The visual lures of spiders exploit insect preferences for flower-like colour and symmetry

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Abstract

Sensory systems capture only a fragment of available information, which creates opportunities for the evolution of deceptive signalling. The sensory traps and sensory bias models have proven valuable for explaining how the structure of visual systems and environments may shape the evolution of sexual signal design, but their potential in deceptive contexts is largely untapped. Here we use the 'jewelled' orb-web spider *Gasteracantha fornicata* to formalise and 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 signal 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 interceptions; a key dimension of fitness. As predicted by the traps model, the most attractive phenotypes were those with flower-like radial symmetry and solid colour patterns, and their attractiveness equaled that of wild-type models. These results demonstrate that deceptive orb-web spider lures function, in part, as inter-kingdom 'sensory traps' via floral mimicry, and support the broader extension of sensory-based models to deceptive signalling contexts.

Introduction

Visual communication is ubiquitous, and the demands of effective information-exchange have driven diverse outcomes (Maia et al. 2013; Thoen et al. 2014; Dalrymple et al. 2015). Understanding this diversity requires examining the relationship between signals, environments, and receivers' sensory systems, for which the sensory traps and bias models — under the umbrella of sensory drive — have proven valuable (among a suite of related models; Christy 1995; Endler 1992; Endler and Basolo 1998; West-Eberhard 1979). According to sensory traps, signals evolve under a model-mimic dynamic to co-opt receiver responses that are adaptive in otherwise unrelated behavioural contexts (Christy et al. 2003). The design of sexual signals, for example, may be shaped by how potential mates detect or recognize food items (Rodd et al. 2002) or shelter (Christy et al. 2003). The sensory bias model, in contrast, emphasises how the existence of underlying sensory and/or perceptual biases may present opportunities for exploitation and hence drive signal evolution (Basolo and Endler 1995; 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; Basolo 1995). Empirically, each of these models have found robust support in the context of sexual signalling, however their ability to explain signal evolution more broadly is largely untested.

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 combining 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; Goncalves and Gawryszewski 2017; White and Kemp 2017). Two

63 hypotheses predominate, which informally mirror the bias and traps models; namely, that lures (1)
64 exploit innate colour preferences, or (2) co-opt the foraging response of prey toward flowers.
65 Empirical support for these hypotheses is presently limited to observational and correlative data,
66 and hence remains equivocal (e.g., Tso et al. 2004; Chuang et al. 2007b; Goncalves and
67 Gawryszewski 2018; White et al. 2017). Formalising these hypotheses within sensory models
68 offers a promising path to progress, with the reciprocal benefit of extending such theory to
69 deceptive contexts.

70 Though elements of the bias and traps models overlap, their core predictions as applied to
71 deceptive lures can be neatly partitioned (White & Kemp 2015). If conspicuous visual lures are
72 exploiting receivers' sensory biases then the most likely perceptual target is colour. The insect
73 prey of luring predators are taxonomically diverse, though pollinating flies and bees are
74 overrepresented (Nentwig 1985; Nentwig 1987; O'Hanlon et al. 2014a). Strong innate preferences
75 for (human-perceived) yellows and whites are well documented (Kay 1976; Lunau 1988; Lunau
76 and Maier 1995), and parallel the biased distribution of these colours among predator lures (White
77 and Kemp 2015). A standing prediction under the bias model, then, is that the presence and size
78 of preferred colours among deceptive signallers should predict their attractiveness to potential
79 prey. The traps hypothesis, in contrast, suggests that lures are exploiting an otherwise-adaptive
80 attraction to flowers, in a dynamic more akin to floral mimicry. Accumulating evidence for the
81 predicted resemblance between lures and sympatric flowers supports this view (Tso et al. 2004;
82 Goncalves and Gawryszewski 2017; White et al. 2017). The key untested prediction, however, is
83 that lures should co-opt the response of prey toward flowers. The strongest evidence to date comes
84 from the orchid mantis, which resembles (O'Hanlon et al. 2013; O'Hanlon et al. 2014b) and is
85 more attractive to pollinators (O'Hanlon et al. 2014a) than sympatric flowers. Though compelling,

86 the restricted range of experimental stimuli offered to pollinators presents a challenge to
87 unambiguously distinguishing between the traps and (more permissive) bias explanations.

