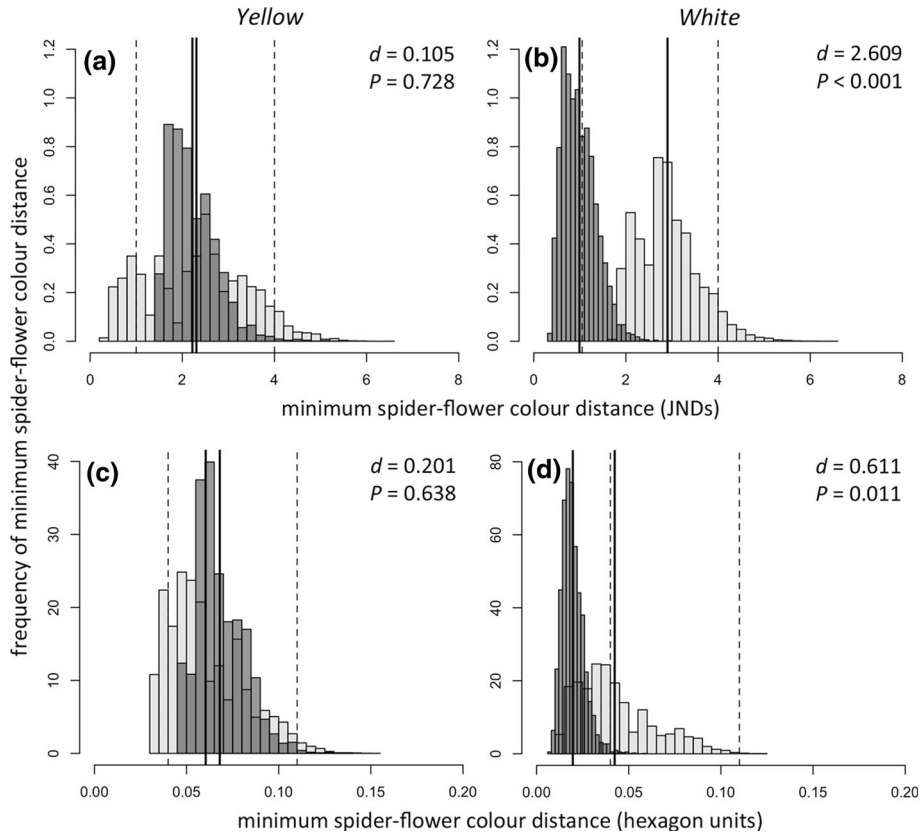


Fig. 4 The subjective colour similarity of polymorphic lures of *G. fornicata* to sympatric (dark bars) versus allopatric (light bars) floral communities. If lures are mimicking particular flowers, we predicted that spiders should be equally or more similar to sympatric as opposed to allopatric flowers. Morphs are indicated by headings. The distributions were generated using a randomisation procedure (see main text), and show the frequency of minimum colour distances between lures and flowers in models of fly (a, b) and bee (c, d) vision. Distribution means are indicated by solid vertical lines. Dashed vertical lines delineate a range of values within which receivers are predicted to have difficulty discriminating between two coloured stimuli under natural conditions. Above this range, receivers should be able to consistently discriminate between coloured stimuli, whereas below this range, accurate discrimination is predicted to become no better than chance. P values (inset, along with Cohen's d) represent the proportion of distance values in the sympatric (dark bars) floral community that were equally or more extreme than the combined distribution of distances from allopatric

deceptive colour-based signals. At the broadest level, our results support the hypothesis that the deceptive colour-based lures of spiders benefit from a resemblance to flowers. Models of fly (Fig. 2a–d) and bee (Figs. 2e–f, 3) vision converged in their predictions of a sensory overlap between the colour signals of flowers and the colour-based lures of spiders, both between and within spider species (Figs. 2, 3). Although these visual models vary in their degree of empirical validation (as discussed above), they each independently predict that lures fall well within the colour ‘envelope’ of local flower communities, given the perspective of putative target receivers (i.e. pollinating Diptera and Hymenoptera). Of course these data alone cannot be interpreted as exclusive evidence for a floral-resemblance hypothesis, since lures and flowers may also have independently converged upon a

