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1 **Title:**

2 Distance-dependent pattern blending can camouflage salient aposematic signals

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17

18 **Abstract**

19 The effect of viewing distance on the perception of visual texture is well known: spatial  
20 frequencies higher than the resolution limit of an observer's visual system will be summed  
21 and perceived as a single combined colour. In animal defensive colour patterns, distance-  
22 dependent pattern blending may allow aposematic patterns, salient at close range, to match  
23 the background to distant observers. Indeed, recent research has indicated that reducing the  
24 distance from which a salient signal can be detected can increase survival over camouflage  
25 or conspicuous aposematism alone. We investigated whether the spatial frequency of  
26 conspicuous and cryptically coloured stripes affects the rate of avian predation. Our results  
27 are consistent with pattern blending acting to camouflage salient aposematic signals  
28 effectively at a distance. Experiments into the relative rate of avian predation on edible  
29 model caterpillars found that increasing spatial frequency (thinner stripes) increased survival.  
30 Similarly, visual modelling of avian predators showed that pattern blending increased the  
31 similarity between caterpillar and background. These results show how a colour pattern can  
32 be tuned to reveal or conceal different information at different distances, and produce  
33 tangible survival benefits.

34 **Key words**

35 aposematism, camouflage, defensive colouration, distance, visual ecology, warning signals.

## 37 **1. Background**

38 Camouflage and aposematism are two seemingly contrasting and mutually exclusive forms  
39 of antipredator colouration: camouflage reduces the likelihood of detection, whereas,  
40 aposematic signals communicate directly with predators [1, 2]. Aposematism is often  
41 associated with high conspicuousness, and increasing conspicuousness has repeatedly  
42 been linked to greater speed and accuracy of predator avoidance learning [3, 4]. However,  
43 rather than developing a complete avoidance of aposematic prey, it is now apparent that  
44 predators learn about prey characteristics, actively managing their consumption of defended  
45 prey depending on their nutritional requirements, toxin burden, and energy expenditure [5-9].

46 As a consequence, under natural levels of environmental heterogeneity and predator  
47 diversity, the costs of increasing conspicuousness can outweigh the benefits of increased  
48 signal efficacy [10]. The conspicuousness of an aposematic signal has, therefore, been  
49 linked to honest signalling of defence strength, as only more heavily defended individuals  
50 can overcome the costs of high detectability [11]. Research into detectability has, however,  
51 predominantly focused on colour saturation and the proportions of conspicuous and  
52 inconspicuous pattern components [11-15].

53 An alternative mechanism, which maintains colour saturation, is to manipulate the visual  
54 texture of an aposematic pattern. As visual systems are limited in their ability to resolve high  
55 spatial frequencies (fine textures), viewing distance can greatly affect the perception of a  
56 pattern [16]. It has been suggested that certain patterns can exploit these limitations and  
57 appear highly conspicuous at close range while also being camouflaged at longer viewing  
58 distances, where fine details can no longer be resolved [12, 13, 17-21].

59 Striped aposematic patterns are common in nature, and often combine a bright colour (e.g.  
60 yellow) with black to produce a highly contrasting and, therefore, salient pattern [22]. Internal  
61 pattern boundaries have been linked to increasing the efficacy of aposematic signalling, with

62 the presence of high contrast patterning being proposed to increase colour contrast above  
63 that which is achievable against the background, produce a consistent signal across multiple  
64 backgrounds, reduce the impact of partial occlusion, or make the pattern more distinct from  
65 palatable species [23-26].

66 When viewed from sufficient distance, however, a striped pattern cannot be resolved and  
67 adjacent stripes will be perceptually summed to produce a combined colour. If this combined  
68 colour matches that of the background, a striped pattern may produce effective camouflage  
69 to distant observers [17, 19, 27].

70 In this study we investigated whether stripe spatial frequency and pattern blending can affect  
71 the detectability and survivability of prey which appear conspicuous (yellow-and-black) or  
72 cryptic (green-and-black). We predicted that blended colours would be a closer match to the  
73 background than their component colours, and that increasing stripe spatial frequency  
74 (thinner stripes) would decrease the rate of avian predation due to the effect of pattern  
75 blending on detectability. As confirmation of the perceptual effects, in a separate experiment  
76 with human observers (Supplementary Material) we predicted that higher spatial frequency  
77 would decrease the distance at which stripes were first visible.

