



Spider lures exploit insect preferences for floral colour and symmetry

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Abstract

Sensory systems can capture only a fraction of available information, which creates opportunities for deceptive signalling. The sensory traps and sensory bias models have proven valuable for explaining how visual systems and environments shape the design of sexual signals, but their application to deceptive signals is largely limited to the context of pollination. Here we use the ‘jewelled’ orb-web spider *Gasteracantha fornicata* to experimentally test two longstanding hypotheses for the function of deceptive visual lures. Namely, that they: (1) exploit generalised preferences for conspicuous colouration (sensory bias), or (2) co-opt the otherwise-adaptive foraging response of prey toward flowers (sensory traps). In a field-based study we manipulated the conspicuous dorsal signals of female spiders along two axes—colour pattern and symmetry—to generate a gradient of floral resemblance and monitored the per-individual consequences for prey interception. As predicted by the sensory traps model, the most attractive phenotypes were those with flower-like radial symmetry and solid colour patterns, and their attractiveness equaled that of natural spiders. Taken with recent work demonstrating a close resemblance between *G. fornicata* and sympatric floral ‘models’, and pollinating insects as primary prey items, our results suggest that the deceptive colour-based lures of spiders function as inter-kingdom sensory traps via floral mimicry, and support the broader extension of sensory-based models to deceptive signalling contexts.

Keywords Sensory trap · Sensory bias · Orb-web spider · Prey lure · Mimicry

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Introduction

Visual communication is widespread, and the demands of effective information-exchange have driven diverse phenotypic outcomes (Maia et al. 2013; Thoen et al. 2014; Dalrymple et al. 2015). Understanding this diversity requires examining the relationship between signals, environments, and sensory systems. The sensory traps and bias models—under the umbrella of sensory drive—have proven valuable to that end (among a suite of related models; Christy 1995; Endler 1992; Endler and Basolo 1998; West-Eberhard 1979). According to the sensory trap model signals evolve to co-opt receiver responses that are adaptive in unrelated contexts, in what is essentially a model-mimic dynamic (Christy et al. 2003). This model accounts for how the design of sexual signals, for example, may be shaped by how potential mates detect or recognize food items (e.g. via colour; Rodd et al. 2002) or shelter (e.g. through innate attraction to raised structures; Christy et al. 2003). The sensory bias model, by contrast, emphasizes how underlying sensory and/or perceptual biases may present opportunities for exploitation and hence drive signal evolution (Basolo and Endler 1995; Nelson et al. 2010; Ryan and Cummings 2013). The elaborate fins of male swordtails present a canonical example (Basolo 1990), having evolved in response to a pre-existing female bias toward such structures (Basolo 1990, 1995). These two models have robust empirical support in the context of sexual signalling, and innovative work in orchids and carnivorous plants continues to demonstrate how sexual- and food-deceptive ‘traps’ attract pollinating insects (reviewed in Gaskett et al. 2014; Lunau and Wester 2017). Nonetheless, much remains to be learned about the ability of bias and traps models to explain signal evolution more broadly.

Visual luring is a widespread predatory strategy and is particularly common among sit-and-wait predators. Orb-web spiders are a model group, with many species using striking body colours and patterns to actively attract insect prey to the web (Tso et al. 2004; Chuang et al. 2007a; White and Kemp 2015). The question of why such conspicuous deceptive signals are attractive to insect viewers has been the focus of considerable attention (Tso et al. 2004; Chuang et al. 2007b; Rao et al. 2015; Ximenes and Gawryszewski 2018; White and Kemp 2017). Two hypotheses predominate in the literature, which informally mirror the bias and traps models; namely, that lures (1) exploit innate colour preferences, or (2) co-opt the foraging response of prey toward flowers. Empirical support for these hypotheses is presently limited to observational and correlative data, and hence remains equivocal (e.g., Tso et al. 2004; Chuang et al. 2007b; Ximenes and Gawryszewski 2018; White et al. 2017). Formalising these hypotheses within the models of sensory drive offers a promising path to progress and may prove reciprocally beneficial in guiding future studies of deceptive signalling.

