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This is a post-peer-review, pre-copyedit version of an article published in *Evolutionary Ecology*. The final authenticated version is available online at:

White, T.E., Kemp, D.J. (2020) Spider lures exploit insect preferences for floral colour and symmetry. *Evolutionary Ecology*, Vol. 34, no. 4, pp. 543–553.

<https://doi.org/10.1007/s10682-020-10047-z>

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1 **Spider lures exploit insect preferences for floral colour and**  
2 **symmetry**

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12 **Keywords:** sensory trap, sensory bias, orb-web spider, prey lure, mimicry

13 **Word count (excluding abstract):** 3555

14 **Number of figures:** 3

15 **Number of tables:** 1

16 **Supplementary information:** Table S1

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18

19 **Abstract**

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

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## 43 **Introduction**

44           Visual communication is widespread, and the demands of effective information-exchange  
45 have driven diverse phenotypic outcomes (Maia et al. 2013; Thoen et al. 2014; Dalrymple et al.  
46 2015). Understanding this diversity requires examining the relationship between signals,  
47 environments, and sensory systems. The sensory traps and bias models — under the umbrella of  
48 sensory drive — have proven valuable to that end (among a suite of related models; Christy 1995;  
49 Endler 1992; Endler and Basolo 1998; West-Eberhard 1979). According to the sensory trap model  
50 signals evolve to co-opt receiver responses that are adaptive in unrelated contexts, in what is  
51 essentially a model-mimic dynamic (Christy et al. 2003). This model accounts for how the design  
52 of sexual signals, for example, may be shaped by how potential mates detect or recognize food  
53 items (e.g. via colour; Rodd et al. 2002) or shelter (e.g. through innate attraction to raised  
54 structures; Christy et al. 2003). The sensory bias model, by contrast, emphasizes how underlying  
55 sensory and/or perceptual biases may present opportunities for exploitation and hence drive signal  
56 evolution (Basolo and Endler 1995; Nelson et al. 2010; Ryan and Cummings 2013). The elaborate  
57 fins of male swordtails present a canonical example (Basolo 1990), having evolved in response to  
58 a pre-existing female bias toward such structures (Basolo 1990; Basolo 1995). These two models  
59 have robust empirical support in the context of sexual signalling, and innovative work in orchids  
60 and carnivorous plants continues to demonstrate how sexual- and food-deceptive 'traps' attract  
61 pollinating insects (reviewed in Gaskett et al. 2014; Lunau & Wester 2017). Nonetheless, much  
62 remains to be learned about the ability of bias and traps models to explain signal evolution more  
63 broadly.

64           Visual luring is a widespread predatory strategy and is particularly common among sit-  
65 and-wait predators. Orb-web spiders are a model group, with many species using striking body

66 colours and patterns to actively attract insect prey to the web (Tso et al. 2004; Chuang et al. 2007a;  
67 White and Kemp 2015). The question of why such conspicuous deceptive signals are attractive to  
68 insect viewers has been the focus of considerable attention (Tso et al. 2004; Chuang et al. 2007b;  
69 Rao et al. 2015; Goncalves and Gawryszewski 2017; White and Kemp 2017). Two hypotheses  
70 predominate in the literature, which informally mirror the bias and traps models; namely, that lures  
71 (1) exploit innate colour preferences, or (2) co-opt the foraging response of prey toward flowers.  
72 Empirical support for these hypotheses is presently limited to observational and correlative data,  
73 and hence remains equivocal (e.g., Tso et al. 2004; Chuang et al. 2007b; Goncalves and  
74 Gawryszewski 2018; White et al. 2017). Formalising these hypotheses within the models of  
75 sensory theory offers a promising path to progress and may prove reciprocally beneficial in guiding  
76 future studies of deceptive signalling.