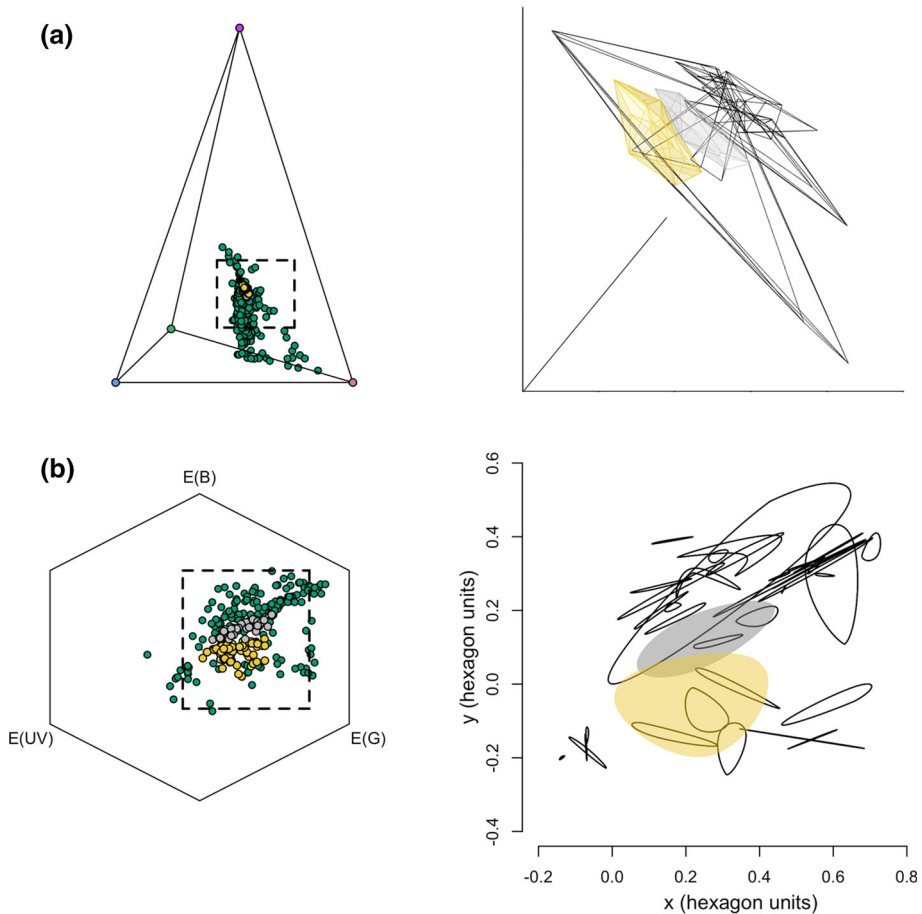


Fig. 5 Sensory overlap between the colour-based lures of *Gasteracantha fornicata* and sympatric individuals of 62 angiosperm species as modelled according to **a** dipteran and **b** hymenopteran vision. Dashed lines on the left indicate the focal areas enlarged on the right. The intraspecific colour variation ‘envelope’ of angiosperms is delineated by black polygons, which are convex hulls containing all individual samples of a given species. Variation within yellow and white morphs of *G. fornicata* is represented by yellow and grey polygons, respectively, which similarly encapsulate all intra-morph spectral samples. Angiosperm species whose envelopes intersect either morph of *G. fornicata* are detailed in Table 1. (Color figure online)

common solution for maximising signal salience. While phylogenetic data are ultimately necessary to resolve this question, the correspondence between model predictions in interspecific analyses, and the results of our further intraspecific analyses (discussed below), favour the hypothesis that lures have adaptively converged upon the colours of flowers.

Through a focal examination of *Gasteracantha fornicata* and sympatric flowers we also found support for the idea that lures resemble particular ‘model’ species. In both fly and bee colour spaces, yellow *G. fornicata* morphs overlapped strongly with *Hibbertia linearis* and *H. riparia* (Fig. 5; Table 1). These are small, insect-pollinated shrubs with ca. 6–12 mm petals (Fig. 6; Wood and Wood 1998; PlantNET 2016). White *G. fornicata* morphs, again in both bee and fly colour spaces (Fig. 5; Table 1), overlapped the most with

Table 1 The volume overlaps, in dipteran and hymenopteran colour spaces, between lures of the colour polymorphic orb spider *Gasteracantha formicata* and the flowers of sympatric angiosperm species from Cairns, Australia (illustrated in Fig. 5)