Though the bias and traps models overlap to some degree, their core predictions as applied to deceptive lures can be neatly partitioned (White and Kemp 2015). If visual lures are exploiting receivers’ sensory biases, then colour is likely to be a primary perceptual target. This follows from the fact that their prey are primarily flies and bees (Nentwig 1985, 1987; O’Hanlon et al. 2014), of which many are pollinators. Strong innate preferences for (human-perceived) yellows and whites are well documented among such groups (Kay 1976; Lunau 1988; Lunau and Maier 1995), which parallels a notably biased distribution of these colours among predator lures (White and Kemp 2015). A standing prediction under the bias model, then, is that the expression of preferred colours among deceptive signalers should predict their attractiveness to potential prey, as informally considered across the literature to date (e.g., Bush et al. 2008; Gawryszewski and Motta 2012; Rao et al. 2015).

The traps hypothesis, by contrast, suggests that lures are exploiting an otherwise-adaptive attraction to flowers in a dynamic more closely akin to floral mimicry. When foraging for flowers, pollinating insects are guided by their aforementioned colour preferences as well as symmetry cues, which they express well-defined preferences for (Chittka and Raine 2006; Kay 1976; Lehrer et al. 1995; Lunau and Maier 1995; Giurfa et al. 1996). Radial symmetry is both the most ancient and common form showcased among angiosperms (Crane et al. 1995; Neal et al. 1998; Endress 2001). Differentiating between the sensory traps and sensory bias hypotheses, then, requires several questions to be answered (Gaskett 2019; de Jager and Anderson 2019; White and Kemp 2015). First, do lures resemble floral ‘models’, as seen by the viewer? There is now good evidence for this across several systems including *Gasteracantha*, which we study here (Ximines and Gawryszewski 2018; O’Hanlon et al. 2013; Tso et al. 2004; White et al. 2017). Second, do the lures and models share the same viewers? This too is apparent in our study system, as *Gasteracantha* nearly exclusively captures Hymenoptera and Diptera that pollinate sympatric flowers (White and Kemp 2016). A critical untested prediction, however, is that lures should co-opt their prey’s natural response towards the model. Thus, any manipulation of the lure’s resemblance to the model should modify the fitness of the deceptive signaller. In our system, this would mean that modifying the signals of *Gasteracantha* spiders so that they look more or less like flowers, should improve and reduce prey capture, respectively. Note that for generalist predators like orb-web spiders this prediction applies to the response of the prey community at large, rather than the preferences of any single viewer.

Here we sought to formalise and test these adaptive hypotheses for deceptive signalling using the jewelled orb-web spider *Gasteracantha fornicata* (Fig. 1). Females of the species are colour polymorphic sit-and-wait predators, whose striking yellow- or white-and-black banded abdomens lure prey—primarily pollinating Diptera and Hymenoptera—to their webs (Kemp et al. 2013; White and Kemp 2016). To distinguish between the traps and bias hypotheses we manipulated the appearance of wild female *G. fornicata* in their natural habitats along two independent axes—colour and symmetry (Fig. 1). Our manipulations consisted of nine different treatments (including the wild-type) that encompassed