## 78 **2. Methods**

### 79 (a) Stimuli

80 Stimuli were designed to mimic free-living lepidopteran larvae with a variety of antipredator  
81 patterns. 'Caterpillars' were, ~16 mm long by ~3 mm diameter, cylinders of coloured dough  
82 (see below). The 12 treatments were based on either yellow-and-black (a common  
83 aposematic colour) or green-and-black (typical of camouflage in vegetative environments),  
84 and were either striped or plain. Striped treatments were designed to differ in spatial  
85 frequency while retaining equal ratios of each component colour (Figure 1).

86 For the yellow-and-black experiment six yellow-and-black treatments were designed:  $Y_P$  –  
87 plain yellow;  $B_P$  – plain black;  $Y_A$  – 1:1 yellow-black average;  $Y_T$  – 16 x 1 mm yellow-and-

88 black stripes (5.00 cycles/cm);  $Y_M$  – 8 x 2 mm yellow-and-black stripes (2.50 cycles/cm);  $Y_L$  –  
89 4 x 4 mm yellow-and-black stripes (1.25 cycles/cm). These patterns were then recreated  
90 based on green-and-black stripes:  $G_P$  – plain green;  $B_P$  – plain black;  $G_A$  – 1:1 green-black  
91 average;  $G_T$  – 16 x 1 mm green-and-black stripes (5.00 cycles/cm);  $G_M$  – 8 x 2 mm green-  
92 and-black stripes (2.50 cycles/cm);  $G_L$  – 4 x 4 mm green-and-black stripes (1.25 cycles/cm).  
93 A 3:1 mix of flour (British Plain Flour by Sainsbury's, J Sainsbury plc., London, UK) and lard  
94 (Sainsbury's Basics Lard) was used to make the dough, which was then coloured yellow (25  
95 ml per 500 g dough; Yellow Food Colouring by Sainsbury's), or black (25 ml per 500 g  
96 dough; Black Food Colouring by Sainsbury's). Green was made from a 1:1 mix of yellow and  
97 black dough, and the average colours were made from a 1:1 mix of either yellow and black  
98 ( $Y_A$ ) or green and black ( $G_A$ ). The stimuli were then built from 16 x 1 mm thick layers of  
99 coloured dough (Figure 1).

#### 100 (b) Image analysis

101 As our experiments used both avian predators (survival experiments) and human  
102 participants (detection experiments - Supplementary Material), assumptions regarding the  
103 conspicuousness of each dough colour were checked in relation to models of avian and  
104 human visual perception using calibrated photography [29, 30].

105 Dough caterpillars were first photographed using a UV-sensitive Nikon D70 Digital SLR  
106 camera, UV-NIKKOR 105 mm lens (Nikon Corporation, Japan), appropriate VIS filters, and a  
107 15% reflectance Spectralon® grey standard (Labsphere Inc., North Sutton, NH, USA). UV  
108 photography revealed minimal UV reflectance from all of the dough colours (Figure 1 top),  
109 and therefore allowed both human and avian vision to be modelled from standard RGB  
110 photography.

111 Photographs (sample sizes:  $Y_A = 9$ ,  $G_A = 9$ ,  $B_P = 8$ ,  $Y_P = 8$ ,  $G_P = 10$ ,  $Y_T = 10$ ,  $G_T = 9$ ) were  
112 taken of each treatment *in situ* on the stems of mature bramble (*Rubus fruticosus* agg.  
113 Rosaceae) plants, as they were presented to wild avian predators in the survival

114 experiments (Figure 1 middle and bottom). Each image was taken with a Nikon D3200  
115 Digital SLR camera and AF-S DX NIKKOR 35 mm prime lens (Nikon Corporation, Tokyo,  
116 Japan) and contained a ColorChecker Passport (X-Rite Inc. 2009. Grand Rapids, MI, USA),  
117 which allowed size-scaling and linearization of colour values [29] in MATLAB 2015a (The  
118 MathWorks Inc. Natick, MA, USA). The locations of the dough caterpillar and the  
119 background were labelled by hand in MATLAB and used to generate masks for subsequent  
120 selection and analysis.

121 To represent the avian predators in the survival experiment visual modelling used the  
122 tetrachromatic vision of the European starling (*Sturnus vulgaris*, Sturnidae), typical of many  
123 songbirds, with single cone peak absorption ( $\lambda_{\max}$ ) of 563 nm (Lw), 504 nm (Mw), 449 nm  
124 (Sw), and 362 nm (UV), and double cones (D) with a peak absorption ( $\lambda_{\max}$ ) of 563 nm [30].  
125 In addition, to allow more intuitive comparison between avian and human vision, and to allow  
126 interpretation of a detection experiment using human participants (Supplementary Material),  
127 we also used two models of human colour perception: L\*a\*b\* and human LMS. L\*a\*b\* is a  
128 perceptually defined colour space produced from discrimination experiments (CIELAB, 1976:  
129 <http://cie.co.at>), however, as there is no avian equivalent of L\*a\*b\*, we also generated a  
130 human LMS colour space analogous to the avian cone space, using cone cell absorption  
131 distributions:  $\lambda_{\max}$  of 564 nm (Lw), 534 nm (Mw), and 420 nm (Sw) [31].

