

Colour change and behavioural choice facilitate chameleon prawn camouflage against different seaweed backgrounds

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1 **Camouflage is driven by matching the visual environment, yet natural habitats are rarely**
2 **uniform and comprise many backgrounds. Therefore, species often exhibit adaptive traits to**
3 **maintain crypsis, including colour change and behavioural choice of substrates. However,**
4 **previous work largely considered these solutions in isolation, whereas many species may**
5 **use a combination of behaviour and appearance to facilitate concealment. Here we show**
6 **that green and red chameleon prawns (*Hippolyte varians*) closely resemble their associated**
7 **seaweed substrates to the vision of predatory fish, and that they can change colour to**
8 **effectively match new backgrounds. Prawns also select colour-matching substrates when**
9 **offered a choice. However, colour change occurs over weeks, consistent with seasonal**
10 **changes in algal cover, whereas behavioural choice of matching substrates occurs in the**
11 **short-term, facilitating matches within heterogeneous environments. We demonstrate how**
12 **colour change and behaviour combine to facilitate camouflage against different substrates**
13 **in environments varying spatially and temporally.**

14 Cryptic coloration allowing visual camouflage is a cosmopolitan antipredator strategy in nature
15 and provides classic examples of evolution by natural selection^{1–5}. Generally, crypsis works by
16 reducing the chance of prey detection or recognition by the visual system of potential
17 predators^{1,6,7}, often through background matching^{1,5,8–10}. However backgrounds within natural
18 habitats are rarely uniform and vary considerably in colour and pattern across space and time¹¹.
19 Therefore, an array of adaptations exist to overcome this problem, including generalist coloration,
20 colour polymorphisms, ontogenetic changes, colour change, and behaviourally-oriented choices^{1,3,12–}
21 ¹⁴. Of these strategies, colour change is widespread in nature and allows individuals of many

22 species to adjust the colour aspect of their camouflage to both the environment and to the visual
23 systems of different predators^{13,15}. Research has tended to focus on animals capable of rapid
24 change (i.e. seconds/minutes) as opposed to slower changes (days/weeks), despite the latter likely
25 being more prevalent across taxonomic groups^{13,15}. The benefit of rapid colour change for crypsis in
26 many animal groups is clear (e.g. chameleons¹⁶, cuttlefish¹⁷, and fish^{18–21}) since it provides a
27 response to environments that change unpredictably in the short term¹¹. The function of slower
28 changes can be less intuitive¹³, though alterations occurring over a period of days-weeks likely
29 improve concealment in response to predictable and slow environmental changes or associated with
30 life history¹¹. This may include seasonal changes in habitat availability. The drivers and outcome of
31 longer-term colour change for camouflage to predator vision has rarely been properly quantified.

32 Aside from direct colour adaptations, animals may also facilitate camouflage by behaviourally
33 choosing appropriate backgrounds^{22–28}. Despite the intuitiveness of this idea there has historically
34 been a lack of consistent experimental investigation into this area²⁷, and few rigorous tests of how and
35 when behavioural choices facilitate crypsis on natural substrates have been conducted. However,
36 recent work has demonstrated the existence of background choice at an individual level for improving
37 concealment. Both the nesting substrate preference of laboratory Japanese quail (*Coturnix*
38 *japonica*)²⁶ and the resting spots of wild Aegean wall lizards (*Podarcis erhardii*)²², for example, have
39 been shown to be closely tied to individual appearance of eggs and adults, respectively. In addition,
40 ground-nesting birds from nine different species improved their level of camouflage by choosing
41 appropriate backgrounds across multiple spatial scales²⁹. Recent work also demonstrates how moths
42 change their resting posture based on individual levels of camouflage²⁸.

43 However, most studies to date have tested background choices in species where individuals are
44 fixed in appearance, and work has yet to fully consider the importance of behavioural preferences
45 affecting concealment of species capable of colour change (but see^{18,30,31}). From a conceptual
46 perspective, individuals from species capable of rapid colour alterations might be under less intense
47 selective pressure to rely on behavioural choices for crypsis, since they can rapidly alter appearance
48 regardless of the background³². For example, cuttlefish (*Sepia officinalis*) do not exhibit substrate
49 preferences for camouflage, but rely on visual environmental cues to adopt camouflage patterns³³.
50 Conversely, individuals from species capable of changing colour over a longer period of time may
51 depend heavily on an ability to select visually appropriate backgrounds. In this manner, individuals

