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1 Disruptive colouration in reef fish: does matching the background reduce predation
2 risk?

3

4 Running title (40 characters):

5 Disruptive colouration in reef fish

6

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13

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15

16 **Summary Statement (15-30 words)**

17 Vertically barred patterns provide protection for prey from visual predators even when they
18 mismatch the spatial frequency of background habitats.

19

20 **Keywords (3-6):**

21 visual ecology; predator-prey relationships; Fourier analysis; behaviour; disruptive camouflage

22 **Abstract (max. 250 words)**

23 Animals use disruptive colouration to prevent detection or recognition by potential predators
24 or prey. Highly contrasting elements of colour patterns, including vertical or horizontal bars, are
25 thought to be effective at distracting attention away from body form and reducing the risk of being
26 detected. However, it is unclear whether such patterns need to be a good match to the spatial
27 characteristics of the background to gain cryptic benefits. We tested this hypothesis using the iconic
28 vertically-banded humbug damselfish, *Dascyllus aruanus*, a small reef fish that lives amongst the
29 finger-like projections of branching coral colonies. Using behavioural experiments, we demonstrate
30 that the spatial frequency of humbug pattern does not need to exactly match the spatial frequency of
31 the coral background to reduce the likelihood of being attacked by two typical reef fish predators:
32 slingjaw wrasse, *Epibulus insidiator* (Pallas, 1770) and coral trout, *Plectropomus leopardus*
33 (Lacépède, 1802). Indeed, backgrounds with a slightly higher spatial frequency than the humbug
34 body pattern provided more protection from predation than well-matched backgrounds. These
35 results were consistent for both predator species, despite differences in their mode of foraging and
36 visual acuity, which was measured using anatomical techniques. We also show that a slight
37 mismatch in the orientation of the vertical bars did not increase the chances of detection. However,
38 the likelihood of attack did increase significantly when bars were perpendicular to the background.
39 Our results provide evidence that fish with highly contrasting patterns do not need to exactly match
40 the spatial characteristics of the background.

41 **Introduction**

42 Animals use visual camouflage to avoid detection and/or recognition by predators and prey
43 (Thayer, 1909, Cott, 1940) by using different strategies such as background matching, masquerade,
44 countershading, and disruptive colouration (defined in (Stevens and Merilaita, 2009a). Background
45 matching requires that the body colour (hue), brightness (luminosity) and/or pattern elements
46 closely resemble that of a specific background (in specialist camouflage), or a number of
47 backgrounds (in generalist camouflage) (Stevens and Merilaita, 2009a, 2011). For example, the
48 body colouration of the green tree frog, *Agalychnis callidryas*, has a similar spectral reflectance to
49 the leaves of the tree on which they rest (Emerson et al., 1990); while the giant cuttlefish, *Sepia*
50 *apama*, is able to change body patterns to match a wide range of backgrounds (Zylinski et al.,
51 2011). Background matching is most effective when animals are relatively stationary, as movement
52 will often break camouflage and cause an animal to become more detectable to predatory visual
53 systems (Julesz, 1971, Ioannou and Krause, 2009, Hall et al., 2013).

54 Disruptive colouration uses highly contrasting pattern elements that occur near the edge of
55 the animal or across the body to break up the body outline, interrupting normal object recognition
56 pathways so the animal form is no longer recognisable (Thayer, 1909, Cott, 1940, Stevens and
57 Cuthill, 2006, Stevens and Merilaita, 2009b, Stevens et al., 2009, Cuthill and Székely, 2009). In
58 Cott's (1940) pioneering work on animal colouration, he suggested that the sub-principle of
59 maximum disruptive contrast (in terms of colour or luminance) between adjacent pattern elements
60 was one of the most effective mechanisms for distracting attention away from a focal animal. Cott
61 used the black and white, vertically-barred humbug damselfish *Dascyllus aranus* as one of the main
62 examples to illustrate this tenet. However, disruptive colouration should also have some
63 resemblance to the background against which it is viewed, in terms of colour, pattern and luminance
64 (Fraser et al., 2007). For example, (Kelman et al. 2007) demonstrate that the degree of luminance
65 contrast in disruptive markings displayed by cuttlefish did not exceed the luminance contrast in the
66 experimental backgrounds. Additionally, others found there that when the luminance contrast

67 between the pattern and background were similar, moths with disruptive edge markings had higher
68 survival rates compared to those with non-disruptive elements, suggesting that disruptive
69 colouration rarely is acting in isolation (Stevens et al., 2006). While matching the background
70 luminance is important in disruptive colouration, whether disruptive markings additionally have to
71 match the background in terms of spatial scale to prevent detection has not been specifically tested,
72 to our knowledge. This is despite knowledge that there are significant differences in the spatial
73 frequency of conspicuous and cryptic animal body patterns (Godfrey et al., 1987, Cheney et al.,
74 2014). Interestingly, Cott (1940) did not make any predictions about the spatial characteristics of
75 optimal disruptive colouration in animal body patterns.

76 In this study, we used humbug damselfish to examine whether the spatial frequency of
77 disruptive pattern elements needs to closely match the spatial frequency of coral backgrounds to
78 provide the fish benefit from a reduction in the likelihood of attack. As outlined in Fig. 1i, fish with
79 a similar pattern to the background, whether that background is plain (a) or patterned (c), is more
80 likely to be cryptic from the perspective of a predator, compared to if a pattern is highly contrasting
81 with the background (b). To understand the design and success of various camouflage strategies, we
82 must consider how colour patterns are viewed by relevant signal receivers (Endler, 1983).
83 Therefore, we first measured the visual acuity of two reef fish predators using information on the
84 anatomy of their eyes and the density of photoreceptors in the area of the eye most likely used for
85 focussing a clear image, similar to the *fovea* in humans (Collin and Pettigrew, 1989, Ullmann et al.,
86 2012). This information was combined to apply relevant blurring to images used in behavioural
87 assays and natural scenes, so that they represent a predators-eye-view of a scene. Next, we used
88 behavioural experiments with the same two predatory fish species to investigate whether there is a
89 reduction in the likelihood of attack for humbugs when viewed against backgrounds of similar and
90 mismatched spatial frequencies (number of within-pattern-elements), measured using Fast Fourier
91 Transform (FFT) analysis (similar to previous methods (Cortesi et al., 2015b). Finally, we assessed
92 field images from the Great Barrier Reef to quantify the spatial frequency of humbug damselfish

93 against natural coral backgrounds. We discuss the implications of our findings in relation to
94 disruptive contrast strategies in both marine and terrestrial predator-prey relationships.