132 For both cone-based visual systems, colour was measured, as in L\*a\*b\*, in terms of a  
133 luminance and two opponent channels, red-green (rg), produced from the relative stimulation  
134 of the longwave and mediumwave cones, and yellow-blue (yb), which was produced from  
135 the relative response of the combined longwave and mediumwave cones compared to the  
136 shortwave cone [28]. Although the opponent mechanisms have not been fully characterised  
137 for birds, it is an efficient way to encode the information because, unlike the photoreceptor  
138 photon catches themselves, these channels are approximately orthogonal (see discussion of  
139 opponent processing in [32] and of this particular representation in [33]).

140 For avian vision, a pseudo-luminance measure ( $L$ ) was calculated from the response of the  
141 double cone, whereas for human LMS,  $L$  was calculated as the mean response of the  
142 longwave and mediumwave cones [30, 31].

143 The colours of the background and high spatial frequency striped 'caterpillars' ( $Y_T$  and  $G_T$ )  
144 were analysed at two spatial scales: at the resolution of the pixels in the photographs  
145 (henceforth 'High') and after spatial averaging, where we applied a Gaussian smoother with  
146 a standard deviation equal to half the length of the caterpillars (henceforth 'Low'; function  
147 `imgaussfilt` in MATLAB 2015a). The High condition, therefore, used all of the available  
148 information and represented close range viewing. For the Low condition, representing a view  
149 from beyond the resolution limit of the pattern, a wavelength equal to half the length of the  
150 caterpillar ensured that all pattern components would blend but the caterpillar itself would  
151 still technically be resolvable against the background.

#### 152 (c) Survival protocol

153 Dough caterpillars were pinned to horizontal stems of bramble bushes (*Rubus fruticosus*  
154 *agg.*, Rosaceae), where they were predated by a variety of small passerine birds  
155 (Passeriformes). Caterpillars were pinned along non-linear transects within suburban areas  
156 of green space in the city of Bristol, UK. A randomised block design was used. Fifteen blocks  
157 of yellow-and-black caterpillars ( $Y_P$ ,  $B_P$ ,  $Y_A$ ,  $Y_T$ ,  $Y_M$ , and  $Y_L$ ) were run between June and  
158 September 2013 (10 of each treatment per block = 900 caterpillars). In a separate  
159 experiment the protocol was repeated with 15 blocks of the green-and-black caterpillars ( $G_P$ ,  
160  $B_P$ ,  $G_A$ ,  $G_T$ ,  $G_M$ , and  $G_L$ ) between November 2013 and June 2014 ( $n = 900$ ). Each block was  
161 conducted in a different location.

162 The survival of each caterpillar was checked at 24, 48, 72, and 96 h. Avian predation was  
163 identified by beak marks in, or complete removal of, the dough caterpillar, whereas  
164 Hymenoptera, principally ants, left small pit marks in the dough. For both experiments  
165 survival was analysed with a mixed effects Cox model from package *coxme* [34] and



166 pairwise tests used the False Discovery Rate from package *multcomp* [35], to gain a suitable  
167 balance between Type I and II errors, in R 3.1.3 (The R Foundation for Statistical  
168 Computing, Vienna, Austria). Avian predation was included as full events, block as a random  
169 factor, and non-avian predation, missing pins, and caterpillars surviving to 96 h were  
170 included as censored values. Data are available in Dryad [36].

### 171 **3. Results**

#### 172 a) Image analysis

173 We found a high correlation between the response of human LMS and the avian visual  
174 model for each visual channel ( $L = 0.997$ ,  $rg = 0.826$ ,  $y_b = 0.996$ ). There was a weaker  
175 correlation between human LMS and  $L^*a^*b^*$  colour space ( $L^*-L = 0.991$ ,  $a^*-rg = 0.489$ ,  $b^*-y_b$   
176  $= 0.524$ ) due to the non-linear relationship between the two visual models (although the  
177 same perceptual trends are conserved, see Supplementary Material). Plotting the avian  
178 visual model response for each treatment indicates that the majority of variation is found in  
179 the luminance (L) and  $y_b$  channels, and that the 'cryptic' treatments ( $B_P$ ,  $Y_A$ ,  $G_P$ , and  $G_A$ ) are  
180 well represented in the background. Yellow dough ( $Y_P$ ), in contrast, differs in both the  
181 luminance and  $y_b$  channels (Figure 2).