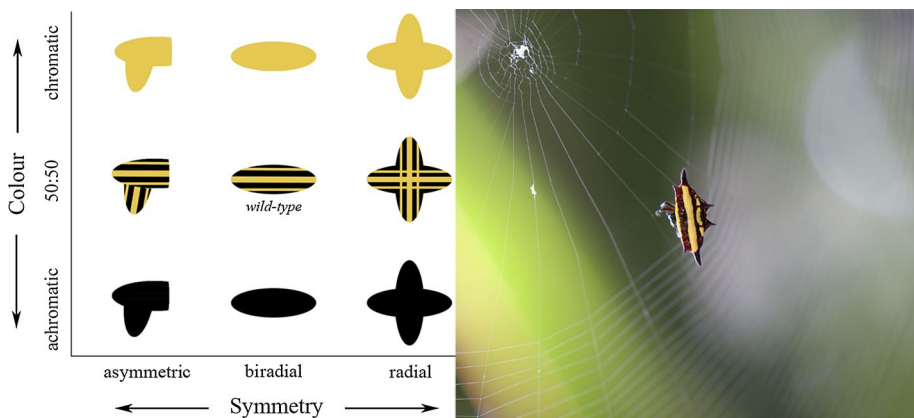


Fig. 1 (Left panel) The colour pattern manipulations as applied to naturally-occurring female *Gasteracantha fornicata*. The aim was to represent an approximate gradient of floral resemblance from most flower-like (top right) to least (bottom left), while including a wild-type model (centre). (Right panel) Female *Gasteracantha fornicata* from the study site in Cairns, QLD, Australia, weaving a web

the full-factorial combination of three levels of colour and three levels of symmetry. The sum of treatments represented an approximate gradient of floral resemblance, with a sensory trap hypothesis predicting positive covariance between capture success and the degree of floral resemblance (the x-axis of Fig. 2). Predicted attractiveness under the sensory bias model is however different, as discussed above, and the attractiveness in this case should scale with stimulus color alone (the y-axis of Fig. 2). We evaluated these predictions according to realized prey capture rates of wild, free-ranging spiders randomly assigned among the nine treatment stimuli.

Methods

Phenotype manipulations and prey interception rates

Our manipulative treatments included asymmetric, biradially symmetric, and radially symmetric shapes, in a fully factorial combination of solid black, black-and-yellow banded, and solid yellow patterns ($n=17\text{--}29$ each; Fig. 1). We manipulated the appearance of spiders by fixing a painted cardboard model (Quill 180 gsm paper) corresponding to a given treatment (Fig. 1) to each individual's otherwise flat dorsal abdomen using a ca. 5 mm^2 square of double-sided tape, such that the cardboard model covered the entirety of their dorsum. Importantly, we controlled the proportionate size of stimuli in each symmetry-class to ensure an equal area of colour coverage. That is, all solid-yellow treatments displayed approximately the same total amount of yellow (ca. 81 mm^2), all striped treatments had equal amounts of yellow and black (ca. 40 mm^2), and all black treatments displayed the same amount of black (ca. 81 mm^2). We used Derivan Matisse Yellow-Mid AZO Series 2 paint to imitate the yellow colouration of *G. fornicata*, which has previously been spectrally matched for this purpose using standard methods and is also a known match to

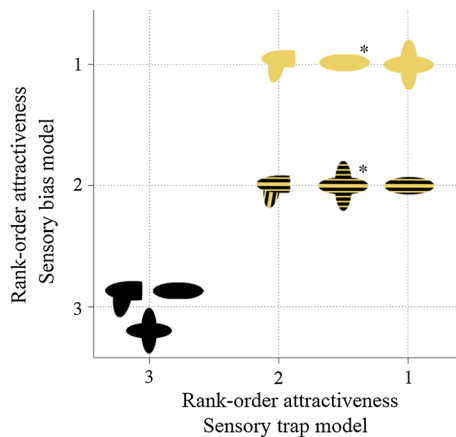


Fig. 2 The predicted attractiveness of artificial phenotypes under the sensory traps and sensory bias models of signal evolution. If lures are exploiting general colour-biases, the attractiveness of models should simply be predicted by yellow coverage. If, in contrast, lures are floral sensory traps, then the natural phenotype should be as equally attractive as the most 'flower-like' phenotype. Note that solid biradial and striped radial models (asterisked) are of intermediate rank on the x axis because it is difficult to derive unambiguous predictions for their rank-order attractiveness under the sensory traps model

sympatric insect-pollinated flora when modelled according to insect viewers (Maia et al. 2019; White and Kemp 2017). In addition to the nine primary treatments we included a further control in which spiders were unmanipulated save for a square of double-sided tape on their ventrum. Although *G. fornicata* are colour polymorphic, we used only yellow colouration in all treatments for simplicity and manipulated both ‘white’ and ‘yellow’ individuals in the field. There is some evidence for microhabitat differentiation between *G. fornicata* morphs (White and Kemp 2016), but our application of treatments was randomised and hence simply contributes unbiased residual variation (i.e., noise). The extent of any microhabitat effects therefore adds conservatism to our focal contrasts.