95

96 **Materials and Methods**

97 Study species

98 The three-barred humbug, *D. aruanus*, (hereafter referred to as a humbug) forms close
99 associations with branching scleractinian coral heads with vertical finger-like protrusions (Randall
100 and Allen, 1977, Randall et al., 1997, Allen et al., 2003). Humbugs are diurnally active, and rarely
101 move more than 1 m from their home coral head, preferring to hide within coral branches when
102 predators approach (Sale, 1970, McCormick and Weaver, 2012, Sale, 1971). The two predators in
103 this study were chosen for their different hunting strategies: slingjaw wrasse (*Epibulus insidiator*)
104 are slow-moving, short-range predators (over a distance of a few cm), while coral trout
105 (*Plectropomus leopardus*) are ambush predators that approach their prey rapidly, attacking from a
106 few metres away (Schott et al., 2014). Predators were caught from the waters surrounding Lizard
107 Island, Great Barrier Reef, Australia [14°41'06" S, 145°26'32" E] using barrier and hand nets
108 (slingjaw wrasse, n = 6), or hook and line (coral trout, n = 9). These two species are also relatively
109 easy to house and train in aquaria (Vail et al., 2013, Vail et al., 2014, Cortesi et al., 2015a), and
110 have been shown to feed on humbugs in the wild (St John, 1999, John et al., 2001).

111

112 Predator spatial acuity

113 We calculated the spatial acuity of both predators to estimate how they would potentially
114 perceive humbug patterns against experimental and natural backgrounds. We used retinal
115 wholemounts from five fish of each species to measure the highest density of photoreceptors in
116 their retinas. This region is likely to be the area of highest acuity within the retina, similar to the
117 *fovea* in humans (Land and Nilsson, 2012). Retinal wholemounts are generated by removing the
118 retina from the eye, fixing the tissue and then mounting the entire retina on a slide with the

119 photoreceptors pointing towards the viewer. Photoreceptors are then counted using specialised
120 software on a modified microscope, using methods previously published elsewhere (Ullmann et al.,
121 2012, de Busserolles et al., Coimbra et al.) and described in detail in the Supplementary
122 Information. Spatial resolution was calculated both as the minimum resolvable angle (θ , in degrees)
123 by the eye, and in the number of cells subtended by 1° of visual arc (spatial resolving power, SRP
124 in cycles per degree). The minimum resolvable angle (θ) can then be used to calculate the smallest
125 detectable size of an object at a given distance. In comparison, the SRP provides us with the
126 reciprocal information, in terms of how many cycles (i.e. black and white lines) could be
127 discriminated in 1° of visual arc (Land and Nilsson, 2012).

128 Calculations of the minimum resolvable angle (θ) followed previously published methods
129 (Land and Nilsson, 2012), where the finest grating an eye can resolve has an angular period of $2\Delta\phi$,
130 where $\Delta\phi$ is the inter-receptor angle and is calculated as follows:

$$131 \quad \Delta\phi = s/f$$

132 where s = distance between photoreceptor centres and f = focal length or posterior nodal distance
133 (PND) = $2.55 \times$ lens radius.

134

135 Only cone cells were used for calculating minimum separation, and we assumed that all
136 cone cells contribute to the visual task. It has been suggested that only double/twin (D/T) cones
137 within fish visual systems convey spatial information, similar to chickens (Osorio et al., 1999).
138 However, as D/T cones make up the majority of cone cells in both species, and as the contribution
139 of single cones remains unknown, only using D/T cones for spatial acuity calculations is potentially
140 incorrect. Minimum separation was measured using the average number of cells in 1 mm in the
141 densest region of cone cells in the retina (Table 1). Our results represent the highest possible visual
142 acuity, before any summation can occur in the ganglion cell layer, or beyond.

143

144 Image analyses

145 We then quantified how well humbug body patterns matched the spatial frequency of
146 experimental and natural backgrounds. To do this, we used Fourier analysis techniques to quantify
147 the frequency characteristics of specific objects within images that had been blurred to reflect
148 predator visual acuity. First, bitmap images of the experimental backgrounds with humbugs were
149 created in Adobe Photoshop (Adobe Photoshop CS5.1) and saved as 2048 x 2048 pixel images
150 (.bmp). These images were then manipulated using previously published methods (Caves et al.,
151 2016) to approximate predator visual acuity. In brief, the Fast Fourier Transform of a single channel
152 of the image was multiplied by a modulation transfer function (MTF) with a contrast of < 2% at the
153 minimum resolvable spatial frequency (i.e. smallest detail). This value was chosen as it represents
154 the minimum contrast threshold for fish under bright light conditions (Douglas and Hawryshyn,
155 1990). Full images were then recovered using a reverse Fourier transform, resulting in an image
156 where spatial information spanning angles $< \theta$ were not present. The following parameters were
157 used to blur the image: distance from the viewer to the image (initially set at 100 cm as this
158 approximates the viewing distance in behavioural trials), the width of the image (estimated using
159 the length of the humbug, set at 5.5 cm total length), and the minimum resolvable angle of the
160 predator in degrees.

161 To analyse the spatial frequency contrast between the vertically barred humbug and the
162 background, we applied a one-dimensional Fast Fourier Transformation (1D FFT) to the blurred
163 images in a custom-designed MATLAB script (R2014a, Mathworks, Nantick, USA). The frequency
164 of ten same-length horizontal transects (0°) through the body of the humbug were averaged to
165 calculate the peak spatial frequency of the vertical bars, which was then compared to an average of
166 ten randomly positioned background transects of the same length and orientation (see
167 Supplementary Information Fig. 1). If the peak frequency of the humbug bars is similar to that of
168 the background, it suggests that the two objects contain similar frequencies along the horizontal
169 plane. The results are plotted showing the peak frequency of the humbug and the background, and
170 also showing the difference between the peak frequency of the fish and the background.

171

172 Behavioural experiments

173 A series of paired-choice experiments were used to test the hypothesis that humbugs benefit
174 from a reduction in the likelihood of attack when their body patterns exactly match the spatial
175 frequency of their coral background. Predators were housed in individual aquaria (slingsjaw: 1.2 x
176 1.2 x 0.4 m; coral trout: 2.2 x 1.2 x 0.4 m) in the flow-through seawater system at Lizard Island
177 Research Station and were fed either pilchards or prawn twice per day during the acclimation
178 period. Each aquarium was divided into two arenas using black corrugated plastic board (thickness
179 = 6 mm) as a partition. A door was cut into the middle of partition to allow fish access into the
180 experimental arena (Fig. 2). Tanks were screened off with shade cloth to minimise external
181 disturbances. A submersible video camera (Hero2, GoPro, San Mateo, USA) was placed on a
182 stainless steel tripod in the middle of the aquarium to film the experiment. The tripod did not
183 interfere with the fish entering the test arena and after a period of acclimation they were not
184 distracted by the camera and tripod.

185 Behavioural experiments took place over five separate periods of 8-12 weeks from January
186 2012 - March 2014. In each trial, individual predators were required to search for humbugs that
187 were placed against experimental backgrounds that varied in spatial frequency. With slingsjaw
188 wrasse, we were able to use a laminated cut-out photograph of a humbug placed against each
189 background, which the wrasse approached and attacked to receive a food reward from above.
190 However, we were unable to train coral trout to perform the experiment without real prey items,
191 therefore we used euthanized humbug individuals.

192 Experimental backgrounds were designed in Adobe Illustrator (CS5.1, Adobe Systems
193 Incorporated, Mountain View, USA). To reduce any response bias that could be caused by hue or
194 saturation contrast, all backgrounds were designed and constructed using black, white or
195 monochromatic grey (50%) with the total number of pixels in the image altered to a 50:50 ratio of
196 black:white. All backgrounds were printed using a Deskjet Printer (HP470, Hewlett-Packard, Palo

197 Alto, USA) and laminated prior to testing. We did not test whether lamination affected the
198 reflectance of the objects or backgrounds as most experimental objects were made using the same
199 materials, thus standardising the glare amongst the backgrounds and objects.