77         Though the bias and traps models overlap to some degree, their core predictions as applied  
78 to deceptive lures can be neatly partitioned (White & Kemp 2015). If visual lures are exploiting  
79 receivers' sensory biases, then colour is likely to be a primary perceptual target. This follows from  
80 the fact that their prey are primarily flies and bees (Nentwig 1985; Nentwig 1987; O'Hanlon et al.  
81 2014a), of which many are pollinators. Strong innate preferences for (human-perceived) yellows  
82 and whites are well documented among such groups (Kay 1976; Lunau 1988; Lunau and Maier  
83 1995), which parallels a notably biased distribution of these colours among predator lures (White  
84 and Kemp 2015). A standing prediction under the bias model, then, is that the expression of  
85 preferred colours among deceptive signallers should predict their attractiveness to potential prey,  
86 as informally considered across the literature to date (e.g. Bush et al. 2008; Gawryszewski & Motta  
87 2012; Rao et al. 2015). The traps hypothesis, by contrast, suggests that lures are exploiting an  
88 otherwise-adaptive attraction to flowers in a dynamic more closely akin to floral mimicry. When

89 foraging for flowers, pollinating insects are guided by their aforementioned colour preferences as  
90 well as symmetry cues, which they express well-defined preferences for (Chittka and Raine 2006;  
91 Kay 1976; Lehrer et al. 1995; Lunau and Maier 1995; Giurfa et al. 1996). Radial symmetry is both  
92 the most ancient and common form showcased among angiosperms (Crane et al. 1995; Neal et al.  
93 1998; Endress 2001). Differentiating between the sensory traps and sensory bias hypotheses, then,  
94 requires several questions to be answered (Gaskett 2019; de Jager & Anderson 2019; White &  
95 Kemp 2015). First, do lures resemble floral 'models', as seen by the viewer? There is now good  
96 evidence for this across several systems including *Gasteracantha*, which we study here (Goncalves  
97 and Gawryszewski 2017; O'Hanlon et al. 2013; Tso et al. 2004; White et al. 2017). Second, do the  
98 lures and models share the same viewers? This too is apparent in our study system, as  
99 *Gasteracantha* nearly exclusively captures Hymenoptera and Diptera that pollinate sympatric  
100 flowers (White & Kemp 2016). A critical untested prediction, however, is that lures should co-opt  
101 their prey's natural response towards the model. Thus, any manipulation of the lure's resemblance  
102 to the model should modify the fitness of the deceptive signaller. In our system, this would mean  
103 that modifying the signals of *Gasteracantha* spiders so that they look more or less like flowers,  
104 should improve and reduce prey capture, respectively. Note that for generalist predators like orb-  
105 web spiders this prediction applies to the response of the prey community at large, rather than the  
106 preferences of any single viewer.

107         Here we sought to formalise and test these adaptive hypotheses for deceptive signalling  
108 using the jewelled orb-web spider *Gasteracantha fornicata* (Fig. 1). Females of the species are  
109 colour polymorphic sit-and-wait predators, whose striking yellow- or white-and-black banded  
110 abdomens lure prey — primarily pollinating Diptera and Hymenoptera — to their webs (Kemp et  
111 al. 2013; White and Kemp 2016). To distinguish between the traps and bias hypotheses we

112 manipulated the appearance of wild female *G. fornicata* in their natural habitats along two  
113 independent axes — colour and symmetry (Fig. 1). Our manipulations consisted of nine different  
114 treatments (including the wild-type) that encompassed the full-factorial combination of three levels  
115 of colour and three levels of symmetry. The sum of treatments represented an approximate gradient  
116 of floral resemblance, with a sensory trap hypothesis predicting positive covariance between  
117 capture success and the degree of floral resemblance (the x-axis of Fig. 2). Predicted attractiveness  
118 under the sensory bias model is however different, as discussed above, and the attractiveness in  
119 this case should scale with stimulus color alone (the y-axis of Fig. 2). We evaluated these  
120 predictions according to realized prey capture rates of wild, free-ranging spiders randomly  
121 assigned among the nine treatment stimuli.

122

## 123 **Methods**

124

### 125 *Phenotype manipulations and prey interception rates*

126 Our manipulative treatments included asymmetric, biradially symmetric, and radially  
127 symmetric shapes, in a fully factorial combination of solid black, black-and-yellow banded, and  
128 solid yellow patterns ( $n = 17-29$  each; Fig. 1). We manipulated the appearance of spiders by fixing  
129 a painted cardboard model (Quill 180 gsm paper) corresponding to a given treatment (Fig. 1) to  
130 each individual's otherwise flat dorsal abdomen using a ca.  $5 \text{ mm}^2$  square of double-sided tape,  
131 such that the cardboard model covered the entirety of their dorsum. Importantly, we controlled the  
132 proportionate size of stimuli in each symmetry-class to ensure an equal area of colour coverage.