182 These data suggest that for the yellow-and-black dough experiments the combined colour  
183 ( $Y_A$ ) is a closer match to the background than the plain yellow ( $Y_P$ ). Similarly, in the green-  
184 and-black experiment, although both constituent colours ( $G_P$  and  $B_P$ ) are represented in the  
185 background, the combined colour ( $G_A$ ) does not contain the high luminance components  
186 found in the plain green ( $G_P$ ).

187 Plotting avian model response at different spatial resolutions shows that at high spatial  
188 resolution (representing close viewing conditions; Figure 3 top) both treatments can be  
189 distinguished from the background, whereas at low spatial resolution (representative of far  
190 viewing conditions; Figure 3 bottom) caterpillar colours converge with those of the  
191 background.

192 These data, therefore, support the hypothesis that the combined colours ( $Y_A$  and  $G_A$ ) were  
193 better matches to the background than their constituent colours ( $Y_P$ , and  $G_P$  respectively),  
194 and that for striped patterns pattern blending at greater viewing distances can produce more  
195 effective camouflage.

196 b) Survival: yellow-and-black

197 There was a significant effect of treatment on the survival of the yellow-and-black caterpillars  
198 ( $\chi^2 = 70.43$ , d.f. = 5,  $p < 0.001$ ; Figure 4 left). Pairwise tests show that there was no  
199 significant difference in survival between plain treatments ( $Y_A - B_P$ :  $z = -0.28$ ,  $p = 1.00$ ;  $Y_A -$   
200  $Y_P$ :  $z = -1.62$ ,  $p = 0.581$ ;  $B_P - Y_P$ :  $z = -1.33$ ,  $p = 0.765$ ), or between the plain treatments and  
201 the lowest spatial frequency stripes ( $Y_L - Y_A$ :  $z = 0.92$ ,  $p = 0.940$ ;  $Y_L - B_P$ :  $z = -0.63$ ,  $p =$   
202  $0.988$ ;  $Y_L - Y_P$ :  $z = -0.72$ ,  $p = 0.980$ ). The medium stripes survived equally to the plain  
203 average and plain black ( $Y_M - Y_A$ :  $z = -2.05$ ,  $p = 0.308$ ;  $Y_M - B_P$ :  $z = -2.32$ ,  $p = 0.185$ ), but  
204 survival was higher than the plain yellow ( $Y_M - Y_P$ :  $z = -3.61$ ,  $p = 0.004$ ). The thinnest stripes  
205 had higher survival than all of plain treatments ( $Y_T - Y_A$ :  $z = -5.49$ ,  $p < 0.001$ ;  $Y_T - B_P$ :  $z = -$   
206  $5.70$ ,  $p < 0.001$ ;  $Y_T - Y_P$ :  $z = -6.74$ ,  $p < 0.001$ ).

207 There was a stepwise decrease in survival as spatial frequency decreased, with the thinnest  
208 stripes having higher survival than the medium and lowest spatial frequencies ( $Y_T - Y_M$ :  $z = -$   
209  $3.73$ ,  $p = 0.003$ ;  $Y_T - Y_L$ :  $z = -6.24$ ,  $p < 0.001$ ), and the medium having higher survival than  
210 the lowest spatial frequency ( $Y_M - Y_L$ :  $z = -2.96$ ,  $p = 0.036$ ).

211 c) Survival: green-and-black

212 For the green-and-black caterpillars there was a significant effect of treatment on survival ( $\chi^2$   
213  $= 90.22$ , d.f. = 5,  $p < 0.001$ ; Figure 4 right).

214 There was no significant difference between the plain black and plain green ( $B_P - G_P$ :  $z =$   
215  $0.33$ ,  $p = 0.999$ ). There was no significant difference between the medium and low spatial  
216 frequency stripes ( $G_M - G_L$ :  $z = 1.00$ ,  $p = 0.918$ ), and no difference between the medium or low  
217 spatial frequency stripes and the plain black or plain green ( $z < 1.68$ ,  $p > 0.546$ ).