200 We tested the hypothesis that experimental backgrounds with the same spatial frequency as
201 the vertical bars of humbugs would provide the most protection from predation (Fig. 1ii). The
202 spatial frequency of backgrounds varied slightly for each of the two predator species, as slingjaw
203 wrasse are likely to target juveniles and sub-adults, while coral trout tend to predate on larger adult
204 humbug damselfish (St John, 1999). The laminated photograph of a humbug used in slingjaw
205 experiments was 3 cm (total length). The width of the middle bar in the pattern of this humbug was
206 4 mm. We used multiple copies of the same humbug photograph, which was presented to slingjaw
207 in a randomised manner. Humbugs used in coral trout experiments were all adults (determined by a
208 lack of blue pigmentation on the ventral fins; size range: standard length (SL) = 26 – 63 mm), and
209 the width of their middle bar was approximately 8 mm.

210 Predators were tested in five separate behavioural experiments in which the prey and the
211 background varied in terms of spatial frequency (Fig. 1ii). Backgrounds were either regular black
212 and white vertical bars (Experiments 1 & 2) or stylised natural coral head backgrounds generated
213 from photographs (Experiment 3). We also tested the hypothesis that humbugs would more likely to
214 be attacked when the orientation contrast between humbug body pattern (based on the middle bar)
215 and background was high (Experiments 4 & 5).

216

217 **Training:** Predators were first trained to associate an A4 laminated paper target mounted on a
218 Perspex board with food. This training was carried out differently for each predator species due to
219 differences in their behaviour and physiology (Randall et al., 1997). Both species of predator were
220 trained to enter an experimental arena and eat a piece of prawn (slingjaw wrasse) or pilchard (coral
221 trout) attached via clear fishing line to a plain white laminated paper background. Once slingjaw
222 wrasse were able to approach and eat food from a background, they were trained using positively

223 reinforced operant conditioning to attack a laminated image of a plain black humbug and given a
224 food reward in the middle of the arena from the experimenter. Images of humbugs and the humbug
225 shape used in training were attached to the backgrounds using double-sided Velcro[®]. Once coral
226 trout entered the arena to eat the pilchard within 60 seconds consistently, they moved on to the
227 testing phase, where the pilchard was replaced with a euthanized humbug. Humbugs were
228 euthanised in a seawater solution of 0.2 ml clove oil per litre of seawater (according to ethics
229 approval QBI/192/13/ARC). Prior to each trial, humbugs were rinsed thoroughly to remove any
230 traces of clove oil and were attached using colourless fishing line to the background.

231

232 **Testing:** A distractor background (with no humbug fish) was present for each trial to ensure that
233 predators searched for humbugs on a background, rather than striking backgrounds at random. We
234 pseudo-randomised the end of tank in which the backgrounds were placed (left or right), the
235 location of each background (left, right, centre), and the spatial frequency of the distractor
236 background (no humbug attached) to prevent the predator associating a particular location or
237 background with food. Fish blood (2-5 ml) from defrosted, commercially available pilchards was
238 added to the experimental arena in front of all three backgrounds to reduce olfactory cues from
239 individual humbugs and to motivate predators to attack humbugs. The water was agitated to
240 distribute the blood and to ensure that it did not interfere with the predator's ability to see the
241 background or humbugs.

242 Trials started when the door was opened and the predator could enter the experimental
243 arena, and ended when the predator attacked a humbug. If the predator took longer than four
244 minutes to attack the humbug, this indicated a lack of motivation to feed and the trial was
245 terminated. In all trials, the humbug and background combinations, time of day of the trial (am or
246 pm), standard length of the humbugs (coral trout only), and the location of the chosen background
247 were recorded. A total of six slingjaw wrasse were used (experiment 1: n = 6; experiment 2: n = 6;
248 experiment 3: n = 5), one of which failed to complete experiment 3 (Supplementary Information

249 Table 1). A total of 9 coral trout were used throughout the study (experiment 1: n = 5; experiment 2:
250 n = 8; experiment 3: n = 6), all of which completed at least one experiment, with three fish
251 completing all three experiments (Supplementary Information Table 1). All predators were
252 presented with a minimum of six repeats of each background combination in each experiment (total
253 trials completed by each predator in individual experiments: minimum n = 14; maximum n = 30).
254 Three predators did not complete all background combinations presented to them: two refused to
255 complete one trial each (BMJ12 & BJF12), while one refused to complete 4 trials (DJF13;
256 Supplementary Information Table 1). Experiments were conducted in early morning and early
257 evening for the coral trout and during daylight hours of 10 am and 3 pm for the slingjaw to simulate
258 their respective crepuscular and diurnal predation behaviours. Additionally, experiments that were
259 trialled during winter months (May – June) were less successful than those in the summer months
260 (January – March) as predators were more motivated to attack prey during these months,
261 presumably due to an increase in metabolism (and therefore hunger) with the increased summer
262 water temperatures.

263

264 Statistical Analyses

265 The likelihood of attack for humbugs against particular backgrounds was analysed using a
266 modified Bradley-Terry generalised mixed effects model (Bradley and Terry, 1952) with a binomial
267 response (background attacked or not attacked). To take into account individual variability between
268 predators and the repetition of tests on each individual, fish identity was added as a random factor
269 within the model. Time of day (am, pm), end of tank in which the backgrounds were placed (left or
270 right), the distractor background used, the location of each of the test backgrounds (left, right, and
271 centre), and the trial number were also included as fixed factors; however, these were insignificant
272 (all $Z > 0.26$ and all $p \geq 0.07$) and removed from the final model. In coral trout experiments,
273 predators did not choose prey based on body size alone: the size of prey that were attacked was not
274 significantly different to the size of prey that was not attacked (Experiment 1, size range = 34 – 55

275 mm, paired $t_{84} = -0.98$, $p = 0.33$; Experiment 2, size range = 26 – 57 mm, $t_{167} = 0.46$, $p = 0.65$;
276 Experiment 3, size range = 32 – 63 mm, $t_{107} = -0.70$, $p = 0.48$). Therefore, we did not consider prey
277 size further in our analyses. The results of the Bradley-Terry model were then fitted to a logistical
278 function (plogis) to determine the probability of the humbug being chosen (based on background).
279 Analyses were performed in R 3.1.3 (2015-03-09, ‘Smooth Sidewalk’ (2015) using the glm, t.test
280 and lmer functions (MASS package, (Venables and Ripley, 2002), kruskal.test (stats package), and
281 the posthoc.kruskal.nemenyi.test functions (PMCMR package, (Pohlert, 2015)).