133 That is, all solid-yellow treatments displayed approximately the same total amount of yellow (ca.  
134 81 mm<sup>2</sup>), all striped treatments had equal amounts of yellow and black (ca. 40 mm<sup>2</sup>), and all black  
135 treatments displayed the same amount of black (ca. 81 mm<sup>2</sup>). We used Derivan Matisse Yellow-  
136 Mid AZO Series 2 paint to imitate the yellow colouration of *G. fornicata*, which has previously  
137 been spectrally matched for this purpose using standard methods and is also a known match to  
138 sympatric insect-pollinated flora when modelled according to insect viewers (Maia et al. 2019;  
139 White and Kemp 2017). In addition to the nine primary treatments we included a further control  
140 in which spiders were unmanipulated save for a square of double-sided tape on their ventrum.  
141 Although *G. fornicata* are colour polymorphic, we used only yellow colouration in all treatments  
142 for simplicity and manipulated both ‘white’ and ‘yellow’ individuals in the field. There is some  
143 evidence for microhabitat differentiation between *G. fornicata* morphs (White and Kemp 2016),  
144 but our application of treatments was randomised and hence simply contributes unbiased residual  
145 variation (i.e., noise). The extent of any microhabitat effects therefore adds conservatism to our  
146 focal contrasts.

147 To estimate prey interceptions as a key component of fitness we used a walking transect-  
148 based method. Namely, after applying the cardboard models we recorded the presence of new prey  
149 and/or web damage at 30-minute intervals over four hours, either in a morning (0800-1200) or,  
150 less often, afternoon (1300-1700) session. We selected this time interval as it allows for the  
151 repeated sampling of a significant number of individuals across the study site, while minimising  
152 the risk of missed interceptions due to web-repair and the rapid processing of prey items. A similar  
153 method has been validated in this system previously and it produced estimates of prey interceptions  
154 comparable to those from continuous observation (White 2017; White et al. 2016). Abiotic  
155 confounds (such as web damage by wind-blown debris) may inflate true interception rates and



156 again contribute residual variation, though past work suggests that this indirect measure of prey  
157 interception is consistent with measures derived from the continuous observation of prey captures  
158 at the same sites and similar times of year (White & Kemp 2016). Spiders whose webs that  
159 sustained >50% damage during an observation period were taken to indicate gross environmental  
160 disturbance and were excluded (n = 12) as well as those whose cardboard model did not remain  
161 affixed (n = 4). We did not (and could not) identify individual prey under this sampling method  
162 nor their behaviour when approaching the web, since our interest for the purpose of this test (as  
163 discussed above) was the aggregate response of *G. fornicata*'s prey community in an ecologically  
164 salient context — the precise conditions in which selection acts to shape phenotypic evolution. All  
165 work took place in November 2018 across populations spanning Cairns to Port Douglas,  
166 Queensland, Australia. The observer (TEW) could not be blind in regard to treatments, but the  
167 unambiguous response variable should work to ameliorate unconscious bias.

168

### 169 *Statistical analyses*

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

177 To test the effects of phenotypic manipulations on capture success we used a GLMM with  
178 interception rate (mean interceptions / 30 minutes) as the response, as above. We specified an  
179 interaction between colour (black/striped/solid) and symmetry (asymmetric/biradial/radial) and  
180 their main effects and included diel session (morning/afternoon) as a random covariate. We then  
181 used Tukey post-hoc contrasts to test for pairwise differences across all treatment combinations.  
182 Should the sensory bias model best explain the attractiveness of phenotypes we predict a main  
183 effect of colour alone (Fig. 2, y axis). In contrast, the sensory traps hypothesis predicts an  
184 interaction between colour and symmetry, with post-hoc tests revealing grouped differences in the  
185 manner specified on the x axis of Figure 2 (and as discussed above). Following the above, we also  
186 ran post-hoc Levene's tests within each of the three symmetry treatments, to test for differences in  
187 the variances of prey interception rates as a function of colour patterning. Summary statistics  
188 reported below are pooled means  $\pm$  standard deviations of prey interception rates (interceptions /  
189 30 minutes). All analyses were run in R v. 3.5.2 (R Core Team 2018) using 'nlme' (Pinheiro et al.  
190 2018) for linear mixed modelling and 'multcomp' (Hothorn et al. 2008) for multiple comparisons.