To estimate prey interceptions as a key component of fitness we used a walking transect-based method. Namely, after applying the cardboard models we recorded the presence of new prey and/or web damage at 30-min intervals over four hours, either in a morning (0800–1200) or, less often, afternoon (1300–1700) session. We selected this time interval as it allows for the repeated sampling of a significant number of individuals across the study site, while minimising the risk of missed interceptions due to web-repair and the rapid processing of prey items. A similar method has been validated in this system previously and it produced estimates of prey interceptions comparable to those from continuous observation (White 2017; White and Kemp 2016). Abiotic confounds (such as web damage by wind-blown debris) may inflate true interception rates and again contribute residual variation, though past work suggests that this indirect measure of prey interception is consistent with measures derived from the continuous observation of prey captures at the same sites and similar times of year (White and Kemp 2016). Spiders whose webs that sustained > 50% damage during an observation period were taken to indicate gross environmental disturbance and were excluded ($n = 12$) as well as those whose cardboard model did not remain affixed ($n = 04$). We did not (and could not) identify individual prey under this sampling method nor their behaviour when approaching the web, since our interest for the purpose of this test (as discussed above) was the aggregate response of *G. fornicata*’s prey community in an ecologically salient context—the precise conditions in which selection acts to shape phenotypic evolution. All work took place in November 2018 across populations spanning Cairns to Port Douglas, Queensland, Australia. The observer (TEW) could not be blind in regard to treatments, but the unambiguous response variable should work to ameliorate unconscious bias.

Statistical analyses

To validate the baseline efficacy of the phenotypic manipulations, we first tested for differences in prey interceptions between the wild-type treatment of *G. fornicata* (biradial striped; Fig. 1 centre) and unmanipulated spiders using a generalised linear mixed-effects model (GLMM). We specified interception rate (mean interceptions/30 min) as the Gaussian response following confirmation of the normality within groups, and treatment (presence/absence) as a main effect, with diel session (morning/afternoon) as a random covariate to account for any systematic differences associated with diel insect activity.

To test the effects of phenotypic manipulations on capture success we used a GLMM with interception rate (mean interceptions/30 min) as the response, as above. We specified an interaction between colour (black/striped/solid) and symmetry (asymmetric/biradial/radial) and their main effects and included diel session (morning/afternoon) as a random covariate. We then used Tukey post-hoc contrasts to test for pairwise differences across all treatment combinations. Should the sensory bias model best explain the attractiveness of

phenotypes we predict a main effect of colour alone (Fig. 2, y axis). In contrast, the sensory traps hypothesis predicts an interaction between colour and symmetry, with post-hoc tests revealing grouped differences in the manner specified on the x axis of Fig. 2 (and as discussed above). Following the above, we also ran post-hoc Levene's tests within each of the three symmetry treatments, to test for differences in the variances of prey interception rates as a function of colour patterning. Summary statistics reported below are pooled means \pm standard deviations of prey interception rates (interceptions/30 min). All analyses were run in R v. 3.5.2 (R Core Team 2018) using 'nlme' (Pinheiro et al. 2018) for linear mixed modelling and 'multcomp' (Hothorn et al. 2008) for multiple comparisons.

Data availability

All data are available via Zenodo (<https://doi.org/10.5281/zenodo.3724934>). Note that an earlier version of this manuscript appeared as a preprint (White and Kemp 2019).