218 There was no significant difference in survival between the highest spatial frequency stripes  
219 and the average colour ( $G_T - G_A$ :  $z = 1.48$ ,  $p = 0.674$ ), but both had significantly higher  
220 survival than the medium and low spatial frequency stripes ( $G_T - G_M$ :  $z = -3.98$ ,  $p < 0.001$ ;  $G_T -$   
221  $G_L$ :  $z = -4.94$ ,  $p < 0.001$ ;  $G_A - G_M$ :  $z = -5.38$ ,  $p < 0.001$ ;  $G_A - G_L$ :  $z = -6.28$ ,  $p < 0.001$ ), as well  
222 as the plain black and plain green caterpillars ( $G_T - B_P$ :  $z = -5.57$ ,  $p < 0.001$ ;  $G_T - G_P$ :  $z = -$   
223  $5.29$ ,  $p < 0.001$ ;  $G_A - B_P$ :  $z = -6.86$ ,  $p < 0.001$ ;  $G_A - G_P$ :  $z = -6.60$ ,  $p < 0.001$ ).

#### 224 **4. Discussion**

225 Aposematic signals are often associated with high contrast patterns [22], which are thought  
226 to increase the saliency, ease of learning, and memorability of the warning signal [23-26]. It  
227 has also been suggested that these pattern components might provide camouflage when  
228 viewed from a distance [12, 13, 17-21, 27]. The latter effect has potentially been  
229 underappreciated, as many studies have been conducted in the laboratory or on unnatural  
230 backgrounds.

231 At greater viewing distances, adjacent patches of colour can no longer be resolved and will  
232 be summed by the visual system and thus perceived as a single combined colour. The  
233 distance at which this summation occurs will depend on the spatial frequency of the pattern  
234 and the visual acuity of the observer. We found that for both yellow-and-black and green-  
235 and-black stripes, the spatially averaged colours were a closer match to the background  
236 than their more conspicuous elements ( $Y_P$  and  $G_P$  respectively) for both human and avian  
237 vision, and increasing spatial frequency (thinner stripes) decreased the rate of predation by  
238 wild avian predators. Furthermore, we found that increasing spatial frequency also  
239 decreased the distance at which human observers could resolve the stripes (Supplementary  
240 Material).

241 Increasing spatial frequency, therefore, decreased the distance at which stripes would blend  
242 to form a more cryptic colour. For our green-and-black striped caterpillars we found that as  
243 spatial frequency increased, survival increased towards that of the average colour ( $G_A = G_T$

244  $> G_M = G_L$ ). In contrast, for the yellow-and-black caterpillars the survival of higher spatial  
245 frequencies surpasses that of the average colour ( $Y_T > Y_M > Y_L = Y_A$ ). We suggest that for  
246 the green-and-black stripes, pattern blending leads to a closer match to the background and  
247 better camouflage, whereas for the yellow-and-black stripes the combination of camouflage  
248 and aversive signalling produces a combined strategy which is more effective than either in  
249 isolation [12,13, 18-21, 27].

250 It has also been suggested that aposematic pattern components could provide disruptive  
251 camouflage (breaking up the organism's outline into incongruent patches) [37], however, the  
252 regular geometric structure of these stimuli are unlike the irregular patterns normally  
253 associated with disruptive camouflage [38]. This possibility, however, does deserve further  
254 research.

255 These data suggest that detection distance can be reduced without necessarily  
256 compromising the effectiveness of salient defensive colouration. For an aposematic pattern,  
257 this is influenced by the internal colour contrasts, the colours themselves, and, perhaps the  
258 ratio of colour components [1, 3, 4, 10, 25, 26-28]. Striped patterns may therefore enable an  
259 animal to combine highly salient aposematic signalling with effective background matching  
260 camouflage. Varying stripe spatial frequency can create a stable and highly salient pattern,  
261 while also controlling the distance at which a pattern is detectable. These mechanisms may  
262 be exploited in order to balance different selection pressures, to alter detectability during  
263 ontogeny as pattern size and defence strength develop together, to minimise the long-range  
264 detectability of other conspicuous signals (i.e. sexual signals where mate attraction and  
265 predation work over different spatial scales), or as a mechanism for Batesian mimic species  
266 to reduce the risk of detection while retaining a pattern which is perceptually grouped with  
267 that of their model [38].

268 Internal pattern boundaries may, therefore, provide a wide range of different benefits to the  
269 aposematic organism, including increased saliency at close range and reduced detection

270 distance. Viewing distance is likely to be an underappreciated aspect of visual ecology, and  
271 a more inclusive study of animal colouration may reveal new insights into how different  
272 functions interact within a single phenotype.

273

274 **Ethics.** Experiments were approved by the University of Bristol Animal Welfare & Ethical  
275 Review Body (birds) and the Faculty of Science Ethics Research Committee (humans:  
276 Supplementary Material). All human participants gave informed consent in accordance with  
277 the Declaration of Helsinki.