191

#### 192 *Data availability*

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

195

## 196 **Results**

197           We found no difference in prey interception rates between control *Gasteracana fornicata*  
198 and wild-type treatments (treatment estimate =  $0.07 \pm 0.25$ ,  $t_{1,41} = 0.29$ ,  $p = 0.77$ ,  $R^2 = 0.02$ ). The  
199 vanishingly small effect size between each group moreover supports the absence of any  
200 biologically relevant consequence of handling. For the main test, we found an interactive effect of  
201 colour and symmetry on prey interception rates ( $F_{4,218} = 4.12$ ,  $p = < 0.01$ , conditional  $R^2 = 0.54$ ;  
202 table 1), as well as main effects of colour ( $F_{2,218} = 107.40$ ,  $p = < 0.01$ ) and symmetry ( $F_{2,218} = 15.08$ ,  
203  $p = < 0.01$ ). Pairwise contrasts (supplementary table S1) revealed considerable variation in prey  
204 interception rates between treatments, with three distinct phenotypic groupings (Fig 3). Spiders  
205 assigned to black control treatments intercepted prey less frequently than all others ( $0.84 \pm 0.77$   
206 intercepts/30 min), while both striped- and solid-coloured asymmetric phenotypes had greater  
207 capture success ( $1.92 \pm 0.70$  intercepts/30 min). The highest rates of prey interception were shared  
208 by radially and biradially symmetric treatments across both striped- and solid-coloured phenotypes  
209 ( $2.86 \pm 0.89$  intercepts/30 min). We found no difference in the variances of prey interception rates  
210 as a function of colour patterning within any of the asymmetric ( $W = 0.26$ ,  $p = 0.77$ ), biradial ( $W$   
211  $= 1.80$ ,  $p = 0.17$ ), or radial ( $W = 2.33$ ,  $p = 0.11$ ) treatments.

212

## 213 **Discussion**

214           Visual lures are a striking adaptation for predation, but the mechanism of deception is  
215 poorly resolved. Here we manipulated the phenotypes of the jewelled spider *Gasteracantha*  
216 *fornicata* along an approximate gradient of floral resemblance to test whether deceptive lures are

217 exploiting simple colour-biases or co-opting foraging preferences, in prey. Consistent with the  
218 sensory traps model (Fig. 2, x axis), we found prey interception rates were similar for the wild type  
219 and the biradially symmetric, solid-yellow (most 'floral') treatment (Fig. 3). By contrast, we found  
220 no support for the sensory bias model; the sheer extent of yellow colouration between treatments  
221 was not solely predictive of prey interceptions. Since the wild type treatment and unmanipulated  
222 (control) spiders were similarly attractive, and black spiders were consistently less attractive than  
223 yellow spiders, we conclude that the manipulations were effective and specific in consequence  
224 (Fig. 3; supplementary table S1). When considered alongside evidence that *G. fornicata* attracts  
225 pollinating Diptera and Hymenoptera (White & Kemp 2016) and bears close resemblance to  
226 sympatric flowers as viewed by these insects (White et al. 2017), our results suggest that the signals  
227 of female *G. fornicata* are a sensory trap which co-opt the foraging responses of prey. Though the  
228 wild-type and most 'flower-like' phenotypes were equally attractive (Fig. 3), *Gasteracantha*  
229 *fornicata* are unlikely to be a simple mimic of any one sympatric flower. Rather, the signals of  
230 spiders are likely presenting a combination of visual cues that are shared by local flowers  
231 including, but not limited to, the spectral, spatial, and symmetric properties of patterns (O'Hanlon  
232 et al. 2014; White et al. 2017). This accords with known features of visual processing among well-  
233 studied insects in which local cues such as (in order of prioritisation) colour, modulation, shape,  
234 area, and orientation are weighed and integrated to guide the choice and classification of stimuli  
235 (Giurfa et al. 1995; Horridge and Zhang 1995; Giurfa et al. 1996; Horridge 2007). These cues can  
236 be readily generalised to novel contexts (Stach et al. 2004), and their relative importance may vary  
237 during assessments of mimetic accuracy (e.g. colour similarity may be prioritised over shape;  
238 Kazemi et al. 2014) or with cognitive load (e.g. in speed-accuracy trade-offs; Chittka & Osorio  
239 2007). This offers a basis for deceptive signal efficacy among luring predators despite their