282

283 **Results**

284 Predator spatial acuity

285 Both predators had distinct differences in photoreceptor density across the retina, with the
286 highest concentrations of cone cells generally falling within the central region. The highest density
287 of cone cells in the slingjaw wrasse was 2569 photoreceptors cm^{-1} compared to 1222 photoreceptors
288 cm^{-1} in the coral trout (Table 1). The highest visual acuity calculated with photoreceptor counts
289 agrees with previously published calculations using ganglion cell densities (*Choerodon albigena*,
290 blue-tusk fish, Labridae): 2880 ganglion cells cm^{-1} ; *P. leopardus*: 1225 ganglion cells cm^{-1}) (Collin,
291 1989, Collin, 2008). Therefore we assume no convergence from photoreceptor to ganglion cell in
292 these retinal regions at least and that photoreceptor densities provide a good estimate of acuity for
293 tasks involving small objects. The minimum resolvable angle (θ) was calculated as 0.092° and
294 0.103° for the slingjaw and coral trout respectively based on the number of cone cells in the highest
295 density regions (Table 1). These spatial acuities correspond to minimum resolvable gratings of 1.74
296 mm and 1.45 mm at a viewing distance of 100 cm respectively. To simplify the subsequent
297 analysis, a minimum resolvable angle of 0.10° to approximate both predators’ visual resolution.

298

299 Image analysis

300 All eight backgrounds used in behavioural experiments were blurred to a minimum
301 resolvable angle of 0.10° to determine how predators would perceive the difference between
302 background and humbug pattern. Fig. 3 shows that the humbug peak frequency was most similar to
303 the 'similar width' barred background (orange lines), while the other barred backgrounds have
304 distinctly different peak frequencies. Unlike the humbug pattern, there is no one distinctive peak
305 frequency in the 'natural' coral backgrounds (Fig. 4), which has peaks both lower and higher in
306 spatial frequency than that of the humbug. When the orientation of the humbug is analysed, it is
307 clear that fish angle influences the peak frequency contrast between the humbug and the
308 background in the horizontal plane, with the greatest differences seen when the fish is at 45° or 90°
309 to the background (Fig. 5).

310 We also blurred an image of humbugs against a coral head from the field (humbugs in the
311 wild) and analysed it using the FFT analysis. Only the green channel of the image was analysed to
312 prevent additional colour information influencing the spatial frequency analysis. At close range, the
313 peak frequencies of the humbug body pattern were very different from the coral background (Fig.
314 6), perhaps due to the wider range of natural frequencies in the background. Additionally, compared
315 to the boldly barred humbug peak in frequency is seen within the fish that is not observed in the
316 coral, possibly corresponding to the regular, bold patterning of the humbug, compared to the
317 irregular, and less-bold patterning of the branching coral head (branching coral heads lose the
318 structure of their branching when flattened in a 2D image). This image was then blurred to represent
319 increasing viewing distances beyond 1m from both a human and predator's perspective, and to
320 identify if at a particular distance, the humbug pattern more closely matched that of the background
321 (Fig. 6). Indeed, by a distance of 5 m, the humbug body statistics do more closely match that of the
322 coral background from a fish predator's perspective, but not a human's perspective.

323

324 Behavioural experiments

325 The likelihood of humbugs being attacked varied depending on the spatial frequency of the
326 background. In Experiment 1 (grey, similar width and $\frac{1}{4}$ width bars), humbugs were least likely to
327 be attacked when viewed against a background with a similar spatial frequency to its own body
328 pattern (Fig. 7a: slingjaw: grey vs. similar width: $z = 2.16$, $n = 6$, d.f. residuals = 15, $p = 0.031$; $\frac{1}{4}$
329 width vs. similar width: $z = 2.75$, $n = 6$, d.f. residuals = 15, $p = 0.006$; coral trout: grey vs. similar
330 width: $z = 5.66$, $n = 5$, d.f. residuals = 12, $p < 0.001$; $\frac{1}{4}$ width vs. similar width: $z = 3.48$, $n = 5$, d.f.
331 residuals = 12, $p = 0.000501$), with the grey background providing the least protection from both
332 predators. When viewed by the slingjaw wrasse, there was no statistical difference in the likelihood
333 of attack for the humbug when viewed against the 1 mm background, compared to the
334 monochromatic grey (Fig. 7a: slingjaw: grey vs. $\frac{1}{4}$ width: $z = 0.405$, $n = 6$, d.f. residuals = 15, $p =$
335 0.686).

336 In Experiment 2 ($\frac{1}{2}$ width, similar width, 2 x width bars), humbugs were again least likely to
337 be attacked when viewed against a background with a similar spatial frequency and, interestingly,
338 when also viewed against a slightly higher spatial frequency to their body pattern (Fig. 7b: slingjaw:
339 $\frac{1}{2}$ width vs. similar width: $z = 1.10$, $n = 6$, d.f. residuals = 15, $p = 0.28$; 2 x width vs. similar width:
340 $z = 2.16$, $n = 6$, d.f. residuals = 15, $p = 0.031$; coral trout: $\frac{1}{2}$ width vs. similar width: $z = -0.93$, $n = 9$,
341 d.f. residuals = 23, $p = 0.35$; 2 x width vs. similar width: $z = 2.38$, $n = 9$, d.f. residuals = 23, $p =$
342 0.017). The lowest frequency background provided the least protection, consistent with results from
343 Experiment 1.

344 In Experiment 3, when stylised coral backgrounds were used, there was a decreased
345 likelihood of being attacked when viewed against the similar width or $\frac{1}{2}$ width branching corals.
346 There was no significant difference in the protection afforded by the coral that was most similar in
347 terms of spatial frequency to the humbug body pattern, and that of the smallest branching coral
348 (Fig. 7c: slingjaw: $\frac{1}{2}$ width vs. similar width branches: $z = -1.50$, $n = 5$, d.f. residuals = 12, $p =$
349 0.134; coral trout: $\frac{1}{2}$ width vs. similar width branches: $z = -1.63$, $n = 6$, d.f. residuals = 15, $p =$
350 0.103). When viewed by the slingjaw, there was no difference in the risk of attack between the

351 similar width and 2 x width branching corals (Fig. 7c: slingjaw: 2 x width vs. similar width
352 branches: $z = 1.06$, $n = 5$, d.f. residuals = 12, $p = 0.29$). In fact, in slingjaw behavioural trials, the
353 only time humbug stimuli showed reduced likelihood of attack against natural backgrounds was
354 when the $\frac{1}{2}$ width branching coral was paired with the 2 x width branching coral. In this case, there
355 was a significant reduction in attack likelihood if viewed against the $\frac{1}{2}$ width branching coral (Fig.
356 7c: slingjaw: 2 x width vs. $\frac{1}{2}$ width branches: $z = -2.49$, $n = 5$, d.f. residuals = 12, $p = 0.0128$). For
357 the coral trout predator, humbugs gained significantly more protection when viewed against the
358 coral with similar spatial frequency to their own body pattern, compared to the widest branching
359 corals (Fig. 7c: coral trout: 2 x width vs. similar width branches: $z = 1.34$, $n = 6$, $p < 0.001$).