Angiosperm species	Pollinator	Bee space (% overlap)		Fly space (% overlap)	
		White morph	Yellow morph	White morph	Yellow morph
<i>Geitonoplesium cymosum</i>	Insect	4	83	0	0
<i>Goodenia lanata</i>	Insect (bee)	0	0	0	9
<i>Grevillea buxifolia buxifolia</i>	Bird	28	6	4	0
<i>Grevillea steiglitziana</i>	Bird	0	8	0	0
<i>Faradaya splendida</i>	Insect	93	0	0	0
<i>Hibbertia linearis</i>	Insect (beetle, bee)	0	100	0	33
<i>Hibbertia riparia</i>	Insect (beetle, bee)	0	100	0	29
<i>Xyris operculata</i>	Insect and bird	0	43	0	0
<i>Zieria arborescens</i>	Insect (fly)	100	0	22	0

Volumes are estimated using a tetrahedral model of dipteran vision, and the hexagon model of hymenopteran vision. Volumes were calculated as the volume of overlap between all individuals of a given flower species and all individuals of a given spider morph, divided by the volume of the smaller of the two (converted to a percentage). A value of 100% thus indicates that one is entirely contained within the other, while a value of 0% indicates that the two do not intersect. We present here only those angiosperm species whose volumes intersect with at least one *G. formicata* morph in at least one model.

the odorous, potentially fly-pollinated shrub *Ziera arborescens* (Fig. 6; Department of Primary Industries, Parks, Water and Environment, Tasmania 2012; PlantNET 2016). This is consistent with evidence from deceptive pollination systems in which comparable levels of colour similarity to rewarding species underlie the success of deceptive flowers (Gigord et al. 2002; Internicola et al. 2007; Peter and Johnson 2008). In further support of the mimicry hypothesis, we found that spider morphs were equally or more similar to sympatric as opposed to allopatric floral communities (Fig. 4, Fig. S1). This is however limited by the fact that floral communities outside of *G. formicata*'s range will still contain sympatric species, as well as the relatively broad scale of sympatry we used (which was determined by the scale at which floral reflectance was sampled for an unrelated study; see methods).

Whereas the attractiveness of conspicuous colouration in many sit-and-wait predators is well established (Hauber 2002; Tso et al. 2004, 2006; Chiao et al. 2009), the ultimate basis of their effectiveness has remained unclear. Recent work has implicated signal detectability as key to lure attractiveness (White and Kemp 2016), and our results suggest that lures may also, in part, function by exploiting prey preferences for typically rewarding floral signals. While it is well established that predators may exploit or modify the visual signals presented by flowers (Elliott and Elliott 1991; Heiling and Herberstein 2004; Heiling et al. 2005), evidence for aggressive pollinator deception—wherein predators exploit receiver preferences for floral signals independent of the flowers themselves—is sparse. The most convincing example to date is that of the orchid mantis *Hymenopus coronatus*. Behavioural (O'Hanlon et al. 2014b), morphological (O'Hanlon et al. 2014a), and ecological (O'Hanlon et al. 2014c) data show that mantids and sympatric flowers overlap in the perceptual space of receivers, and that they are probably mistaken for otherwise rewarding flowers. Our results similarly suggest that spiders and sympatric

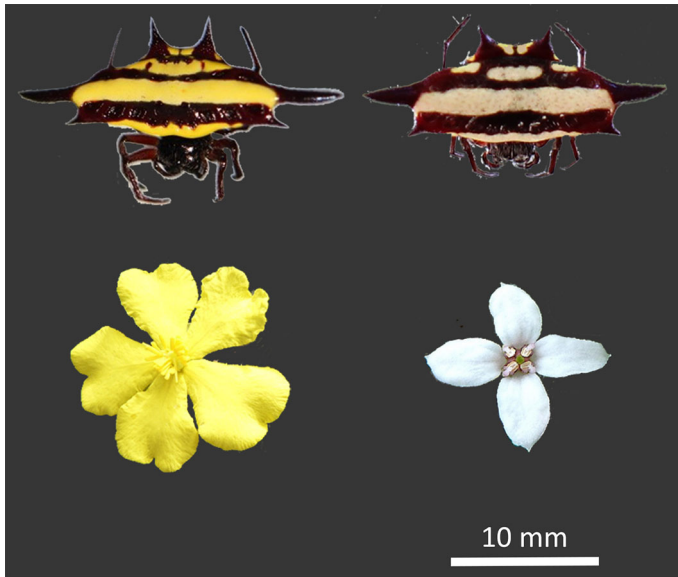


Fig. 6 Colour morphs of the spiny orb spider *Gasteracantha fornicata*, and inflorescences from flower species whose colour signals are most similar, as modelled according to dipteran and hymenopteran vision (Table 1). *Left* yellow morph, and the insect pollinated shrub *Hibbertia linearis*. *Right* white morph, and the possibly fly pollinated ‘stinkwood’ shrub *Zieria arborescens*. (Color figure online)

flowers present considerable colour-convergence to receivers, and target shared receivers (Fig. 5; also see table S1 in White and Kemp 2016).