88 Here we sought to formalise and test these adaptive hypotheses for visual luring using the
89 jewelled orb-web spider *Gasteracantha fornicata* (supplementary Fig. S1). Females of the species
90 are colour polymorphic sit-and-wait predators, whose striking yellow- or white-and-black banded
91 abdomens actively attract prey — primarily pollinating Diptera and Hymenoptera — to their webs
92 (Hauber 2002; Kemp et al. 2013; White and Kemp 2016). To distinguish between the traps and
93 bias hypotheses in a field-based assay we manipulated the appearance of female *G. fornicata* in
94 the wild along two axes — colour and symmetry (Fig. 1). This served two purposes. First, it varied
95 the presence and size of a colour patch for which pollinating insects have a known bias (as
96 discussed above). Second, the selected combinations of colour and symmetry generated an
97 approximate gradient of floral resemblance. Colour is a central channel of information for insects
98 that aids in the detection, discrimination, and memorisation of rewarding resources (Chittka and
99 Raine 2006), and the floral colour gamut itself is thought to have evolved in response to the colour
100 vision of pollinators (Chittka and Menzel 1992; Chittka 1996; Shrestha et al. 2013). When
101 foraging, pollinating insects integrate these colour preferences with information on different forms
102 of floral symmetry, which they can readily perceive and express preferences for (as contrasted
103 with asymmetry, which is aversive: Kay 1976; Lehrer et al. 1995; Lunau and Maier 1995; Giurfa
104 et al. 1996). The two main forms of symmetry described in angiosperms are radial (actinomorphy)
105 and bilateral (zygomorphy), with radial symmetry pre-dating other forms by some 40 MYA,
106 actively preferred by model insects (Giurfa et al. 1996), and outnumbering bilateral species 2:1
107 (Crane et al. 1995; Neal et al. 1998; Endress 2001). This manipulation thus allows for
108 discrimination between the predictions of the biases and traps hypotheses as applied to deceptive

lures. If lures are exploiting simple colour biases, then the sheer area of yellow coverage within signals should best predict the attractiveness of phenotypes (Fig 2a). If lures are instead mimicking flowers, then the traps model predicts an equivalently heighted response to natural phenotypes and the most 'flower-like' stimulus specifically (Fig. 2b).

Methods

Phenotype manipulations and prey interception rates

Our phenotypic manipulations included asymmetric, biradially symmetric, and radially symmetric shapes, in a fully crossed combination of solid black, black-and-yellow banded, and solid yellow patterns (n = 17-29 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 dorsum using a ca. 5 mm^2 square of double-sided tape. 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 models displayed approximately the same total amount of yellow (ca. 81 mm^2), all striped models had equal amounts of yellow and black (ca. 40 mm^2), and all black models 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 sympatric insect-pollinated flora (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

130 save for a square of double-sided tape on their ventrum. Though *G. fornicata* are colour
131 polymorphic we used only yellow colouration in all treatments for simplicity, and manipulated
132 both 'white' and 'yellow' individuals in the field.

133 To estimate prey interceptions, a key component of spider fitness, we used a transect-base
134 method comparable to one previously used in this system (White 2017). After applying the
135 cardboard models, we recorded the presence of new prey and/or web damage at 30 minute intervals
136 for four hours, either in a morning (0800-1200) or, less often, afternoon (1300-1700) session.
137 Abiotic confounds may inflate true interception rates, but the effects should be randomly
138 distributed across treatments. Spiders whose webs that sustained >50% damage (indicating gross
139 environmental disturbance) during an observation period were excluded (n = 12) as well as those
140 whose model did not remain affixed (n = 4), and the experiments took place in November 2018
141 across populations spanning Cairns to Port Douglas, Queensland, Australia. The observer (TEW)
142 was not blind to treatments, but the unambiguous response variable and simultaneous testing of
143 multiple hypotheses should work to ameliorate unconscious bias.

144

145 *Statistical analyses*

146 To validate the baseline efficacy of the phenotypic manipulations, we first tested for
147 differences in prey interceptions between the wild-type models of *G. fornicata* (biradial striped;
148 Fig. 1 centre) and unmanipulated spiders using a generalised linear mixed-effects model (GLMM).
149 We specified interception rate (mean interceptions / 30 minutes) as the gaussian response
150 following confirmation of the normality within groups, and treatment (presence/absence) as a main

151 effect, with diel session (morning/afternoon) as a random covariate to account for any systematic
152 differences associated with diel insect activity.