278 **Data accessibility.** Raw data can be accessed from the Dryad data repository [36]:  
279 doi:10.5061/dryad.2h6nf.

280 **Competing interests.** We have no competing interests.

281 **Authors' contributions.** J.B.B. collected the data, and all authors participated in  
282 experimental design, analysis, and writing of the manuscript.

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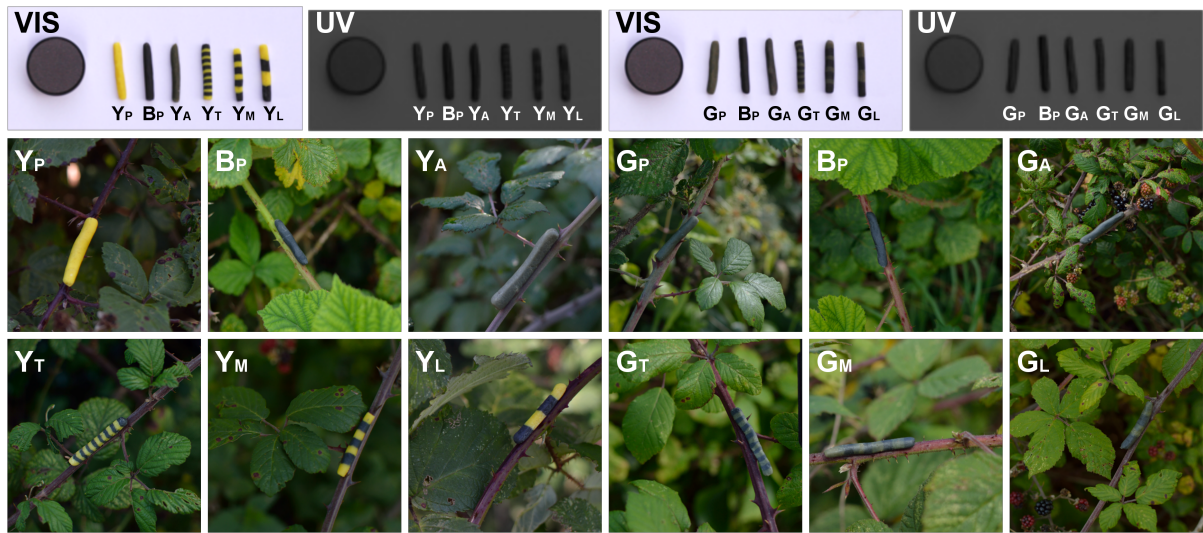
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392 **Figure 1.** Yellow-and-black, (left), and green-and-black, (right), dough caterpillars  
393 photographed in human visible (VIS) and ultraviolet (UV) light, with a 15% reflectance  
394 Spectralon® grey standard (Labsphere, Inc. North Sutton, NH, USA), and photographed *in*  
395 *situ* on bramble stems (*Rubus fruticosus* agg. Rosaceae). ‘Caterpillars’ are approximately 16  
396 mm long by 3 mm diameter.



