

1 **Supplementary Material**

2 **Background matching and disruptive coloration as habitat-specific strategies for**
3 **camouflage**

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11 This file contains the following supplementary information

12 **Further methods for calculating camouflage metrics**

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16 **Calculating Metrics of Camouflage**

17 *Background matching: colour and luminance*

18 To quantify colour and luminance match to the background we used a widely employed log version
19 of a model of predator discrimination¹. This calculates just noticeable differences (JNDs) between
20 two objects to determine discriminability. Based on a recent evaluation of estimates of receptor
21 noise², we used Weber fractions of 0.1 and 0.05 for the bird and fish vision model respectively, and
22 cone proportions of LW = 0.92, MW = 1.00, SW = 0.81, UV = 0.54 for the peafowl³ and LW = 1.0
23 and SW = 0.5 for the pollack⁴. For luminance, we used a modified achromatic version of the model⁵
24 based on the double cones for birds and LW cones for the pollack⁶, with Weber fractions of 0.2 and
25 0.05 for the bird and fish models². The output of the model, JNDs, predicts whether two objects can

be discriminated (values < 1.00), with increasing values equating to a reduction in the level of camouflage match. We measured the cone values for each crab ROI for each visual system, and then the same for each background image. Using the above models, we then compared the colour and luminance match of each crab carapace to every background image, followed by calculating average colour and luminance JNDs for each crab to each habitat. We therefore derived an average level of background matching for each crab to each of the two habitat types, across all samples.

Background matching: pattern

To assess background pattern matching between crab carapace and the background for each habitat, a granularity analysis was conducted. This method has previously been successfully used to analyse patterns in other animals, including cuttlefish (e.g.^{7,8}) and cuckoo-host bird eggs (e.g.^{9,10}). It has also been used to measure shore crab carapace markings^{11,12}. During granularity analysis, each image is filtered using Fast Fourier bandpass filtering, at multiple spatial frequency scales, resulting in each filter measuring information or ‘energy’ at different spatial bands (see^{7,9}). The energy at each of these scales can be measured as the standard deviation of the pixel values¹³, such that larger markings (of low spatial frequency) are captured by smaller filter sizes, and smaller markings (higher spatial frequency) are captured by larger filter sizes. While granularity analyses of intrinsic animal patterns can provide valuable measures of appearance, the process has recently been extended to allow direct comparisons between the body markings of an animal and the substrate (‘pattern energy difference’, PED), giving a measure of background pattern matching. This has been used to measure background matching in birds¹⁴ and fish¹⁵, and has been shown to predict detection times of predators searching for wild bird nests (e.g. predict survival¹⁶) and of humans searching for hidden computer targets¹⁷.

While colour is important in many detection and discrimination tasks, achromatic vision is widely thought to be key for analysing much spatial information, especially pattern, and in birds this seems based on the double cones⁶. Therefore, for pattern analysis we used the double cone

(luminance) values of the peafowl (*Pavo cristatus*)³. Here, because previous work has shown close similarities between avian and fish crab pattern achromatic metrics¹⁸, and because achromatic information tends to be more conserved among species and based on middle to longer-wave parts of the spectrum⁶, we only model avian and not fish based pattern measures. PED values were generated in ImageJ as part of a granularity analysis, which calculates the absolute difference between the spectra of two images/samples across all spatial scales measured. Any two patterns with similar energy across all spatial scales will produce low pattern difference values, indicative of background matching, whereas deviation in either amplitude or shape of the spectra will produce larger differences. Here, the absolute difference between the spectra of crab carapaces and habitat backgrounds was assessed (both rock pool and mudflat separately). For each background image, we measured the granularity spectrum of the entire image. The granularity spectrum of each crab carapace was then compared to the spectrum of every background image, and the average per habitat taken. As above, we therefore derived an average level of pattern matching for each crab to each of the two habitat types.

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67 *Disruptive coloration*

68 To quantify disruption, we used a recently developed method inspired by visual processing that has
69 been shown to be one of the most important predictors of human detection times of disruptive
70 targets (and superior to other pattern metrics¹⁷). This method, unlike other metrics of disruption
71 (e.g.^{19,20}), takes account the direction of perceived edges versus actual body outlines, enabling it to
72 distinguish ‘false edges’ (markings that run at right angles to the prey’s outline and are maximally
73 disruptive) from ‘coherent edges’ (markings that match the outline of the animals body, potentially
74 making the prey’s shape easier to detect). The resultant edge disruption metric, ‘GabRat’, uses
75 angle sensitive filters to measure the ratio of false edges to coherent edges around the target
76 outline²³. A high ratio of false edges to coherent edges should be more disruptive, and therefore
77 indicates that prey are more difficult to detect, while lower values suggest salient coherent edges.

78 First, images were exported as binary mask images (the crab carapace being white against a
79 black background) in TIFF format, and a Gabor filter was applied to each of the pixels around the
80 edge of the carapace, using a sigma level (filter size) of 5 as this was most relevant for objects
81 around 5-15 mm¹⁷. The filter size is dependent on the px/mm of the carapace and controls the size
82 of the pattern markings that are detected; larger sigma levels would detect larger disruptive patterns.
83 The edge disruption of each crab was in this way measured against a neutral background. This
84 enabled the angle of the crab's outline at each point of the carapace to be measured independent of
85 the background, since the metric involves comparing the presence of edges perpendicular to, and
86 intersecting the body outline. This process was then repeated, but for the actual crab when against
87 all rock pool and mudflat image backgrounds, using the same sigma level. A custom function in
88 ImageJ randomly placed each crab onto a background and measured the carapace edge disruption
89 by applying the Gabor filter. This measured each point around the crab's outline at an angle parallel
90 to and at right angles to the true outline, enabling measurements of the interaction between the crab
91 and its background to be made. An aspect of image analysis of the background samples was to
92 ensure that only relevant areas of substrate for potential camouflage were selected. As such, any
93 possible areas that a crab would not normally be found on in the wild (at least during the day; e.g.
94 sitting on top of large rocks), were labelled exclusion zones in the image processing and ignored.
95 To avoid ambiguity, we selected exclusion zones as any substrate object (e.g. exposed rock) that
96 had a width larger than 7.5 mm. A disruption ratio was calculated at each point on the crab's
97 outline, and the mean of these ratios across the whole carapace outline was calculated, resulting in
98 the final Gabor edge disruption ratio (GabRat). GabRat values range from 0 - 1, with < 0.2 being
99 considered as equating to a low level of edge disruption and > 0.4 to high edge disruption¹⁷.