240 apparent distinctiveness from flowers to humans. That is, lures may need only present an ensemble  
241 of a few salient cues, rather than a faithful analogue of floral signals, to exploit the foraging  
242 response of insect prey (discussed further below). This possibility is further enabled by both the  
243 phenotypic diversity of sympatric flora, which present a suite of shapes, symmetries, and colour  
244 patterns from which deceptive signallers may draw (see White et al. 2017 for data relevant to *G.*  
245 *fornicata* specifically), and gross variation in the sensory systems of viewers (such as flies and  
246 bees), since differences in the rank-order importance of individual cues and combinations thereof  
247 may generate a broader perceptual canvas for signallers (Song & Lee 2018). Our finding that  
248 colour alone was attractive to insects, and even more so when combined with floral symmetry  
249 cues, is consistent with such a view (Fig. 3), though awaits closely controlled behavioural work to  
250 test in further detail.

251         While the presence of colour in any form was associated with improved attractiveness, the  
252 colour pattern — be it solid or striped — had no further effect (Fig. 3). There are two plausible  
253 explanations for the lack of a pattern effect. One is that the stripes cannot be visually resolved by  
254 the insect when it views the flower, and a striped pattern would instead only generate a subtly  
255 duller, though still ‘solid’, signal that is functionally equivalent to their block-coloured  
256 counterparts. Although the stripes are indeed likely to be resolved only at close distances by typical  
257 fly and bee viewers (Land 1997), past work has shown that interception rates are directly modified  
258 by the orientation of the stripes of *G. fornicata* in the web (White 2017), thereby establishing the  
259 discriminability of the patterns at relevant viewing distances. A simple alternative, related to the  
260 above, is that both striped and solid variants present attractive cues to viewers that are shared by  
261 flowers. Solid colours are typical among flowers, though some 33% of radially symmetric and  
262 14% of bilaterally symmetric species also present patterned ‘floral guides’ (Dafni and Giurfa

263 1999). Such guides take the form of repeated stripes and/or radiating elements, which serve to  
264 draw pollinators to the location of nectar and pollen centers (Dafni and Kevan 1996; Dafni and  
265 Giurfa 1999). The banded pattern of *G. fornicata* and our striped, radial treatment are thus unlikely  
266 to be entirely novel to experienced receivers and may merely present another cue that pollinators  
267 recognise as broadly 'floral'.

268         The role of colour in visual deception is widespread, and our results support the extension  
269 of sensory models to formalise the study of its causes and predicted consequences more generally.  
270 The dynamic displays of crab spiders (Heiling et al. 2003), red rims of pitcher plants (Bennett &  
271 Ellison 2009; Schaefer and Ruxton 2008), and decorated webs of spiders (Herberstein et al. 2000)  
272 are striking examples, though identifying the underlying mechanism in each case has proven  
273 difficult (Herberstein et al. 2000; Schaefer and Ruxton 2009). Our results reiterate the well  
274 understood necessity of considering the perspective of receivers, since human-subjective  
275 assessments of similarity are a poor guide to the existence and extent of mimicry (Fig. 3). Though  
276 our wild-type and 'floral' spider treatments bear little resemblance (to humans), our results are  
277 consistent with the view that they converge at some stage of sensory processing in insect viewers  
278 to elicit a shared foraging response, as noted above. This accords with evidence from sexual  
279 signalling systems in which the co-option of food detection pathways underlies the attractiveness  
280 and early evolution of male sexual ornaments, such as the yellow caudal bands of male swordtail  
281 characins (Garcia & Ramirez 2005; Rodd et al. 2002). By the same token, the sexually deceptive  
282 signals of orchids may regularly evolve through the initial exploitation of foraging preferences  
283 among pollinators (Reiter et al. 2018; Lunau & Wester 2017). Interestingly once such signals  
284 become common within a population, receivers may 'escape' the sensory trap via selection for  
285 increased response thresholds or improved discriminability (Garcia & Ramirez 2005). We may