Unlike the orchid mantis, however, orb-web spiders are generalist predators that capture prey including non-pollinating arthropods (Nentwig 1987; Tso et al. 2005). This is particularly true for tropically distributed species such as *G. fornicata*, because the tropics are characterised by greater arthropod diversity, with lower and more temporally variable abundance of any one species (relative to temperate zones; Stork 1988; Basset 2001; Basset et al. 2012). Such prey community diversity argues for a generalist element in colour-lure systems. Hence, within the range of effective lure colours (here defined, in a receiver-bias framework, by sympatric flowers; Figs. 2, 3), we may expect selection to favour lures that best appeal to the ‘aggregate’ viewer. This could have predictable consequences for adaptive signal designs. Yellow, for example, is a particularly common lure colour (Craig 1994; Craig and Ebert 1994; Tso et al. 2002; e.g. Bush et al. 2008; Kemp et al. 2013). A working hypothesis is that yellow is broadly favoured both by pollinators because of their resemblance to rewarding flowers (Figs. 2, 3), and by many non-pollinating insects for whom yellow may act as a ‘supernormal foliage’ (i.e. green) stimulus (Prokopy and Owens 1983; Chittka and Döring 2007).

Receiver-bias models predict several routes to signal diversification that depend on the type of biases being exploited (Christy 1995; Endler and Basolo 1998; White and Kemp 2015). If, as our results suggest, deceptive predators target receiver’s preferences for rewarding floral signals, then lure diversity, including polymorphism, may be adaptively favoured by the fitness benefits of ‘matching’ multiple models in space and/or time. The considerable diversity in these deceptive signals (reviewed in White and Kemp 2015) may therefore have arisen through the convergence of lures upon the signals of varied

rewarding stimuli, as consistent with our findings (Figs. 5, 6). The extent to which lures need match the signals of particular flowers, however, will depend on both receivers' accuracy in colour discrimination, and their tendency to generalise learned colours. Common insect pollinators, such as honeybees, are known to imperfectly discriminate between learned colours (Gumbert 2000; Gigord et al. 2002; Internicola et al. 2007; Peter and Johnson 2008; Dyer and Murphy 2009). This will generate a broader perceptual target for deceptive signallers to exploit, and has also been extended as an explanation for the enduring question of why lures are often discretely polymorphic (e.g. Levi 1978; Tso et al. 2002; Kemp et al. 2013; Rao et al. 2015). Recent theoretical work on sexually deceptive orchids has shown that pollinators are more likely to mistake extreme coloured forms with an intermediate form, than with one another (Kagawa and Takimoto 2016). Intermediate forms will therefore be learned more rapidly, since they will be more often categorised as a negative stimulus, relative to extreme forms. Disruptive selection against intermediate forms arising from this could subsequently favour polymorphism. While the cost of a mistake in lure systems may be more severe than in deceptive orchids, the significant rates of prey escape from orb-web spiders (up to 80%; Craig et al. 1996; Zschokke et al. 2006) could foster learned avoidance and, hence, generate disruptive selection in the manner outlined above. The role of innate versus learned colour preferences in the adaptive success of deceptive lures is not well understood, and is worthy of further study.

In sum, data both across and within spider and flower species suggest that the ultimate basis of colour-lure efficacy in orb-web spiders relates, in part, to their resemblance to floral signals. Our results also imply a model/mimic dynamic between lures and flowers, although a key outstanding question is whether and under what circumstances prey mistake lures for flowers (Christy 1995). This could be profitably tested through receiver-behaviour experiments across a range of variation in spider appearance, while also manipulating receivers' prior experience of colour stimuli. Finer-scale data on the geographic distribution of colour-luring spiders and flower models would also be valuable, particularly for examining the maintenance of geographic variation in morph composition among polymorphic species (e.g. the geographic cline of *G. fornicata*; Kemp et al. 2013). Phylogenetic data on the evolutionary history of lure and flower colouration will ultimately be essential for establishing whether lures adaptively converged upon floral signals, or arose as a consequence of receiver biases unrelated to flower/pollinator ecology.