Results

We found no difference in prey interception rates between control *Gasteracana fornicata* and wild-type treatments (treatment estimate = 0.07 ± 0.25 , $t_{1,41} = 0.29$, $p = 0.77$, $R^2 = 0.02$). The vanishingly small effect size between each group moreover supports the absence of any biologically relevant consequence of handling. For the main test, we found an interactive effect of colour and symmetry on prey interception rates ($F_{4,218} = 4.12$, $p \leq 0.01$, conditional $R^2 = 0.54$; Table 1), as well as main effects of colour ($F_{2,218} = 107.40$, $p \leq 0.01$) and symmetry ($F_{2,218} = 15.08$, $p \leq 0.01$). Pairwise contrasts (Supplementary Table S1) revealed considerable variation in prey interception rates between treatments, with three distinct phenotypic groupings (Fig. 3). Spiders assigned to black control treatments intercepted prey less frequently than all others (0.84 ± 0.77 interceptions/30 min), while both striped- and solid-coloured asymmetric phenotypes had greater capture success (1.92 ± 0.70 interceptions/30 min). The highest rates of prey interception were shared by radially and biradially symmetric treatments across both striped- and solid-coloured phenotypes (2.86 ± 0.89

Table 1 Parameter estimates from a linear mixed-effects model of phenotypic manipulations of colour (black, striped, solid yellow) and symmetry (asymmetric, biradial, radial) on prey interceptions by *Gasteracantha fornicata*

Parameter	Estimate	Std. err.	t	p
Intercept	0.85	0.15	5.63	< 0.001
Colour (stripe)	0.89	0.23	3.94	< 0.001
Colour (yellow)	1.24	0.21	5.77	< 0.001
Symmetry (biradial)	0.06	0.21	0.26	0.794
Symmetry (radial)	- 0.08	0.25	- 0.33	0.744
Colour (striped) \times symmetry (biradial)	0.97	0.31	3.10	0.002
Colour (yellow) \times symmetry (biradial)	0.77	0.30	2.56	0.011
Colour (striped) \times symmetry (radial)	1.19	0.35	3.45	< 0.001
Colour (yellow) \times symmetry (radial)	0.89	0.34	2.60	0.010

Diel session was a random effect with a variance of 0.816. Conditional $R^2 = 0.54$

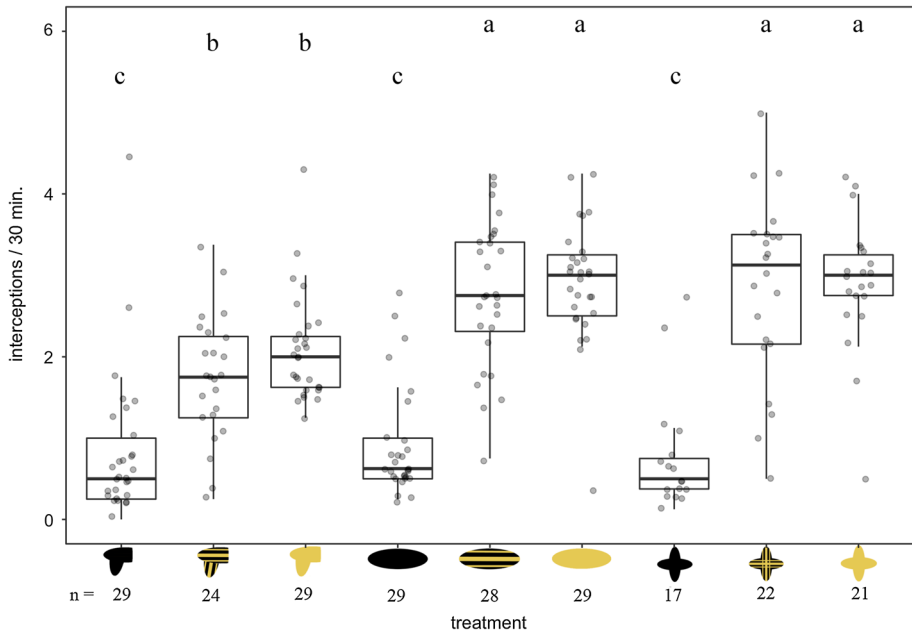


Fig. 3 The effect of phenotypic manipulations (Fig. 1) on prey interception rates in *G. fornicata*. Boxes denote the median and first and third quartiles, while whiskers extend to values at a maximum of 1.5 times the inter-quartile range. Horizontal lines indicate statistically distinct treatment groupings based on post-hoc multiple comparisons. Sample sizes are indicated below each treatment