100 For each image, each crab was randomly placed in 50 different positions that did not overlap
101 with each other or any exclusion zones. This was repeated on all 94 backgrounds (47 rock pool and
102 47 mudflat), resulting in a total of 4700 edge disruption measurements per individual crab. This
103 process accounted for variation in positioning of crabs in the wild. The average GabRat value of the

total 50 positions was calculated for each background, so that one value was generated per crab/image combination. Means per individual were then calculated across both rock pool and mudflat backgrounds, so that each crab had an average edge disruption value for both habitat types.

References

1. Vorobyev, M. & Osorio, D. Receptor noise as a determinant of colour thresholds. *Proc R Soc B* **265**, 351-358 (1998).
2. Olsson, P., Lind, J. & Kelber, A. Chromatic and achromatic vision: parameter choice and limitations for reliable model predictions. *Behav Ecol* **29**, 273-282 (2018).
3. Hart, N. S. Vision in the peafowl (Aves: *Pavo cristatus*). *J Exp Biol* **205**, 3925-3935 (2002).
4. Shand, J., Partridge, J. C., Acher, S. N., Potts, G. W. & Lythgoe, J. N. Spectral absorbance changes in the violet/blue sensitive cones of the juvenile pollack, *Pollachius pollachius*. *J Comp Physiol A* **163**, 699-703 (1988).
5. Siddiqi, A., Cronin, T. W., Loew, E. R., Vorobyev, M. & Summers, K. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J Exp Biol* **207**, 2471-2485 (2004).
6. Osorio, D. & Vorobyev, M. Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proc R Soc B* **272**, 1745-1752 (2005).
7. Chiao, C.-C., Chubb, C., Buresch, K. C., Siemann, L. & Hanlon, R. T. The scaling effects of substrate texture on camouflage patterning in cuttlefish. *Vis Res* **49**, 1647-1656 (2009).
8. Barbosa, A. *et al.* Cuttlefish camouflage: the effects of substrate contrast and size in evoking uniform, mottle or disruptive body patterns. *Vis Res* **48**, 1242-1253 (2008).
9. Stoddard, M. C. & Stevens, M. Pattern mimicry of host eggs by the common cuckoo, as seen through a bird's eye. *Proc R Soc B* **277**, 1387-1393 (2010).
10. Stevens, M., Troscianko, J. & Spottiswoode, C. N. Repeated targeting of the same hosts by a brood parasite compromises host egg rejection. *Nat Comm* **4**, 2475 (2013).

- 130 11. Nokelainen, O., Hubbard, N., Lown, A. E., Wood, L. E. & Stevens, M. Through predators' eyes
131 – phenotype-environment associations in shore crab coloration at different spatial scales. *Biol J*
132 *Linn Soc* **122**, 738–751 (2017).
- 133 12. Stevens, M., Wood, L. E. & Lown, A. E. Camouflage and individual variation in shore crabs
134 (*Carcinus maenas*) from different habitats. *PLoS ONE* **9**, e115586 (2014).
- 135 13. Troscianko, J. & Stevens, M. Image calibration and analysis toolbox – a free software suite for
136 objectively measuring reflectance, colour and pattern. *Meth Ecol Evol* **6**, 1320–1331 (2015).
- 137 14. Stevens, M., Troscianko, J., Wilson-Aggarwal, J. & Spottiswoode, C. N. Improvement of
138 individual camouflage through background choice in ground-nesting birds. *Nat Ecol Evol* **1**,
139 1325–1333 (2017).
- 140 15. Smithers, S. P., Wilson, A. & Stevens, M. Rock pool gobies change their body pattern in
141 response to background features. *Biol J Linn Soc* **121**, 109–121 (2017).
- 142 16. Troscianko, J., Wilson-Aggarwal, J., Stevens, M. & Spottiswoode, C. N. Camouflage predicts
143 survival in ground-nesting birds. *Sci Rep* **6**, 19966 (2016).
- 144 17. Troscianko, J., Skelhorn, J. & Stevens, M. Quantifying camouflage: how to predict detectability
145 from appearance. *BMC Evol Biol* **17**, 7 (2017).
- 146 18. Nokelainen, O., Hubbard, N., Lown, A. E., Wood, L. E. & Stevens, M. Through predators' eyes
147 – phenotype-environment associations in shore crab coloration at different spatial scales. *Biol J*
148 *Linn Soc* **122**, 738–751 (2017).
- 149 19. Stevens, M. & Cuthill, I. C. Disruptive coloration, crypsis and edge detection in early visual
150 processing. *Proc R Soc B* **273**, 2141–2147 (2006).
- 151 20. Lovell, P. G., Ruxton, G. D., Langridge, K. V. & Spencer, K. A. Individual quail select egg-
152 laying substrate providing optimal camouflage for their egg phenotype. *Curr Biol* **23**, 260–264
153 (2013).
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