Acknowledgements TEW was supported by an Australian Postgraduate Award and the Australasian Evolution Society, and thanks Elizabeth Mulvenna for all her support. DJK was supported by the Australian Research Council (Grant DP140104107). RLD was supported by an Australian Postgraduate Award, UNSW Research Excellence Award, an E&ERC Postgraduate Research Start-Up Grant, and the Wiley Blackwell fundamental ecology award. We thank Manuel Leal, John Endler, and anonymous reviewers for valuable comments.

References

- Adams DC, Anthony CD (1996) Using randomization techniques to analyse behavioural data. *Anim Behav* 51:733–738
- Ames A (2000) CNS energy metabolism as related to function. *Brain Res Rev* 34:42–68
- Avaughès-Weber A, de Brito Sanchez MG, Giurfa M, Dyer AG (2010) Aversive reinforcement improves visual discrimination learning in free-flying honeybees. *PLoS ONE* 5:e15370
- Basset Y (2001) Invertebrates in the canopy of tropical rain forests how much do we really know? In: Linsenmair KE, Davis CM, Fiala B, Speight MR (eds) *Tropical forest canopies: ecology and management*. Springer, Berlin, pp 87–107

- Basset Y, Cizek L, Cuénoud P, Didham RK, Guilhaumon F, Missa O, Novotny V et al (2012) Arthropod diversity in a tropical forest. *Science* 338:1481–1484
- Bernhardt P (1984) The pollination biology of *Hibbertia stricta* (dilleniaceae). *Plant Syst Evol* 147:267–277
- Bernhardt P (1986) Bee-pollination in *Hibbertia fasciculata* (dilleniaceae). *Plant Syst Evol* 152:231–241
- Blamires SJ, Hou C, Chen L-F, Liao CP, Tso I-M (2014) A predator's body coloration enhances its foraging profitability by day and night. *Behav Ecol Sociobiol* 8:1253–1260
- Brembs B, de Ibarra NH (2006) Different parameters support generalization and discrimination learning in *Drosophila* at the flight simulator. *Learn Memory* 13:629–637
- Briscoe AD, Chittka L (2001) The evolution of color vision in insects. *Annu Rev Entomol* 46:471–510
- Burley NT, Symanski R (1998) A taste for the beautiful: latent aesthetic mate preferences for white crests in two species of Australian grassfinches. *Am Nat* 152:792–802
- Bush AA, Yu DW, Herberstein ME (2008) Function of bright coloration in the wasp spider *Argiope bruennichi* (Araneae : Araneidae). *Proc R Soc B* 275:1337–1342
- Chiao C-C, Wu W-Y, Chen S-H, Yang E-C (2009) Visualization of the spatial and spectral signals of orb-weaving spiders, *Nephila pilipes*, through the eyes of a honeybee. *J Exp Biol* 212:2269–2278
- Chittka L (1992) The colour hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *J Comp Physiol A* 170:533–543
- Chittka L, Döring TF (2007) Are autumn foliage colors red signals to aphids? *PLoS Biol* 5:e187
- Chittka L, Shmida A, Troje N, Menzel R (1994) Ultraviolet as a component of flower reflections, and the colour perception of hymenoptera. *Vis Res* 34:1489–1508
- Chittka L, Dyer AG, Bock F, Dornhaus A (2003) Psychophysics: bees trade off foraging speed for accuracy. *Nature* 424:388