intercepts/30 min). We found no difference in the variances of prey interception rates as a function of colour patterning within any of the asymmetric ($W=0.26$, $p=0.77$), biradial ($W=1.80$, $p=0.17$), or radial ($W=2.33$, $p=0.11$) treatments.

Discussion

Visual lures are a striking adaptation for predation, but the mechanism of deception is poorly resolved. Here we manipulated the phenotypes of the jewelled spider *Gasteracantha fornicata* along an approximate gradient of floral resemblance to test whether deceptive lures are exploiting simple colour-biases or co-opting foraging preferences, in prey. Consistent with the sensory traps model (Fig. 2, x axis), we found prey interception rates were similar for the wild type and the biradially symmetric, solid-yellow (most ‘floral’) treatment (Fig. 3). By contrast, we found no support for the sensory bias model; the sheer extent of yellow colouration between treatments was not solely predictive of prey interceptions. Since the wild type treatment and unmanipulated (control) spiders were similarly attractive, and black spiders were consistently less attractive than yellow spiders, we conclude that the manipulations were effective and specific in consequence (Fig. 3; Supplementary Table S1). When considered alongside evidence that *G. fornicata* attracts pollinating Diptera and Hymenoptera (White and Kemp 2016) and bears close resemblance to sympatric flowers as viewed by these insects (White et al. 2017), our results suggest that the signals of female *G. fornicata* are a sensory trap which co-opt the foraging responses of prey.

Though the wild-type and most ‘flower-like’ phenotypes were equally attractive (Fig. 3), *Gasteracantha fornicata* are unlikely to be a simple mimic of any one sympatric flower. Rather, the signals of spiders are likely presenting a combination of visual cues that are shared by local flowers including, but not limited to, the spectral, spatial, and symmetric properties of patterns (O’Hanlon et al. 2014; White et al. 2017). This accords with known features of visual processing among well-studied insects in which local cues such as (in order of prioritisation) colour, modulation, shape, area, and orientation are weighed and integrated to guide the choice and classification of stimuli (Giurfa et al. 1995, 1996; Horridge and Zhang 1995; Horridge 2007). These cues can be readily generalised to novel contexts (Stach et al. 2004), and their relative importance may vary during assessments of mimetic accuracy (e.g. colour similarity may be prioritised over shape; Kazemi et al. 2014) or with cognitive load (e.g. in speed-accuracy trade-offs; Chittka and Osorio 2007). This offers a basis for deceptive signal efficacy among luring predators despite their apparent distinctiveness from flowers to humans. That is, lures may need only present an ensemble of a few salient cues, rather than a faithful analogue of floral signals, to exploit the foraging response of insect prey (discussed further below). This possibility is further enabled by both the phenotypic diversity of sympatric flora, which present a suite of shapes, symmetries, and colour patterns from which deceptive signallers may draw (see White et al. 2017 for data relevant to *G. fornicata* specifically), and gross variation in the sensory systems of viewers (such as flies and bees), since differences in the rank-order importance of individual cues and combinations thereof may generate a broader perceptual canvas for signallers (Song and Lee 2018). Our finding that colour alone was attractive to insects, and even more so when combined with floral symmetry cues, is consistent with such a view (Fig. 3), though awaits closely controlled behavioural work to test in further detail.