360 In Experiments 4 and 5, there was a significant increase in the likelihood of being attacked
361 when the angle of the humbug was at 90° to the background (Fig. 8a: slingjaw: 90° vs. 180° : $z =$
362 2.081 , d.f. residuals = 2, $n = 4$, $p = 0.038$; coral trout: 90° vs. 180° : $z = 2.94$, $n = 4$, d.f. residuals =
363 14, $p = 0.003$). In all other angle contrast scenarios, the likelihood of attack did not significantly
364 change with angle contrast although for both species there was a non-significant trend for decreased
365 attack likelihood (Fig. 8b; slingjaw: stripe matched vs. 45° : $z = -1.81$, $n = 5$, d.f. residuals = 16, $p =$
366 0.071 ; stripe matched vs. 180° : $z = -0.51$, $n = 5$, d.f. residuals = 16, $p = 0.608$; 45° vs. 180° : $z =$
367 0.383 , $n = 5$, d.f. residuals = 16, $p = 0.702$; coral trout: stripe matched vs. 45° : $z = -1.317$, $n = 4$, d.f.
368 residuals = 13, $p = 0.188$; stripe matched vs. 180° : $z = -1.615$, $n = 4$, d.f. residuals = 13, $p = 0.106$;
369 45° vs. 180° : $z = -0.932$, $n = 4$, d.f. residuals = 13, $p = 0.351$).

370

371

372

373

374 **Discussion**

375 *Summary*

376 Our results demonstrate that highly contrasting pattern elements used in disruptive
377 colouration do not have to exactly match the spatial characteristics of the background to reduce the
378 likelihood of attack by potential predators. Interestingly, backgrounds with a slightly higher spatial
379 frequency provided humbugs with a reduction in the likelihood of attack, presumably due to
380 predators being unable to detect the prey items against these backgrounds compared to other
381 backgrounds. Our results are consistent when considering the orientation of the humbug against the
382 background, as the likelihood of attack only increased when the orientation contrast was maximised
383 (humbug at 90° to the background). The results for both behavioural testing and image analysis
384 were similar between the two predator species, despite differences between their visual systems and
385 hunting strategies, suggesting that the humbug body pattern has evolved to be effective against a
386 wide range of vertebrate visual systems.

387

388 *Background matching & disruptive colouration*

389 Predator behavioural trials suggest that perfect background-matching is not necessary for
390 increased survival. Our results with fish predators are similar to those found with avian predators,
391 where the disruptive elements of moth body patterns (in particular, the spatial positioning of highly
392 contrasting elements across the body) provided increased survival (or reduction in likelihood of
393 attack) without perfect background-matching (Schaefer and Stobbe, 2006, Stevens et al., 2006).
394 Our results suggest an additional benefit to having a body pattern that is both background-matching
395 and disruptive (so-called differential blending; (Cott, 1940)), as the disruptive colouration provides
396 crypsis on a range of backgrounds, possibly due to the varying angle and width of the highly
397 contrasting black and white bars within the body pattern. Humbugs are therefore likely to be
398 protected from detection by fish predators when they are viewed against a range of spatial
399 frequency backgrounds, supporting the idea that disruptive elements are particularly important in

400 concealing animals that reside in heterogenous environments (Thayer, 1909). Indeed, the humbug
401 lives around and within several species of branching corals that are likely to have a range of spatial
402 frequencies (Sale, 1972).

403

404 *Higher spatial frequency background decreases likelihood of attack*

405 It was particularly interesting to us that a higher spatial frequency background provided as
406 much (or even greater) reduction in the likelihood of predatory attack than backgrounds with a
407 similar spatial frequency to the humbug body pattern. There are a number of possible explanations
408 why this may occur. Backgrounds that have a greater degree of complexity could be distracting to
409 the visual system of the predator (Dimitrova and Merilaita, 2009) and indeed, avian predators take
410 longer to find prey on more complex backgrounds, regardless of the spatial frequency contrast
411 (Dimitrova and Merilaita, 2011). This suggests that a greater number of elements within the
412 background transfers visual attention away from the target or prey. A slight mismatch with the
413 background may also enhance the disruptive effect of the humbug body pattern by decreasing
414 predatory edge detection. Edge detection is a key phase in early visual processing in vertebrates,
415 occurring in the retinal ganglion cells (Land and Nilsson, 2012). Body form can be detected by
416 luminance contrast between the animal and the background (Canny, 1986, Hubel and Wiesel, 1962,
417 Marr and Hildreth, 1980). However, the disruptive vertical bars of the humbug body pattern would
418 create ‘false edges’ that breakup the body shape of the fish, termed coincident disruptive
419 colouration (Cott, 1940). In frogs, highly contrasting body patterns and enhanced borders unlike
420 those seen in natural scenes have also shown to act as a camouflage strategy due to the lack of
421 suitable detection methods in predator visual systems (Osorio and Srinivasan, 1991). The disruptive
422 effect may be greater on a background that contains more ‘natural edges’ than the body pattern (as
423 found on a higher spatial frequency background), as the contrast between the body outline and
424 background would be further blurred, causing a greater visual illusion to the predators.

425

426 *Viewing distance and disruptive colouration*

427 Our experimental trials, and subsequent Fourier Analyses were performed at a set predator
428 viewing distance of 100 cm. With increased viewing distances (similar to those used by coral trout
429 when attacking prey in the wild) it is likely that the black-and-white bars on the humbug merge into
430 one grey object, as is predicted with many of the bright and intricate reef fish colour patterns
431 (Marshall, 2000, Vorobyev et al., 1999, Wilkins et al., 2016). Indeed, as the reef contains many
432 dappled shadows and grey-areas, merged grey objects are likely to be well camouflaged through a
433 direct match to background luminous intensity. We took an underwater field image of humbugs
434 against a coral head and blurred it to examine how well humbugs would match the natural
435 background at a range of viewing distances. To human visual systems, humbugs will remain
436 conspicuous even at a distance of 10 m in clear ocean water. However, when modelled using the
437 predators' visual acuity, the effectiveness of the humbug's camouflage increased with increasing
438 viewing distance, until the spatial frequency of the humbug and coral appear to be similar at a
439 distance of 5m.

440 Coral trout ambush prey from a distance of a few metres and therefore it is likely that the
441 combination of their limited spatial acuity, the visual complexity of the reef background, and the
442 unique characteristics of the humbug body pattern, allow this species to avoid being eaten as often
443 as other damselfish species, as suggested by gut contents analyses (John, 1995, 1999, 2001). The
444 slingjaw wrasse approaches prey at close distances, suggesting other aspects of the humbug ecology
445 play a role in avoiding predatory attacks, such as sheltering within the coral head, or the effect of
446 movement combined with the disruptive body pattern.

447

448 *Visual acuity of predators*

449 Our backgrounds were designed to be at the limit of spatial discrimination for both
450 predators, and therefore the predators may have been unable to distinguish the individual bars
451 within the background, due to behavioural visual resolution being lower than theoretical resolution,

452 as demonstrated in other fish (Champ et al., 2014). We calculated minimum resolvable angles using
453 the distance between two cone photoreceptors (both double and single cones), and did not take into
454 account potential summation within the retinal ganglion cell (RGC) layer, optic nerve, or optic
455 tectum. Further processing may reduce the spatial acuity of the predator (Collin and Pettigrew,
456 1989) thereby enhancing the cryptic potential of the prey body pattern against the background.
457 Additionally, lower light levels would encourage regional summation of the signal within the retina,
458 further reducing visual acuity. As the light levels in this experiment were high (all the experiments
459 were carried out during daylight hours), it is unlikely that summation had a significant effect on the
460 visual acuity of the predators.