153 For the central tests we used a GLMM with interception rate (mean interceptions / 30
154 minutes) as the response, as above. We specified an interaction between colour
155 (black/striped/solid) and symmetry (asymmetric/biradial/radial) and their main effects, and
156 included diel session (morning/afternoon) as a random covariate. We then used Tukey post-hoc
157 contrasts to test for pairwise differences across all treatment combinations. Should the sensory bias
158 model best explain the attractiveness of phenotypes, we predict a main effect of colour alone (Fig.
159 2a). In contrast, the sensory traps hypothesis predicts an interaction between colour and symmetry,
160 with post-hoc tests revealing grouped differences in the manner specified in Figure 2b (and as
161 discussed above). Summary statistics reported below are pooled means ± standard deviations of
162 prey interceptions rates (interceptions / 30 minutes). All analyses were run in R v. 3.5.2 (R Core
163 Team 2018) using 'nlme' (Pinheiro et al. 2018) for linear mixed modelling and 'multcomp'
164 (Hothorn et al. 2008) for multiple comparisons.

165

166 *Data availability*

167 All data and code will be made persistently available via Github and Zenodo upon acceptance.

168

169 Results

170 We found no difference in prey interception rates between unmanipulated *Gasteracana.*
171 *fornicata* and wild-type models ($F_{1,41} = 0.65$, $p = 0.43$, $R^2 = 0.02$). For the main test, we found an

interactive effect of colour and symmetry on prey interception rates ($F_{4,218}$ = 4.12, p = < 0.01, conditional R^2 = 0.54), as well as main effects of colour ($F_{2,218}$ = 107.40, p = < 0.01) and symmetry ($F_{2,218}$ = 15.08, p = < 0.01). Pairwise contrasts (supplementary table S1) revealed considerable variation in prey interception rates between treatments, with three distinct groupings of experimental phenotypes (Fig. 3). Spiders assigned to black control treatments intercepted prey less frequently than all others (0.84 ± 0.77), while both striped- and solid-coloured asymmetric phenotypes had greater capture success (1.92 ± 0.70). 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).

Discussion

Visual lures are a striking adaptation for predation, but the underlying mechanism of deception is poorly resolved. In a field-based assay, 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. As predicted by the sensory traps model (Fig. 2b), we found equivalently heightened prey interception rates between the natural phenotype and the biradially symmetric, solid-yellow (most 'floral') model (Fig. 3). In contrast, the sheer coverage of yellow colouration on models was not singularly predictive of prey interceptions as expected under a bias explanation (Fig. 2a). Control tests suggest that the manipulations were convincing and effective, with no difference in interception rates between the wild-type model and unmanipulated spiders, and significant differences between black models and all others (Fig. 3; supplementary table S1). The deceptive

194 lures of *G. fornicata* thus appear to co-opt the foraging responses of prey toward flowers, in a
195 deceptive inter-kingdom sensory trap.

196 Though the wild-type and most 'flower-like' phenotypes were equally attractive (Fig. 3),
197 *Gasteracantha. fornicata* are unlikely to be a simple mimic of any one sympatric flower. Rather,
198 the signals of spiders are likely presenting a combination of visual cues that are shared by local
199 flowers including, but not limited to, the spectral, spatial, and symmetric properties of patterns
200 (O'Hanlon et al. 2014a; O'Hanlon et al. 2014b; White et al. 2017). This accords with known
201 features of visual processing among well-studied insects in which local cues such as (in order of
202 prioritisation) colour, modulation, shape, area, and orientation are weighed and integrated to guide
203 the choice and classification of stimuli (Giurfa et al. 1995; Horridge and Zhang 1995; Giurfa et al.
204 1996; Horridge 2007). These cues can be readily generalised to novel contexts (Stach et al. 2004),
205 and their relative importance may vary during assessments of mimetic accuracy (e.g. colour
206 similarity may prioritised over shape; Kazemi et al. 2014) or with cognitive load (e.g. in speed-
207 accuracy tradeoffs; Chittka & Osorio 2007). This offers a basis for deceptive signal efficacy among
208 luring predators despite their human-subjective distinctiveness from flowers. That is, lures may
209 need only present an ensemble of a few salient cues, rather than a faithful analogue of floral signals,
210 to exploit the foraging response of insect prey (discussed further below). This possibility is further
211 enabled by the phenotypic diversity of sympatric flora, which present a suite of shapes,
212 symmetries, and colour patterns from which deceptive signallers may draw (see White et al. 2017
213 for data relevant to *G. fornicata* specifically). Our finding that colour alone was attractive to
214 insects, yet moreso when combined with floral symmetry cues, is consistent with such a view (Fig.
215 3), though awaits closely controlled behavioural work to test in 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 this equivalence. One is that the stripes cannot be resolved at meaningful distances, 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 only resolvable 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 model are thus unlikely to be entirely novel to experienced receivers and may merely present another cue that pollinators recognise as broadly 'floral'.