- Chittka L, Skorupski P, Raine NE (2009) Speed–accuracy tradeoffs in animal decision making. *Trends Ecol Evol* 24:400–407
- Christy JH (1995) Mimicry, mate choice, and the sensory trap hypothesis. *Am Nat* 146:171–181
- Christy JH, Backwell PRY (1995) The sensory exploitation hypothesis. *Trends Ecol Evol* 10:417
- Christy JH, Baum JK, Backwell PR (2003a) Attractiveness of sand hoods built by courting male fiddler crabs, *Uca musica*: test of a sensory trap hypothesis. *Anim Behav* 66:89–94
- Christy J, Backwell P, Schober U (2003b) Interspecific attractiveness of structures built by courting male fiddler crabs: experimental evidence of a sensory trap. *Behav Ecol Sociobiol* 53:84–91
- Chuang CY, Yang EC, Tso I-M (2008) Deceptive color signaling in the night: a nocturnal predator attracts prey with visual lures. *Behav Ecol* 19:237–244
- Craig CL (1994) Limits to learning—effects of predator pattern and color on perception and avoidance learning by prey. *Anim Behav* 47:1087–1099
- Craig CL, Ebert K (1994) Colour and pattern in predator–prey interactions: the bright body colours and patterns of a tropical orb-spinning spider attract flower-seeking prey. *Funct Ecol* 8:616–620
- Craig CL, Weber RS, Bernard GD (1996) Evolution of predator-prey systems: spider foraging plasticity in response to the visual ecology of prey. *Am Nat* 147:205–229
- Cummings ME (2007) Sensory trade-offs predict signal divergence in surfperch. *Evolution* 61:530–545
- Dalrymple R, Kemp D, Flores-Moreno H, Laffan S, White T, Hemmings F, Tindall M, Moles AT (2015) Birds, butterflies and flowers in the tropics are not more colourful than those in higher latitudes. *Global Ecol Biogeogr* 24:848–860
- Department of Primary Industries, Parks, Water and Environment, Tasmania (2012) Listing Statement for *Zieria veronicea* subsp. *veronicea* (pink zieria), pp 1–5
- Dyer AG, Chittka L (2004a) Bumblebees (*Bombus terrestris*) sacrifice foraging speed to solve difficult colour discrimination tasks. *J Comp Physiol A* 190:759–763
- Dyer AG, Chittka L (2004b) Fine colour discrimination requires differential conditioning in bumblebees. *Naturwissenschaften* 91:224–227
- Dyer AG, Murphy AH (2009) Honeybees choose “incorrect” colors that are similar to target flowers in preference to novel colors. *Isr J Plant Sci* 57:203–210
- Dyer A, Neumeyer C (2005) Simultaneous and successive colour discrimination in the honeybee (*Apis mellifera*). *J Comp Physiol A* 191:547–557
- Dyer AG, Spaethe J, Prack S (2008) Comparative psychophysics of bumblebee and honeybee colour discrimination and object detection. *J Comp Physiol A* 194:617–627
- Dyer AG, Boyd-Gerny S, McLoughlin S, Rosa MGP, Simonov V, Wong BBM (2012) Parallel evolution of angiosperm colour signals: Common evolutionary pressures linked to hymenopteran vision. *Proc R Soc B* 279:3606–3615
- Elliott NB, Elliott WM (1991) Effect of an ambush predator, *Phymata americana melin*, on behavior of insects visiting *Daucus carota*. *Am Midl Nat* 126:198–202