461

462 *Movement and orientation of prey*

463 When swimming up and down in the water column, and moving to different areas of the
464 coral head, humbugs do not always swim at the same orientation to the coral. We show that
465 humbugs still retain a significant reduction in predation risk even when they are not completely
466 aligned with the background habitat. Indeed, the orientation of an animal against a background can
467 enhance or reduce the individual's crypsis depending on the alignment of features within the
468 background and body pattern (Webster et al., 2009). It has been shown that in some species of
469 moth, individuals rest in non-random orientations that maximise crypsis with the background
470 (Endler, 1984). Moths will change their orientation to a more cryptic position (Kang et al., 2013)
471 using both visual and tactile information (Kang et al., 2015), thereby reducing predator detection
472 (Webster et al., 2009) and suggesting an adaptive advantage of being in-phase with the background.
473 Our results agree to some extent with the alignment hypothesis: the humbug only suffered increased
474 predation when its patterns were perpendicular (90°) to the background, which would be rare in the
475 natural environment.

476 In this study, we did not incorporate movement, and although high contrast markings are
477 likely to increase predator search times in comparison to low contrast markings independent of

478 motion (e.g.(Dimitrova et al., 2009), high contrast patterns are hypothesised to increase protection
479 when moving (Allen et al., 2013, Thayer, 1909). This ‘motion dazzle’ (sensu Cott, 1942) has been
480 shown to be particularly effective when the pattern is striped or barred as opposed to spotty or plain
481 (Stevens et al., 2008) and can affect the distance travelled, speed and directional information
482 relayed to the viewer’s visual system (Ashida and Kitaoka, 2003, Conway and Livingstone, 2005,
483 Jackson et al., 1976). It has been suggested that, in terrestrial animals, bars and stripes in body
484 patterns may distract predator’s visual systems and provide misinformation about the direction of
485 movement of a group of animals (How and Zanker, 2014). However, some studies have shown that
486 the details of the pattern (i.e. whether background matching or disruptive) are not influential in
487 decreasing predation likelihood, as long as the pattern is at least similar to the background. It is the
488 presence of other similarly patterned objects that increase protection (Hall et al., 2013, Stevens et
489 al., 2011). For interest, we have included a blurred movie of the humbug in its natural environment
490 to simulate how they may appear to predators in the wild (Supplementary Information Movie 1).
491 The humbug has a body pattern similar to that of a zebra and congregates in small groups
492 suggesting an increased confusion effect due to the presence of similarly patterned objects (both
493 humbug and branching coral background). When combined with the attenuating properties of water,
494 it is likely that movement will only serve to increase the camouflage potential of the humbug body
495 pattern. Clearly this is an area that warrants further research.

496

497 *Limitations of study*

498 In this study we have looked exclusively at the humbug and background in greyscale and
499 not incorporated colour into any visual models. As the humbug is black and white, and coral is
500 likely to vary in spectral reflectance between individual colonies, there will be colour contrast
501 between the coral background and humbug body pattern, particularly as many coral reef fish
502 predators are likely to have functional colour vision (Losey et al., 2003, Marshall et al., 2003a,
503 Marshall et al., 2003b, Phillips et al., 2016). It would be interesting to identify whether colour adds

504 another element of disruption to the humbug body pattern, and recent methods have been developed
505 to answer exactly these types of question (Endler, 2012).

506

507 *Conclusions*

508 In summary, the results of this study are the first to show quantitatively that although coral
509 head backgrounds serve to increase the crypsis of disruptive colouration, it is not achieved through
510 matching the spatial frequency of the background as previously assumed (Cott, 1940). Instead, a
511 slight mismatch to a higher spatial frequency background enhances the crypsis of disruptive
512 colouration. Therefore, humbugs should be found in environments with a variety of spatial
513 frequency backgrounds, including many higher spatial frequency backgrounds. Further research
514 should identify whether humbugs actively choose higher spatial frequency backgrounds to reduce
515 the likelihood of detection when approached by predators, as has been suggested in killifish
516 (Kjernsmo and Merilaita, 2012).

517

518

References

519

- 520 ALLEN, G., STEENE, R., HUMANN, P. & DELOACH, N. 2003. *Reef Fish Identification:*
521 *Tropical Pacific*, Jacksonville, Florida, New World Publications, Inc.
- 522 ALLEN, W. L., BADDELEY, R., SCOTT-SAMUEL, N. E. & CUTHILL, I. C. 2013. The
523 evolution and function of pattern diversity in snakes. *Behavioral Ecology*.
- 524 ASHIDA, H. & KITAOKA, A. 2003. A gradient-based model of the peripheral drift illusion.
525 *Perception ECVF abstract*, 32, 0-0.
- 526 BRADLEY, R. A. & TERRY, M. E. 1952. Rank analysis of incomplete block designs: I. The
527 method of paired comparisons. *Biometrika*, 39, 324-345.
- 528 CANNY, J. 1986. A computational approach to edge detection. *Pattern Analysis and Machine*
529 *Intelligence, IEEE Transactions on*, 679-698.
- 530 CAVES, E. M., FRANK, T. M. & JOHNSEN, S. 2016. Spectral sensitivity, spatial resolution, and
531 temporal resolution and their implications for conspecific signalling in cleaner shrimp.
532 *Journal of Experimental Biology*, 219, 597-608.
- 533 CHAMP, C., WALLIS, G., VOROBYEV, M., SIEBECK, U. & MARSHALL, J. 2014. Visual
534 acuity in a species of coral reef fish: *Rhinocanthus aculeatus*. *Brain Behav Evol*, 83, 31-42.
- 535 CHENEY, K. L., CORTESI, F., HOW, M. J., WILSON, N. G., BLOMBERG, S. P., WINTERS, A.
536 E., UMANZOR, S. & MARSHALL, N. J. 2014. Conspicuous visual signals do not coevolve
537 with increased body size in marine sea slugs. *J Evol Biol*, 27, 676-87.
- 538 COIMBRA, J. P., NOLAN, P. M., COLLIN, S. P. & HART, N. S. 2012. Retinal ganglion cell
539 topography and spatial resolving power in penguins. *Brain Behav Evol*, 80, 254-68.