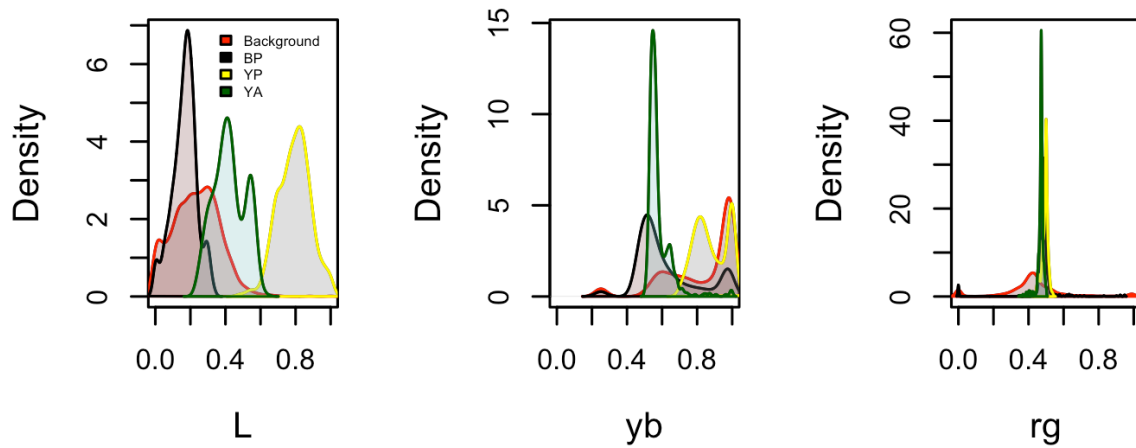
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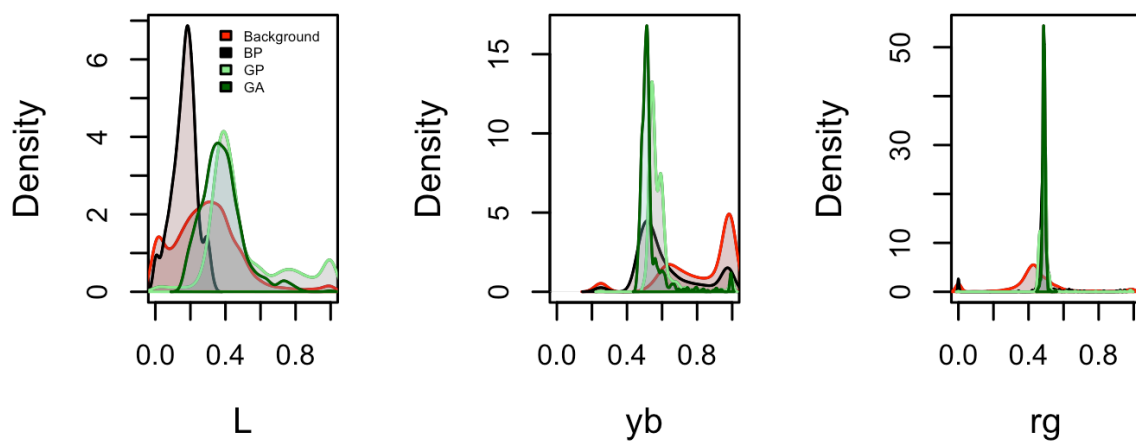
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399 **Figure 2.** Dough caterpillar and bramble colours as viewed by a model of avian visual  
400 perception (top - yellow-and-black; bottom – green-and-black). All colours are well  
401 represented in the background (red) apart from  $Y_P$  (yellow) which forms an obvious outlier in  
402 luminance.