- Endler JA, Basolo AL (1998) Sensory ecology, receiver biases and sexual selection. *Trends Ecol Evol* 13:415–420
- Endler JA, Mielke PW (2005) Comparing entire colour patterns as birds see them. *Biol J Linn Soc* 86:405–431
- Fukushi T (1994) Colour perception of single and mixed monochromatic lights in the blowfly *Lucilia cuprina*. *J Comp Physiol A* 175:15–22
- Fuller RC (2002) Lighting environment predicts the relative abundance of male colour morphs in bluefin killifish (*Lucania goodei*) populations. *Proc R Soc Lond Ser B* 269:1457–1465
- Gaskett AC, Herberstein ME (2010) Colour mimicry and sexual deception by tongue orchids (cryptostylis). *Naturwissenschaften* 97:97–102
- Gaskett A, Winnick C, Herberstein ME (2008) Orchid sexual deceit provokes ejaculation. *Am Nat* 171:E206–E212
- Gigord LDB, Macnair MR, Stritsky M, Smithson A (2002) The potential for floral mimicry in rewardless orchids: an experimental study. *Proc R Soc B* 269:1389–1395
- Govardovskii V, Fyhrquist N, Reuter T, Kuzmin D, Donner K (2000) In search of the visual pigment template. *Vis Neurosci* 17:509–528
- Gumbert A (2000) Color choices by bumble bees (*Bombus terrestris*): innate preferences and generalization after learning. *Behav Ecol Sociobiol* 48:36–43
- Hauber ME (2002) Conspicuous colouration attracts prey to a stationary predator. *Ecol Entomol* 27:686–691
- Heiling AM, Herberstein ME (2004) Predator-prey coevolution: Australian native bees avoid their spider predators. *Proc R Soc B* 271:S196–S198
- Heiling AM, Chittka L, Cheng K, Herberstein ME (2005) Colouration in crab spiders: substrate choice and prey attraction. *J Exp Biol* 208:1785–1792
- Herberstein M, Craig C, Coddington J, Elgar M (2000) The functional significance of silk decorations of orb-web spiders: a critical review of the empirical evidence. *Biol Rev* 75:649–669
- Herberstein ME, Heiling AM, Cheng K (2009) Evidence for UV-based sensory exploitation in Australian but not European crab spiders. *Evol Ecol* 23:621–634
- Hoese F, Law E, Rao D, Herberstein M (2006) Distinctive yellow bands on a sit-and-wait predator: Prey attractant or camouflage? *Behaviour* 143:763–781
- Internicola AI, Page PA, Bernasconi G, Gigord LDB (2007) Competition for pollinator visitation between deceptive and rewarding artificial inflorescences: an experimental test of the effects of floral colour similarity and spatial mingling. *Funct Ecol* 21:864–872
- Kagawa K, Takimoto G (2016) Inaccurate color discrimination by pollinators promotes evolution of discrete color polymorphism in food-deceptive flowers. *Am Nat* 187:194–204
- Keighery G (1975) Pollination of *Hibbertia hypericoides* (dilleniaceae) and its evolutionary significance. *Journal of Natural History* 9:681–684
- Kemp DJ, Holmes C, Congdon BC, Edwards W (2013) Color polymorphism in spiny spiders (*Gasteracantha fornicata*): testing the adaptive significance of a geographically clinal lure. *Ethology* 119:1126–1137
- Kelly M, Gaskett A (2014) UV reflectance but no evidence for colour mimicry in a putative brood-deceptive orchid *Corybas cheesemani*. *Curr Zool* 60:104–113
- Kemp DJ, Herberstein ME, Fleishman LJ, Endler JA, Bennett ATD, Dyer AG, Hart NS, Marshal J, Whiting MJ (2015) An integrative framework for the appraisal of coloration in nature. *Am Nat* 185:705–724
- Kirschfeld K, Feiler R, Franceschini N (1978) A photostable pigment within the rhabdomere of fly photoreceptors no. 7. *J Comp Physiol* 125:275–284
- Leal M, Fleishman LJ (2002) Evidence for habitat partitioning based on adaptation to environmental light in a pair of sympatric lizard species. *Proc R Soc Lond B* 269:351–359
- Levi HW (1978) The American orb-weaver genera *Colpopeira*, *Micrathena*, and *Gasteracantha* north of Mexico (Araneae, Araneidae). *Bull Mus Comp Zool* 148:417–442
- Lunau K (2014) Visual ecology of flies with particular reference to colour vision and colour preferences. *J Comp Physiol A* 200:1–16
- Maia R, Eliason CM, Bitton P-P, Doucet SM, Shawkey MD (2013) Pavo: an R package for the analysis, visualization and organization of spectral data. *Methods Ecol Evol* 4:906–913
- Moran D, Softley R, Warrant EJ (2015) The energetic cost of vision and the evolution of eyeless Mexican cavefish. *Sci Adv* 1:e1500363
- Morante J, Desplan C (2008) The color-vision circuit in the medulla of *Drosophila*. *Curr Biol* 18:553–565
- Morawetz L, Svoboda A, Spaethe J, Dyer AG (2013) Blue colour preference in honeybees distracts visual attention for learning closed shapes. *J Comp Physiol A* 199:817–827
- Nentwig W (1987) The prey of spiders. In: Nentwig W (ed) *Ecophysiology of spiders*. Springer, Berlin, pp 249–263