- 540 COLLIN, S. P. 1989. Topography and morphology of retinal ganglion cells in the coral trout
541 *Plectropomus leopardus* (Serranidae): A retrograde colbaltous-lysine study. *The Journal of*
542 *Comparative Neurology*, 281, 143-158.
- 543 COLLIN, S. P. 2008. A web-based archive for topographic maps of retinal cell distribution in
544 vertebrates. *Clinical & experimental optometry : journal of the Australian Optometrical*
545 *Association*. 2007/11/30 ed.
- 546 COLLIN, S. P. & PETTIGREW, J. D. 1989. Quantitative comparison of the limits on visual spatial
547 resolution set by the ganglion cell layer in twelve species of reef teleosts. *Brain, Behavior*
548 *and Evolution*, 34, 184-192.
- 549 CONWAY, B. R. & LIVINGSTONE, M. S. 2005. A different point of hue. *Proceedings of the*
550 *National Academy of Sciences of the United States of America*, 102, 10761-10762.
- 551 CORTESI, F., FEENEY, W. E., FERRARI, M. C. O., WALDIE, P. A., PHILLIPS, G. A. C.,
552 MCCLURE, E. C., SKÖLD, H. N., SALZBURGER, W., MARSHALL, N. J. & CHENEY, K. L. 2015a. Phenotypic plasticity confers multiple fitness benefits to a mimic. *Current*
553 *Biology*, 25, 1-6.
- 554
555 CORTESI, F., MUSILOVÁ, Z., STIEB, S. M., HART, N. S., SIEBECK, U. E., MALMSTRØM,
556 M., TØRRESEN, O. K., JENTOFT, S., CHENEY, K. L., MARSHALL, N. J., CARLETON,
557 K. L. & SALZBURGER, W. 2015b. Ancestral duplications and highly dynamic opsin gene
558 evolution in percomorph fishes. *PNAS*, 112, 1-6.
- 559 COTT, H. B. 1940. *Adaptive coloration in animals*, Oxford, England, Oxford.
- 560 CUTHILL, I. C. & SZÉKELY, A. 2009. Coincident disruptive coloration. *Philos Trans R Soc Lond*
561 *B Biol Sci*, 364, 489-96.
- 562 DE BUSSEROLLES, F., FITZPATRICK, J. L., MARSHALL, N. J. & COLLIN, S. P. 2014. The
563 influence of photoreceptor size and distribution on optical sensitivity in the eyes of
564 lanternfishes (Myctophidae). *PLoS ONE*, 9, e99957.
- 565 DIMITROVA, M. & MERILAITA, S. 2009. Prey concealment: visual background complexity and
566 prey contrast distribution. *Behavioral Ecology*, 21, 176-181.
- 567 DIMITROVA, M. & MERILAITA, S. 2011. Prey pattern regularity and background complexity
568 affect detectability of background-matching prey. *Behavioral Ecology*, 23, 384-390.
- 569 DIMITROVA, M., STOBBE, N., SCHAEFER, H. M. & MERILAITA, S. 2009. Concealed by
570 conspicuousness: distractive prey markings and backgrounds. *Proc Biol Sci*, 276, 1905-10.
- 571 DOUGLAS, R. H. & HAWRYSHYN, C. W. 1990. Behavioural studies of fish vision: an analysis
572 of visual capabilities. In: DOUGLAS, R. H. & DJAMGOZ, M. B. A. (eds.) *The Visual*
573 *System of Fish*. London: Chapman and Hall Ltd.
- 574 EMERSON, S. B., COOPER, T. A. & EHLERINGER, J. R. 1990. Convergence in reflectance
575 spectra among treefrogs. *Functional Ecology*, 4, 47-51.
- 576 ENDLER, J. A. 1983. Natural and sexual selection on color patterns in poeciliid fishes.
577 *Environmental Biology of Fishes*, 9, 173-190.
- 578 ENDLER, J. A. 1984. Progressive background matching in moths, and a quantitative measure of
579 crypsis. *Biological Journal of the Linnean Society*.
- 580 ENDLER, J. A. 2012. A framework for analysing colour pattern geometry: adjacent colours.
581 *Biological Journal of the Linnean Society*, 107, 233-253.
- 582 FRASER, S., CALLAHAN, A., KLASSEN, D. & SHERRATT, T. N. 2007. Empirical tests of the
583 role of disruptive coloration in reducing detectability. *Proceedings of the Royal Society B:*
584 *Biological Sciences*, 274, 1325-1331.
- 585 GODFREY, D., LYTHGOE, J. N. & RUMBALL, D. A. 1987. Zebra stripes and tiger stripes: the
586 spatial frequency distribution of the pattern compared to that of the background is
587 significant in display and crypsis. *Biological Journal of the Linnean Society*, 32, 427-433.
- 588 HALL, J. R., CUTHILL, I. C., BADDELEY, R., SHOHET, A. J. & SCOTT-SAMUEL, N. E. 2013.
589 Camouflage, detection and identification of moving targets. *Proceedings of the Royal*
590 *Society B: Biological Sciences*, 280.

591 HOW, M. J. & ZANKER, J. M. 2014. Motion camouflage induced by zebra stripes. *Zoology*
592 (*Jena*), 117, 163-70.

593 HUBEL, D. H. & WIESEL, T. N. 1962. Receptive fields, binocular interaction and functional
594 architecture in the cat's visual cortex. *The Journal of Physiology*, 160, 106-154.

595 IOANNOU, C. C. & KRAUSE, J. 2009. Interactions between background matching and motion
596 during visual detection can explain why cryptic animals keep still. *Biology Letters*, 5, 191-
597 193.

598 JACKSON, J. F., INGRAM III, W. & CAMPBELL, H. W. 1976. The dorsal pigmentation pattern
599 of snakes as an antipredator strategy: a multivariate approach. *American Naturalist*, 1029-
600 1053.

601 JOHN, J. S. 1995. *Feeding ecology of the coral trout, Plectropomus leopardus (Serranidae), on the*
602 *Great Barrier Reef, Australia*.

603 JOHN, J. S. 1999. Ontogenetic changes in the diet of the coral reef grouper *Plectropomus leopardus*
604 (Serranidae): patterns in taxa, size and habitat of prey. *Marine Ecology Progress Series*,
605 180, 233-246.

606 JOHN, J. S., RUSS, G. R., BROWN, I. W. & SQUIRE, L. C. 2001. The diet of the large coral reef
607 serranid *Plectropomus leopardus* in two fishing zones on the Great Barrier Reef, Australia.
608 *Fishery Bulletin*, 99, 180-192.

609 JULESZ, B. 1971. *Foundations of cyclopean perception.* , Oxford, England, University of Chicago
610 Press.

611 KANG, C., STEVENS, M., MOON, J. Y., LEE, S. I. & JABLONSKI, P. G. 2015. Camouflage
612 through behavior in moths: the role of background matching and disruptive coloration.
613 *Behavioral Ecology*, 26, 45-54.

614 KANG, C.-K., MOON, J.-Y., LEE, S.-I. & JABLONSKI, P. G. 2013. Moths on tree trunks seek out
615 more cryptic positions when their current crypticity is low. *Animal Behaviour*, 86, 587-594.

616 KJERNSMO, K. & MERILAITA, S. 2012. Background choice as an anti-predator strategy: the
617 roles of background matching and visual complexity in the habitat choice of the least
618 killifish. *Proc Biol Sci*, 279, 4192-8.

619 LAND, M. F. & NILSSON, D.-E. 2012. *Animal Eyes*, Oxford University Press.

620 LOSEY, G. S., MCFARLAND, W. N., LOEW, E. R., ZAMZOW, J. P., NELSON, P. A. &
621 MARSHALL, N. J. 2003. Visual biology of Hawaiian coral reef fishes. I. Ocular
622 transmission and visual pigments. *Copeia*, 3, 433-454.

623 MARR, D. & HILDRETH, E. 1980. Theory of Edge Detection. *Proceedings of the Royal Society B:*
624 *Biological Sciences*, 207, 187-217.

625 MARSHALL, N. J. 2000. Communication and camouflage with the same 'bright' colours in reef
626 fishes. *Philos Trans R Soc Lond B Biol Sci*, 355, 1243-8.