286 predict a similar course in luring systems, though the consequences for signal evolution will  
287 diverge due to differences in the alignment of interests between signallers and receivers. In sexual  
288 contexts the interests of both parties are broadly aligned toward reproduction. Although selection  
289 may favour the partitioning of receivers' feeding and sexual responses through improved  
290 discrimination of mimetic traps, they will ultimately respond positively to both sexual and foraging  
291 cues (Basolo and Endler 1995; Ryan and Cummings 2013). With respect to signallers, a known  
292 consequence is a shift toward signal honesty which also reduces the foraging costs to receivers of  
293 responding to deceptive cues (Garcia & Ramirez 2005). Luring systems, in contrast, cannot follow  
294 such a trajectory since they are entirely antagonistic. Thus, while selection for improved  
295 discrimination and response thresholds in receivers is a predictable outcome, the consequences for  
296 deceptive, as opposed to sexual, signal evolution will diverge. Possible outcomes include selection  
297 for improved mimetic fidelity via the integration of new cues or refinement of existing ones (e.g.  
298 a move toward closer spectral or morphological resemblance to models), a shift toward dietary  
299 specialisation or generalisation depending on the composition of available prey (and their foraging  
300 preferences), or the evolution of signal polymorphism if available prey and models are diverse  
301 enough to generate multiple fitness optima (Kazemi et al. 2014; Kikuchi & Pfenning 2013; White  
302 & Kemp 2016), all of which depend, in part, on the frequency and costs of interactions between  
303 signallers and receivers (Lehtonen & Whitehead 2014). These are intriguing avenues for future  
304 work and highlight the reciprocal promise of luring systems for fueling both empirical insight and  
305 theoretical development.

306

307 **Acknowledgments**

308 We thank Matthew Symonds, Anne Gaskett, and two anonymous reviewers for their thoughtful  
309 feedback, which greatly improved the manuscript. TEW thanks Elizabeth Mulvenna and Cormac  
310 White for their endless support. We have no conflicts of interest to declare.

311

312 **Funding**

313 None to report.



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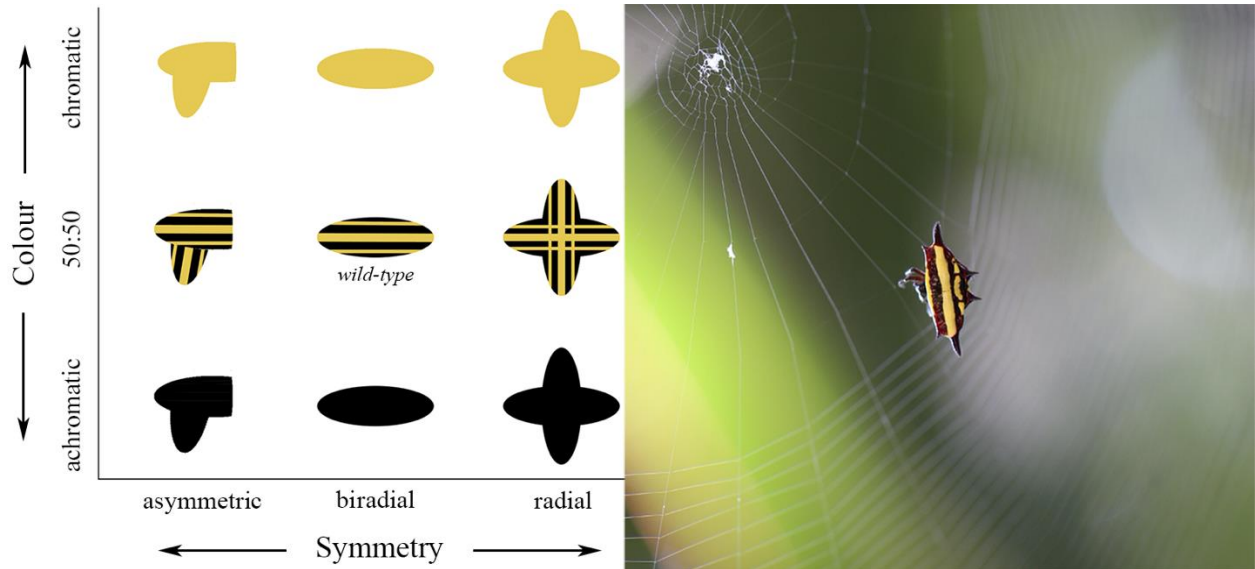
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476 **Figures & tables**