- Niven JE, Anderson JC, Laughlin SB (2007) Fly photoreceptors demonstrate energy-information trade-offs in neural coding. *PLoS Biol* 5:e116
- O'Hanlon JC, Holwell GI, Herberstein ME (2014a) Predatory pollinator deception: Does the orchid mantis resemble a model species? *Curr Zool* 60:90–103
- O'Hanlon JC, Holwell GI, Herberstein ME (2014b) Pollinator deception in the orchid mantis. *Am Nat* 183:126–132
- O'Hanlon J, Herberstein M, Holwell G (2014c) Habitat selection in a deceptive predator: maximizing resource availability and signal efficacy. *Behav Ecol* 26:194–199
- Peng P, Blamires SJ, Agnarsson I, Lin H-C, Tso I-M (2013) A color-mediated mutualism between two arthropod predators. *Curr Biol* 23:172–176
- Peter CI, Johnson SD (2008) Mimics and magnets: the importance of color and ecological facilitation in floral deception. *Ecology* 89:1583–1595
- PlantNET (2016). <http://plantnet.rbg Syd.nsw.gov.au>
- Poisot T (2011) The digitize Package: extracting numerical data from scatterplots. *R J* 25:3–5
- Prokopy RJ, Owens ED (1983) Visual detection of plants by herbivorous insects. *Annu Rev Entomol* 28:337–364
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rao D, Castañeda-Barbosa E, Nuñez-Beverido N, Díaz-Fleischer F (2015) Foraging benefits in a colour polymorphic neotropical orb web spider. *Ethology* 121:187–195
- Renoult JP, Valido A, Jordano P, Schaefer HM (2014) Adaptation of flower and fruit colours to multiple, distinct mutualists. *New Phytol* 201:678–686
- Ryan MJ, Cummings ME (2013) Perceptual biases and mate choice. *Annu Rev Ecol Evol Syst* 44:437–459
- Salcedo E, Huber A, Henrich S, Chadwell LV, Chou WH, Paulsen R, Britt SG (1999) Blue- and green-absorbing visual pigments of *Drosophila*: ectopic expression and physiological characterization of the r8 photoreceptor cell-specific rh5 and rh6 rhodopsins. *J Neurosci* 19:10716–10726
- Skorupski P, Spaethe J, Chittka L (2006) Visual search and decision making in bees: time, speed, and accuracy. *Int J Comp Psychol* 19:342–357
- Spaethe J, Streinzer M, Eckert J, May S, Dyer A (2014) Behavioural evidence of colour vision in free flying stingless bees. *J Comp Physiol A* 200:485–496
- Stevens M, Cuthill IC, Windsor AMM, Walker HJ (2006) Disruptive contrast in animal camouflage. *Proc R Soc B* 273:2433–2438
- Stoddard MC, Stevens M (2011) Avian vision and the evolution of egg color mimicry in the common cuckoo. *Evolution* 65:2004–2013
- Stork NE (1988) Insect diversity: facts, fiction and speculation. *Biol J Linn Soc* 35:321–337
- Stuart-Fox D, Moussalli A, Whiting MJ (2007) Natural selection on social signals: signal efficacy and the evolution of chameleon display coloration. *Am Nat* 170:916–930
- Sutherland JP, Sullivan MS, Poppy GM (1999) The influence of floral character on the foraging behaviour of the hoverfly, *Episyrphus balteatus*. *Entomol Exp Appl* 93:157–164
- Troje N (1993) Spectral categories in the learning behaviour of blowflies. *Zeitschrift fur Naturforschung C* 48:96
- Tso I-M, Tai P-L, Ku T-H, Kuo C-H, Yang E-C (2002) Colour-associated foraging success and population genetic structure in a sit-and-wait predator *Nephila maculata* (Araneae: Tetragnathidae). *Anim Behav* 63:175–182
- Tso I-M, Lin C-W, Yang E-C (2004) Colourful orb-weaving spiders, *Nephila pilipes*, through a bee's eyes. *J Exp Biol* 207:2631–2637
- Tso I-M, Wu H-C, Hwang I-R (2005) Giant wood spider *Nephila pilipes* alters silk protein in response to prey variation. *J Exp Biol* 208:1053–1061
- Tso I-M, Liao CP, Huang RP, Yang EC (2006) Function of being colorful in web spiders: Attracting prey or camouflaging oneself? *Behav Ecol* 17:606–613
- Vorobyev M, Osorio D (1998) Receptor noise as a determinant of colour thresholds. *Proc R Soc Lond Ser B* 265:351–358
- Vorobyev M, Brandt R, Peitsch D, Laughlin SB, Menzel R (2001) Colour thresholds and receptor noise: behaviour and physiology compared. *Vis Res* 41:639–653
- Warrant EJ (2008) Seeing in the dark: vision and visual behaviour in nocturnal bees and wasps. *J Exp Biol* 211:1737–1746
- White TE, Kemp DJ (2015) Technicolour deceit: a sensory basis for the study of colour-based lures. *Anim Behav* 105:231–243
- White TE, Kemp DJ (2016) Colour polymorphic lures target different visual channels in prey. *Evolution* 70:1398–1408

- White TE, Dalrymple RL, Noble DWA, O'Hanlon JC, Zurek DB, Umbers KDL (2015) Reproducible research in the study of biological coloration. *Anim Behav* 106:51–57
- Wood B, Wood D (1998) *Flowers of the south coast and ranges of New South Wales: a field guide*. Wood's Books
- Yamaguchi S, Desplan C, Heisenberg M (2010) Contribution of photoreceptor subtypes to spectral wavelength preference in *Drosophila*. *Proc Natl Acad Sci* 107:5634–5639
- Zschokke S, Hénaut Y, Benjamin SP, García-Ballinas JA (2006) Prey-capture strategies in sympatric web-building spiders. *Can J Zool* 84:964–973