While the presence of colour in any form was associated with improved attractiveness, the colour pattern—be it solid or striped—had no further effect (Fig. 3). There are two plausible explanations for the lack of a pattern effect. One is that the stripes cannot be visually resolved by the insect when it views the flower, and a striped pattern would instead only generate a subtly duller, though still ‘solid’, signal that is functionally equivalent to their block-coloured counterparts. Although the stripes are indeed likely to be resolved only at close distances by typical fly and bee viewers (Land 1997), past work has shown that interception rates are directly modified by the orientation of the stripes of *G. fornicata* in the web (White 2017), thereby establishing the discriminability of the patterns at relevant viewing distances. A simple alternative, related to the above, is that both striped and solid variants present attractive cues to viewers that are shared by flowers. Solid colours are typical among flowers, though some 33% of radially symmetric and 14% of bilaterally symmetric species also present patterned ‘floral guides’ (Dafni and Giurfa 1999). Such guides take the form of repeated stripes and/or radiating elements, which serve to draw pollinators to the location of nectar and pollen centers (Dafni and Kevan 1996; Dafni and Giurfa 1999). The banded pattern of *G. fornicata* and our striped, radial treatment are thus unlikely to be entirely novel to experienced receivers and may merely present another cue that pollinators recognise as broadly ‘floral’.

The role of colour in visual deception is widespread, and our results support the extension of sensory models to formalise the study of its causes and predicted consequences more generally. The dynamic displays of crab spiders (Heiling et al. 2003), red rims of pitcher plants (Bennett and Ellison 2009; Schaefer and Ruxton 2008), and decorated webs of spiders (Herberstein et al. 2000) are striking examples, though identifying the underlying mechanism in each case has proven difficult (Herberstein et al. 2000; Schaefer and Ruxton 2009). Our results reiterate the well understood necessity of considering the

perspective of receivers, since human-subjective assessments of similarity are a poor guide to the existence and extent of mimicry (Fig. 3). Though our wild-type and ‘floral’ spider treatments bear little resemblance (to humans), our results are consistent with the view that they converge at some stage of sensory processing in insect viewers to elicit a shared foraging response, as noted above.

This accords with evidence from sexual signalling systems in which the co-option of food detection pathways underlies the attractiveness and early evolution of male sexual ornaments, such as the yellow caudal bands of male swordtail characins (Garcia and Ramirez 2005; Rodd et al. 2002). By the same token, the sexually deceptive signals of orchids may regularly evolve through the initial exploitation of foraging preferences among pollinators (Reiter et al. 2018; Lunau and Wester 2017). Interestingly once such signals become common within a population, receivers may ‘escape’ the sensory trap via selection for increased response thresholds or improved discriminability (Garcia and Ramirez 2005). We may predict a similar course in luring systems, though the consequences for signal evolution will diverge due to differences in the alignment of interests between signallers and receivers. In sexual contexts the interests of both parties are broadly aligned toward reproduction. Although selection may favour the partitioning of receivers’ feeding and sexual responses through improved discrimination of mimetic traps, they will ultimately respond positively to both sexual and foraging cues (Basolo and Endler 1995; Ryan and Cummings 2013). With respect to signallers, a known consequence is a shift toward signal honesty which also reduces the foraging costs to receivers of responding to deceptive cues (Garcia and Ramirez 2005). Luring systems, in contrast, cannot follow such a trajectory since they are entirely antagonistic. Thus, while selection for improved discrimination and response thresholds in receivers is a predictable outcome, the consequences for deceptive, as opposed to sexual, signal evolution will diverge. Possible outcomes include selection for improved mimetic fidelity via the integration of new cues or refinement of existing ones (e.g. a move toward closer spectral or morphological resemblance to models), a shift toward dietary specialisation or generalisation depending on the composition of available prey (and their foraging preferences), or the evolution of signal polymorphism if available prey and models are diverse enough to generate multiple fitness optima (Kazemi et al. 2014; Kikuchi and Pfennig 2013; White and Kemp 2016), all of which depend, in part, on the frequency and costs of interactions between signallers and receivers (Lehtonen and Whitehead 2014). These are intriguing avenues for future work and highlight the reciprocal promise of luring systems for fueling both empirical insight and theoretical development.

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