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

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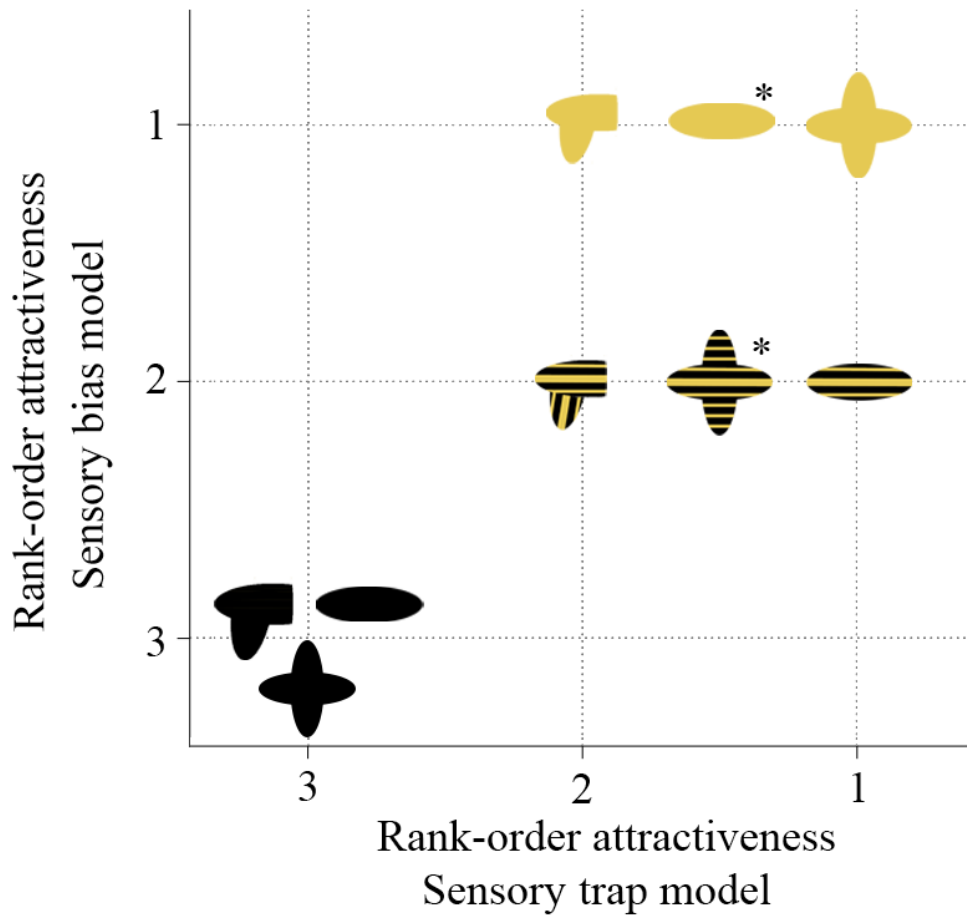
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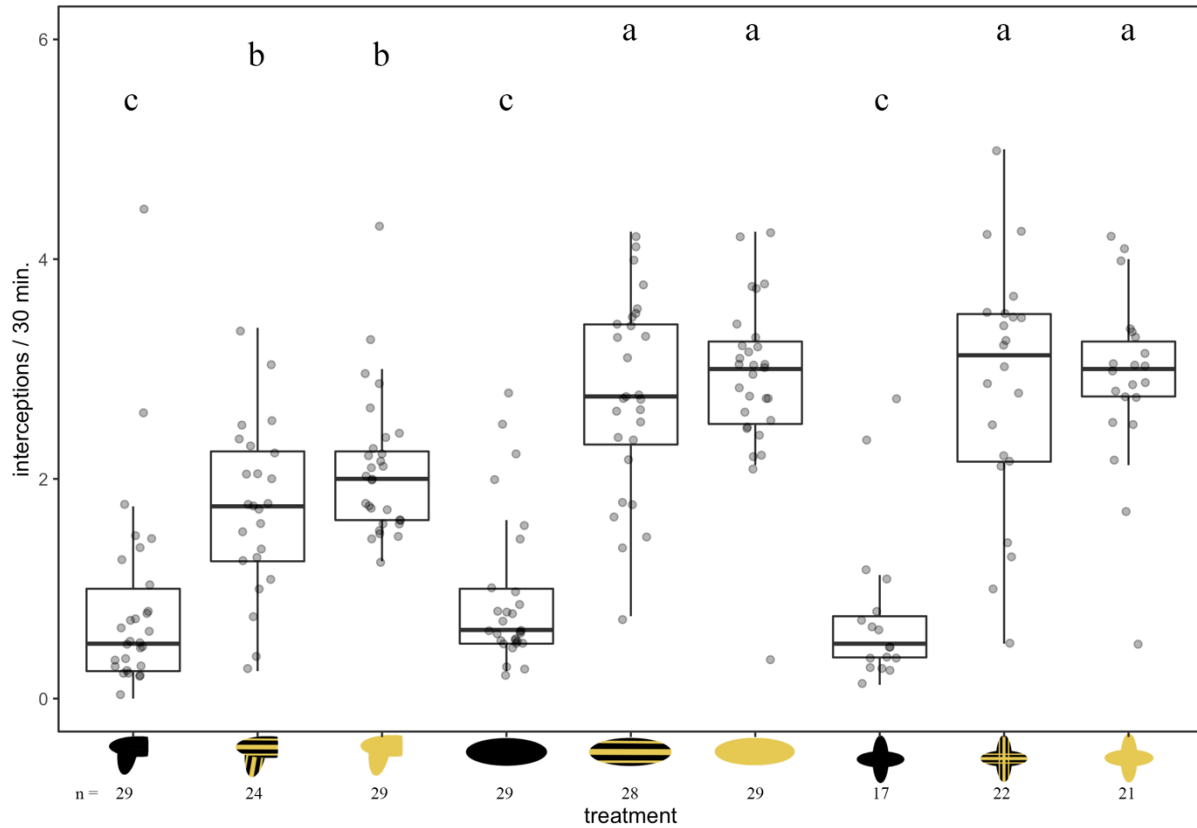


**Figure 2:** The predicted attractiveness of artificial phenotypes under the sensory traps and sensory bias models of signal evolution. If lures are exploiting general colour-biases, the attractiveness of models should simply be predicted by yellow coverage. If, in contrast, lures are floral sensory 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.



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

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529 **Table 1:** Parameter estimates from a linear mixed-effects model of phenotypic manipulations of  
530 colour (black, striped, solid yellow) and symmetry (asymmetric, biradial, radial) on prey  
531 interceptions by *Gasteracantha fornicata*. Diel session was a random effect with a variance of  
532 0.816 . Conditional  $R^2 = 0.54$ .

<i>parameter</i>	<i>Estimate</i>	<i>Std. Err.</i>	<i>t</i>	<i>P</i>
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) x symmetry (biradial)	0.97	0.31	3.10	0.002
colour (yellow) x symmetry (biradial)	0.77	0.30	2.56	0.011
colour (striped) x symmetry (radial)	1.19	0.35	3.45	< 0.001
colour (yellow) x symmetry (radial)	0.89	0.34	2.60	0.010

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