52 may maintain a level of protection by reducing the level of mismatch during the process of colour
53 change^{11,27}. However, the relationship between these two strategies is more complex and likely
54 depends on a number of additional factors. The larvae of two different salamander species, for
55 example, change colour over a few hours when placed in mismatched substrates but the capacity for
56 choosing concealing backgrounds differed between species and was affected by predation risk³⁴.
57 Also, rock gobies (*Gobius paganellus*) are able to rapidly alter coloration to improve camouflage, but
58 individuals also selected darker backgrounds that improved matching, indicating that a combination of
59 behaviour and colour change may reduce limitations of each strategy¹⁸. Similarly, behavioural choices
60 for colour matching backgrounds potentially improving camouflage were also demonstrated in fish
61 species, both in the laboratory³¹ and field¹⁹. Therefore, colour change and oriented-choice behaviours
62 are non-mutually exclusive traits that are widely utilised by cryptic species to maximise colour
63 concealment and reduce prey detection by predators^{18,27,30}.

64 Crustaceans, particularly those living in dynamic intertidal habitats, have frequently been used
65 as key organisms to investigate the fitness advantages conveyed by cryptic traits^{35,36}. Within this
66 group, caridean shrimps are well known to exhibit remarkable variation in coloration often allied to a
67 cryptic lifestyle^{24,37-43}. The chameleon prawn (*Hippolyte varians*) is a small species that exhibits a
68 variety of colour forms that, subjectively, show a close similarity to the seaweed species on which
69 they associate (Fig. 1). Research at the end of the 19th century revealed that this species was capable
70 of changing colour over different time-scales, including driven by light-intensity, periodic shifts
71 between diurnal/nocturnal forms, and slow changes in response to novel substrates^{39,40,43}. In addition,
72 the different colour forms of chameleon prawns may choose concealing algal substrates when
73 displaced⁴⁴. However, there is little information on how colour change and behavioural traits may
74 operate in tandem in order to improve camouflage and reduce detection by predators over different
75 spatial and temporal scales.

76 Here, we use digital photography, image analysis, and vision models of ecologically relevant
77 predators (fish) to quantify how chameleon prawn camouflage is mediated by colour change and
78 behavioural choices. We focus on the homogenous green and red prawns (Fig. 1) against natural
79 seaweed substrates: the 'green' sea lettuce (*Ulva lactuca*) and the 'red' dulse (*Palmaria palmata*). We
80 first assessed the level of camouflage achieved by the different prawn forms against seaweed in the
81 field, and conducted laboratory and field experiments to test whether prawn camouflage is improved

82 by longer-duration colour change, and whether prawns show behavioural preferences for matching
83 seaweed types, respectively. We expected that if coloration is adaptive and increases prawn survival,
84 the different colour forms will exhibit increased camouflage against their main seaweed substrate.
85 Similarly, we expected that colour change will induce alteration on prawn coloration towards the
86 colour of the new substrate, reducing the level of colour mismatch; and that prawns will show a strong
87 behavioural preference for matching seaweed backgrounds when given a choice. Our results clearly
88 demonstrate that, to predator vision, prawns exhibit effective camouflage against their associated
89 seaweed substrate and are able to alter coloration improving camouflage in response to changes to
90 their background. Additionally, prawns show strong behavioural preferences for selecting substrates
91 that match their own appearance. Our findings support the notion that, since longer-duration colour
92 changes inevitable lead to some degree of mismatch between individuals and backgrounds, slow-
93 change species likely have evolved convergent behavioural strategies to ensure that a cryptic benefit
94 is maintained in a species overall cryptic stratagem.

95 **Results**

96 We modelled the coloration of both green and red prawns and natural seaweed substrates (green sea
97 lettuce and red dulse) to predator vision using the spectral sensitivity data of the dichromatic pollack
98 (*Pollachius pollachius*)⁴⁵ and the trichromatic two-spotted goby (*Gobiusculus flavescens*)⁴⁶. We used
99 a polynomial mapping function to convert prawn and seaweed multispectral images from the camera
100 colour space to fish vision^{47,48}, generating values for pollack and goby predicted cone catches (see
101 Methods).