The use of colour as a deceptive instrument 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 (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

239 similarity are a poor guide to the existence and extent of mimicry (Fig. 3). Though our wild-type
240 and 'floral' spider models bear little human-subjective resemblance, our results are consistent with
241 the view that they converge at some stage of sensory processing in insect viewers to elicit a shared
242 foraging response (as noted above). This accords with evidence from sexual signalling systems in
243 which the co-option of food detection pathways underlies the attractiveness and early evolution of
244 male sexual ornaments, such as the yellow caudal bands of male swordtail characins (Garcia &
245 Ramirez 2005; Rodd et al. 2002). Interestingly, once such signals become common within a
246 population, receivers may 'escape' the sensory trap via selection for increased response thresholds
247 or improved discriminability (Garcia & Ramirez 2005). We may predict a similar course in luring
248 systems, though the consequences for signal evolution will diverge due to differences in the
249 alignment of interests between signallers and receivers. In sexual contexts the interests of both
250 parties are broadly aligned toward reproduction. Although selection may favour the partitioning
251 of receivers' feeding and sexual responses through improved discrimination of mimetic traps, they
252 will ultimately respond positively to both sexual and foraging cues (Basolo and Endler 1995; Ryan
253 and Cummings 2013). With respect to signallers, a known consequence is a shift toward signal
254 honesty which also reduces the foraging costs to receivers of responding to deceptive cues (Garcia
255 & Ramirez 2005). Luring systems, in contrast, cannot follow such a trajectory since they are
256 entirely antagonistic. Thus while selection for improved discrimination and response thresholds in
257 receivers is a predictable outcome, the consequences for deceptive, as opposed to sexual, signal
258 evolution will diverge. These include selection for improved mimetic fidelity via the integration
259 of new cues and/or refinement of existing ones (e.g. a move toward closer spectral or
260 morphological resemblance to models), a shift toward dietary specialisation or generalisation
261 depending on the composition of available prey and their foraging preferences, and/or the

evolution of signal polymorphism if extant prey or models are diverse enough to generate multiple fitness optima (Kazemi et al. 2014; Kikuchi & Pfenning 2013; White & Kemp 2016). 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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Figures and Tables