### Yellow-and-black



### Green-and-black

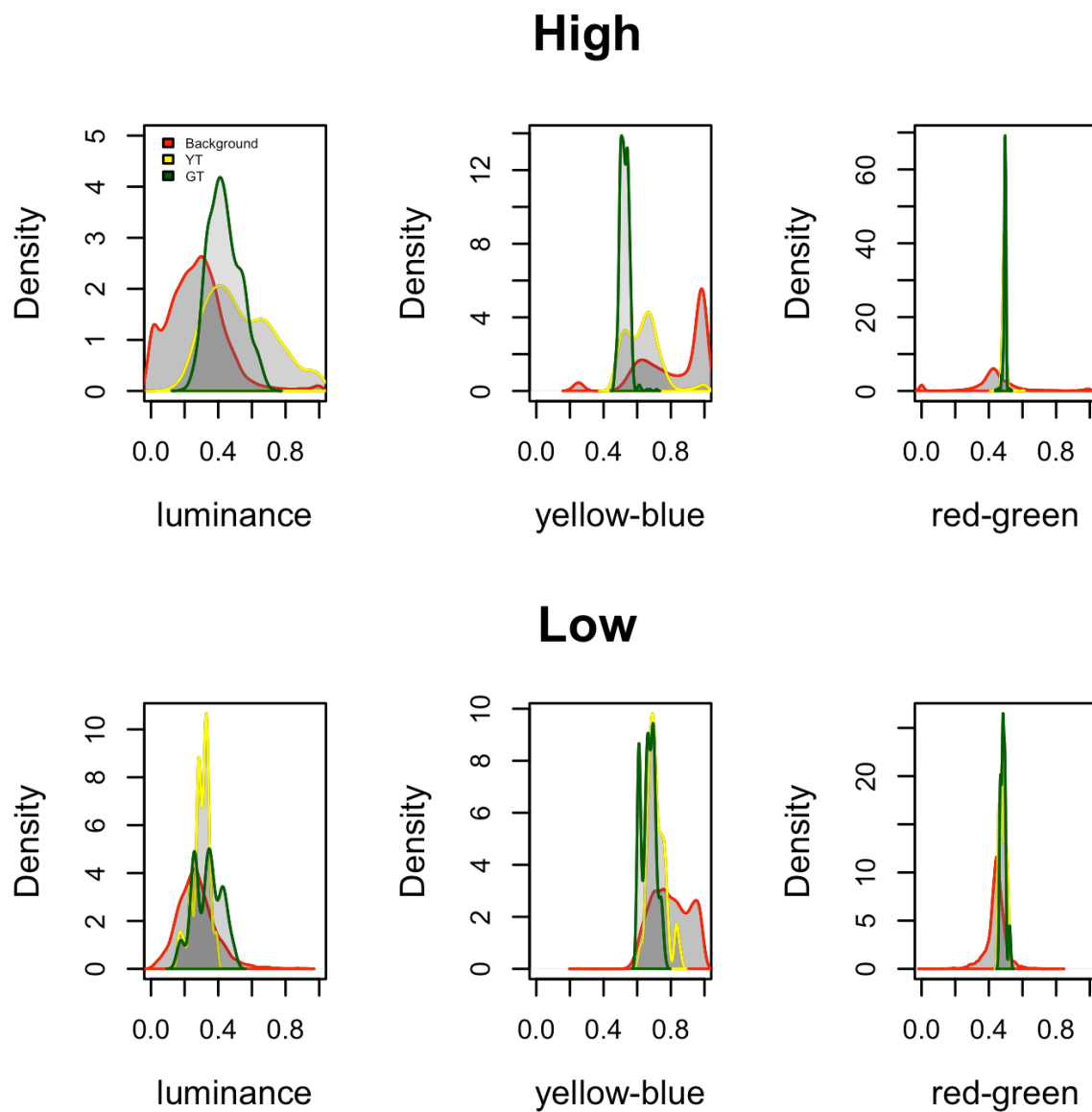


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405 **Figure 3.** High spatial frequency striped dough caterpillar treatments (yellow –  $Y_T$ ; green –  
406  $G_T$ ) viewed by the avian visual model in relation to the bramble background (red) at high,  
407 (top), and low, (bottom), spatial resolutions. At low spatial resolutions the colours of both  
408 striped targets blend together and converge with the colours of the background across all  
409 three channels.

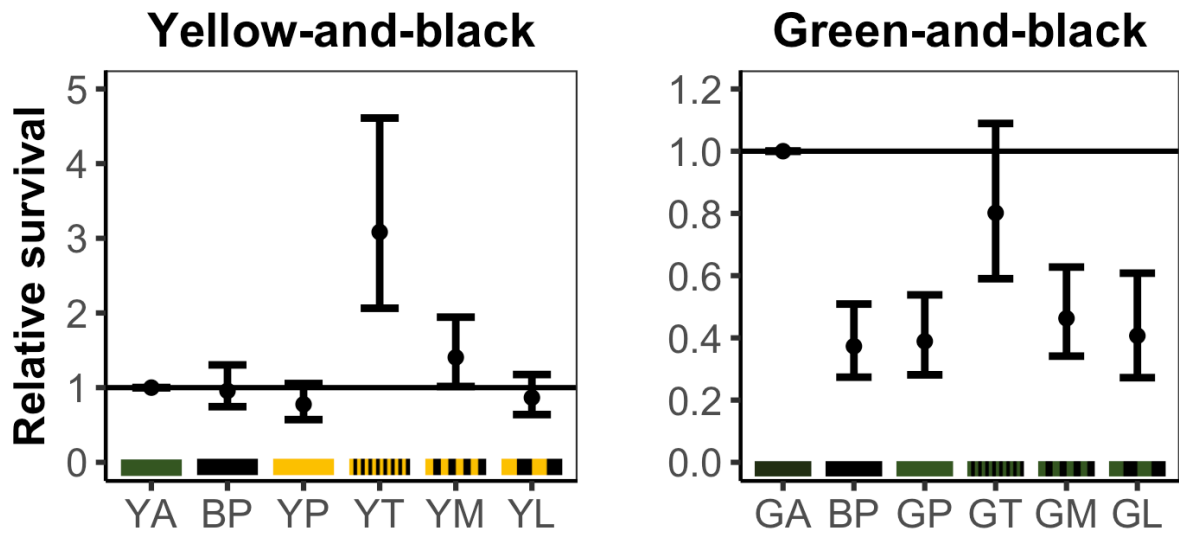


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412 **Figure 4.** Relative survival of dough caterpillars (odds ratios compared to the average colour  
413 treatment with 95% CI from the model). For both the yellow-and-black, (left), and the green-  
414 and-black, (right), stripes, increasing spatial frequency increases survival. For the yellow-  
415 and-black stripes survival increases beyond that of the average colour ( $Y_A$ ); whereas, for the  
416 green-and-black stripes, as spatial frequency increases, the survival of striped patterns  
417 moves towards than of the more cryptic average ( $G_A$ ).



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