627 MARSHALL, N. J., JENNINGS, K., MCFARLAND, W. N., LOEW, E. R. & LOSEY, G. S.
628 2003a. Visual biology of Hawaiian coral reef fishes. II. Colours of Hawaiian coral reef fish.
629 *Copeia*, 3, 455-466.

630 MARSHALL, N. J., JENNINGS, K., MCFARLAND, W. N., LOEW, E. R. & LOSEY, G. S.
631 2003b. Visual biology of Hawaiian coral reef fishes. III. Environmental light and an
632 integrated approach to the ecology of reef fish vision. *Copeia*, 3, 467-480.

633 MCCORMICK, M. I. & WEAVER, C. J. 2012. It pays to be pushy: intracohort interference
634 competition between two reef fishes. *PloS one*, 7, e42590-e42590.

635 OSORIO, D. & SRINIVASAN, M. V. 1991. Camouflage by edge enhancement in animal
636 coloration patterns and its implications for visual mechanisms. *Proc Biol Sci*, 244, 81-5.

637 OSORIO, D., VOROBYEV, M. & JONES, C. 1999. Colour vision of domestic chicks. *The Journal*
638 *of Experimental Biology*, 202, 2951-2959.

639 PHILLIPS, G. A. C., CARLETON, K. L. & MARSHALL, N. J. 2016. Multiple Genetic
640 Mechanisms Contribute to Visual Sensitivity Variation in the Labridae. *Molecular Biology*
641 *and Evolution*, 33, 201-215.

- 642 POHLERT, T. 2015. PMCMR: Calculate Pairwise Multiple Comparisons of Mean Rank Sums. .
643 1.1 ed. <http://cran.r-project.org/package=PMCMR>.
- 644 RANDALL, H. A. & ALLEN, G. R. 1977. A revision of the damselfish genus *Dascyllus*
645 (Pomacentridae) with the description of a new species. *Records of the Australian Museum*,
646 31, 349-385.
- 647 RANDALL, J. E., ALLEN, G. R. & STEENE, R. C. 1997. *Fishes of the Great Barrier Reef and*
648 *Coral Sea*, Hawaii, University of Hawai'i Press.
- 649 SALE, P. F. 1970. Behaviour of the humbug fish. *Australian Natural History*, 16, 362-366.
- 650 SALE, P. F. 1971. Extremely limited home range in a coral reef fish, *Dascyllus aruanus* (Pisces;
651 Pomacentridae). *Copeia*, 2, 324-327.
- 652 SALE, P. F. 1972. Influence of corals in the dispersion of the Pomacentrid fish, *Dascyllus aruanus*.
653 *Ecology*, 53, 741-744.
- 654 SCHAEFER, H. M. & STOBBE, N. 2006. Disruptive coloration provides camouflage independent
655 of background matching. *Proc Biol Sci*, 273, 2427-32.
- 656 SCHOTT, R. K., REFVIK, S. P., HAUSER, F. E., LÓPEZ-FERNÁNDEZ, H. & CHANG, B. S. W.
657 2014. Divergent positive selection in rhodopsin from lake and riverine cichlid fishes. *Mol*
658 *Biol Evol*, 31, 1149-65.
- 659 ST JOHN, J. 1999. Ontogenetic changes in the diet of the coral reef grouper *Plectropomus*
660 *leopardus* (Serranidae): patterns in taxa, size and habitat of prey. *Marine Ecology Progress*
661 *Series*, 180, 233-246.
- 662 STEVENS, M. & CUTHILL, I. C. 2006. Disruptive coloration, crypsis and edge detection in early
663 visual processing. *Proc Biol Sci*, 273, 2141-7.
- 664 STEVENS, M., CUTHILL, I. C., WINDSOR, A. M. M. & WALKER, H. J. 2006. Disruptive
665 contrast in animal camouflage. *Proceedings of the Royal Society B: Biological Sciences*,
666 273, 2433-2438.
- 667 STEVENS, M. & MERILAITA, S. 2009a. Animal camouflage: current issues and new
668 perspectives. *Philos Trans R Soc Lond B Biol Sci*, 364, 423-7.
- 669 STEVENS, M. & MERILAITA, S. 2009b. Defining disruptive coloration and distinguishing its
670 functions. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 364, 481-
671 488.
- 672 STEVENS, M., SEARLE, W. T., SEYMOUR, J. E., MARSHALL, K. L. & RUXTON, G. D. 2011.
673 Motion dazzle and camouflage as distinct anti-predator defenses. *BMC Biol*, 9, 81.
- 674 STEVENS, M., WINNEY, I. S., CANTOR, A. & GRAHAM, J. 2009. Outline and surface
675 disruption in animal camouflage. *Proceedings of the Royal Society B: Biological Sciences*,
676 276, 781-786.
- 677 STEVENS, M., YULE, D. H. & RUXTON, G. D. 2008. Dazzle coloration and prey movement.
678 *Proceedings of the Royal Society B-Biological Sciences*, 275, 2639-2643.
- 679 TEAM, R. C. 2015. R: A language and environment for statistical computing. 3.1.2. "Smooth
680 Sidewalk" ed. Vienna, Austria: R Foundation for Statistical Computing, Vienna, Austria.
- 681 THAYER, G. H. 1909. *Concealing-coloration in the animal kingdom: an exposition of the laws of*
682 *disguise through color and pattern: being a summary of Abbott H. Thayer's discoveries.*,
683 New York, NY, Macmillan.
- 684 ULLMANN, J. F., MOORE, B. A., TEMPLE, S. E., FERNANDEZ-JURICIC, E. & COLLIN, S. P.
685 2012. The retinal wholemount technique: a window to understanding the brain and
686 behaviour. *Brain, behavior and evolution*, 79, 26-44.
- 687 VAIL, A. L., MANICA, A. & BSHARY, R. 2013. Referential gestures in fish collaborative
688 hunting. *Nature Communications*, 4, 1765.
- 689 VAIL, A. L., MANICA, A. & BSHARY, R. 2014. Fish choose appropriately when and with whom
690 to collaborate. *Current Biology*, 24, R791-3.
- 691 VENABLES, W. N. & RIPLEY, B. D. 2002. *Modern Applied Statistics with S*, Springer, New
692 York.

- 693 VOROBYEV, M., MARSHALL, J., OSORIO, D., HEMPEL DE IBARRA, N. & MENZEL, R.
694 1999. Colourful objects through animal eyes. *COLOR research and application*,
695 Supplement Volume 26, S214-217.
- 696 WEBSTER, R. J., CALLAHAN, A., GODIN, J.-G. J. & SHERRATT, T. N. 2009. Behaviourally
697 mediated crypsis in two nocturnal moths with contrasting appearance. *Philosophical*
698 *Transactions of the Royal Society B: Biological Sciences*, 364, 503-510.
- 699 WILKINS, L., MARSHALL, N. J., JOHNSEN, S. & OSORIO, D. 2016. Modelling fish colour
700 constancy, and the implications for vision and signalling in water. *J Exp Biol*.
- 701 ZYLINSKI, S., HOW, M. J., OSORIO, D., HANLON, R. T. & MARSHALL, N. J. 2011. To be
702 seen or to hide: visual characteristics of body patterns for camouflage and communication in
703 the Australian giant cuttlefish *Sepia apama*. *Am Nat*, 177, 681-90.
- 704
- 705