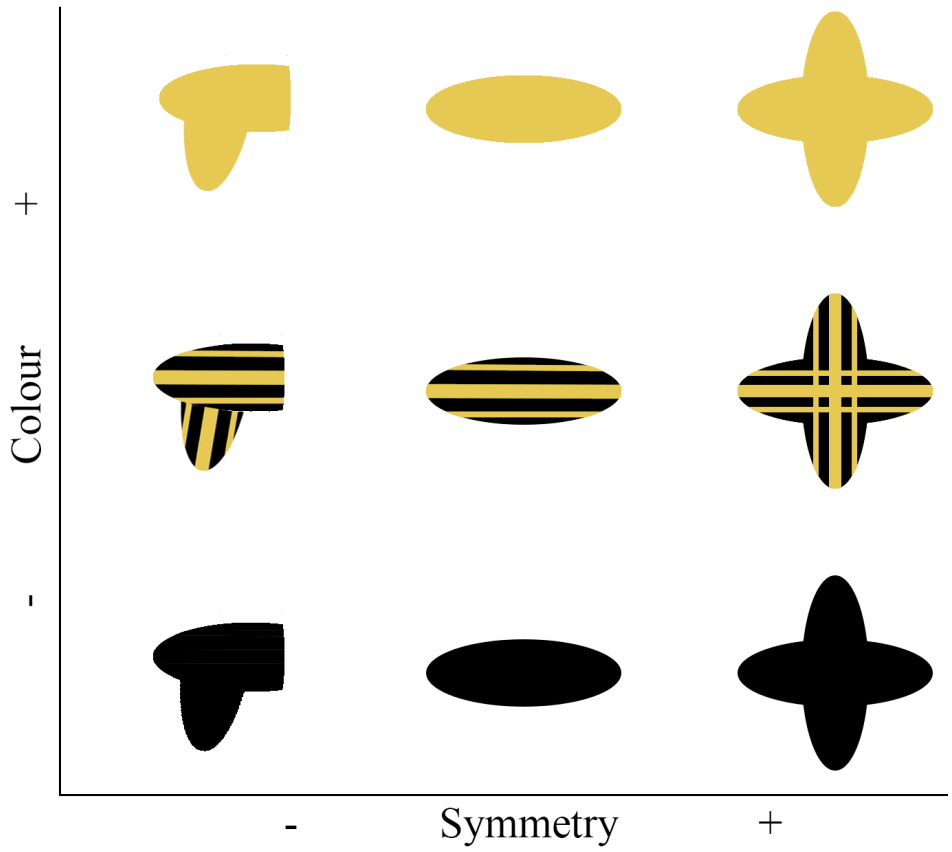


Figure 1: The models applied to female *G. fornicata*. The aim was to generate an approximate gradient of floral resemblance from most flower-like (top right) to least (bottom left), while including a wild-type model (center; also see Supplementary Fig. S1).

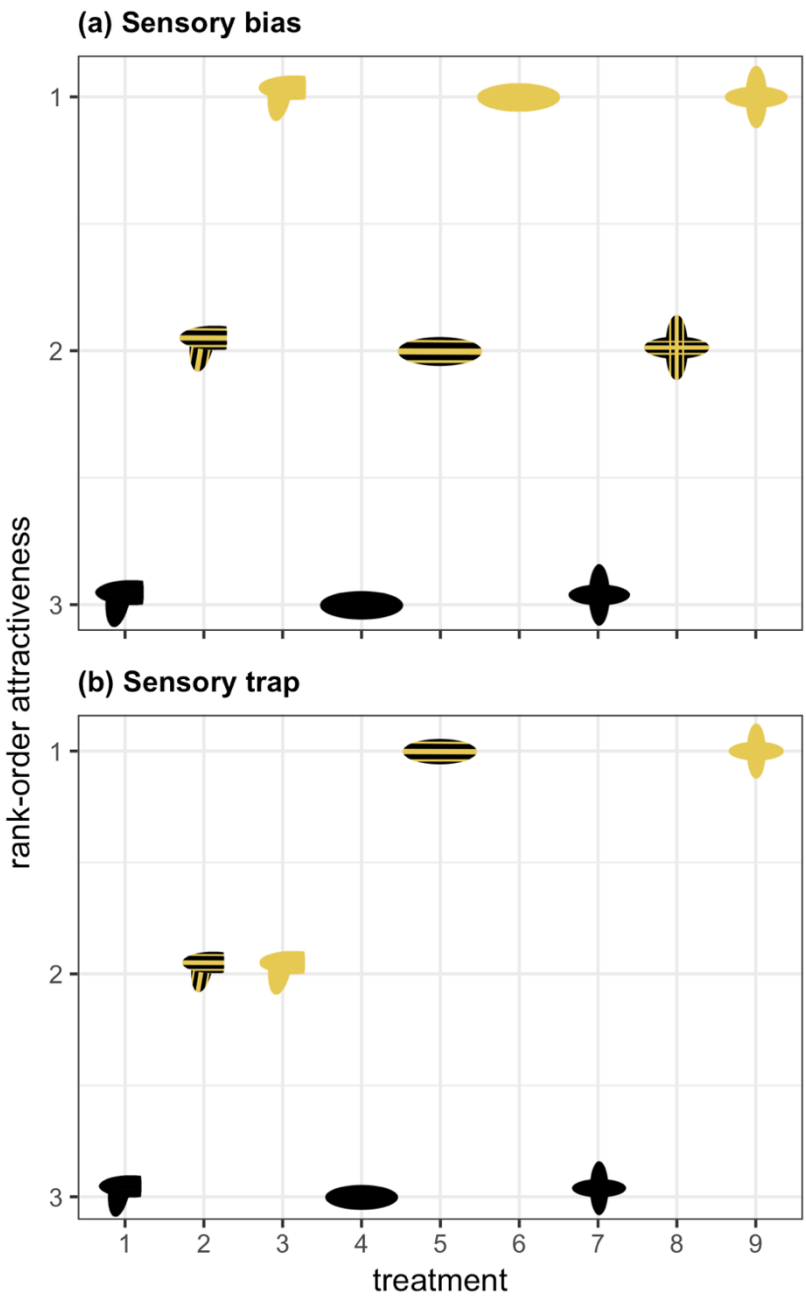
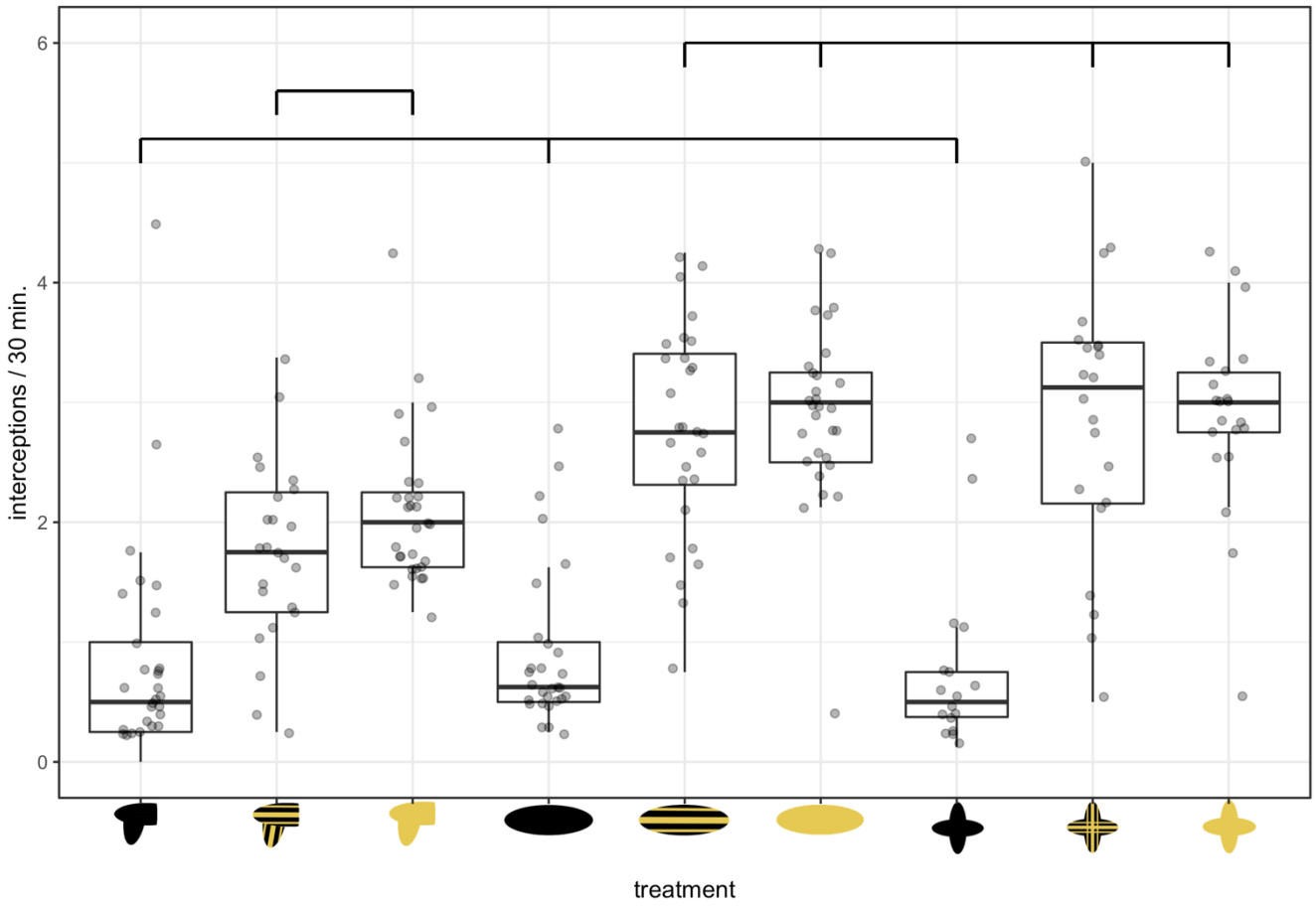


Figure 2: The predicted attractiveness of artificial phenotypes under the traps and bias models of signal evolution. If lures are exploiting general colour-biases, the attractiveness of models should simply be predicted by yellow coverage. If, in contrast, lures are floral sensory traps, then the natural phenotype should be as equally attractive as the most 'flower-like' phenotype. Note that solid biradial and striped radial models (6 and 9) are excluded from (b) for simplicity, since it is difficult to derive unambiguous predictions for their rank-order attractiveness from the sensory traps model.



460 **Figure 3:** The effect of phenotypic manipulations (Fig. 1) on prey interception rates in *G.*
461 *fornicata*. Boxes denote the median and first and third quartiles, while whiskers extend to values
462 at a maximum of 1.5 times the inter-quartile range. Horizontal lines indicate statistically distinct
463 treatment groupings based on post-hoc multiple comparisons. Sample sizes, left-to-right; 29, 24,
464 29, 29, 28, 29, 17, 22, 21.

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