102 ***Coloration provides camouflage against natural substrates***

103 In order to assess the level of camouflage between prawn colour types and seaweed species from the
104 modelled perspectives of fish vision we used the widely implemented noise model for colour
105 discrimination of Vorobyev and Osorio⁴⁹, which predicts chromatic signal discriminability as units of
106 “just noticeable differences” (JNDs). Colour JND comparisons across combinations of ‘colour type’
107 and ‘seaweed species’ showed type-specific colour matches to seaweed species for both pollack and
108 goby on distinct backgrounds (LMM: pollack: $F_{1,252} = 544.18$, $p < 0.001$; goby: $F_{1,252} = 339.27$, $p <$
109 0.001). Specifically, colour contrasts of green prawns against green sea lettuce (mean \pm SE = $1.73 \pm$
110 0.15 for pollack, and 1.91 ± 0.17 for goby vision) were around the threshold of discriminability and

111 much lower than against red dulse (6.66 ± 0.34 for pollack, and 6.38 ± 0.36 for goby vision).
112 Concurrently, the opposite pattern was found for red prawns, with individuals showing small colour
113 differences against red dulse (mean \pm SE = 1.44 ± 0.12 for pollack, and 2.48 ± 0.19 for goby vision)
114 and higher contrasts against green sea lettuce (8.04 ± 0.31 for pollack, and 8.15 ± 0.33 for goby
115 vision) (Fig. 2). This shows that green and red prawns are a very close match to their respective
116 substrates in the field.

117 ***Prawns change colour over time in response to new substrates***

118 In order to test the ability of *H. varians* to change colour in response to new substrates we conducted
119 a laboratory experiment where both colour forms were kept on colour-contrasting seaweeds over a
120 period of 30 days. Hue values (i.e. a measure of colour type, see Methods for details) of green
121 prawns kept on red dulse significantly increased over time to both pollack (LMM: $F_{6,124} = 51.03$, $p <$
122 0.001) and goby vision (LMM: $F_{6,124} = 45.65$, $p < 0.001$). Conversely, hue of red prawns maintained on
123 green sea lettuce significantly decreased over time to both visual systems (pollack: $F_{6,118} = 65.48$, $p <$
124 0.001 ; goby: $F_{6,118} = 44.31$, $p < 0.001$ - Fig. 3). These results can be explained by changes in the
125 relative proportion of reflectance in the short-wave (SW) channel of prawns over time. At the
126 beginning of the experiment, green prawns have relatively low short-wave reflectance compared to
127 red prawns. However, after a few days exposed to colour contrasting seaweed, there was a crossover
128 in this pattern, with green prawns exhibiting larger SW reflectance than red individuals (Fig. 3). These
129 changes resulted in green prawns kept on red dulse becoming redder, and red prawns kept on green
130 sea lettuce becoming greener, to human vision (Fig. 4). Hue changes of both colour types occurred
131 faster in the initial 10 days of the experiment (comparisons between days 0, 5 and 10 all significant –
132 Tukey t -tests; $p < 0.05$), becoming smaller and non-significant over the next 20 days (Fig. 3). The
133 body size of individuals, included as a covariate in the model, was significantly correlated with hue
134 only for green prawns (pollack: $F_{1,22} = 16.21$, $p < 0.001$; goby: $F_{1,22} = 16.18$, $p < 0.001$), indicating that
135 larger green individuals change less for hue along time compared to smaller prawns.

136 ***Colour change enables better camouflage on new substrates***

137 Overall, the colour JNDs of green and red prawns against red dulse and green sea lettuce
138 significantly reduced over time to both pollack (LMM – green prawns: $F_{6,124} = 44.16$, $p < 0.001$, day 0
139 [mean \pm SE] = 14.83 ± 0.48 \rightarrow day 30 = 5.53 ± 0.76 ; red prawns: $F_{6,118} = 49.44$, $p < 0.001$, day 0 =

140 $11.25 \pm 0.25 \rightarrow$ day 30 = 3.65 ± 0.68 ; Fig. 3), and goby vision (LMM – green prawns: $F_{6,124} = 44.68$, p
141 < 0.001 , day 0 = $14.81 \pm 0.46 \rightarrow$ day 30 = 5.52 ± 0.79 ; red prawns: $F_{6,124} = 47.33$, $p < 0.001$, day 0 =
142 $10.66 \pm 0.20 \rightarrow$ day 30 = 4.07 ± 0.71 ; Fig. 3). These results show that both prawn types increased
143 their chromatic similarity to the new seaweed background over time, improving their camouflage (Fig.
144 4). Similar to hue, prawn size was significantly correlated with JNDs only for green prawns (LMM -
145 pollack: $F_{1,22} = 16.42$, $p < 0.001$; goby: $F_{1,22} = 15.45$, $p < 0.001$), with larger individuals being more
146 poorly concealed against red dulse (i.e. exhibiting larger JNDs) than small prawns over the
147 experiment.

148 ***Behavioural substrate choice facilitates crypsis***

149 We performed a series of behavioural trials using a Y-choice decision chamber (see Methods) to
150 determine whether prawns actively selected a background that improved their level of camouflage.
151 For each trial, lasting 10 minutes, we gave a choice between red dulse and green sea lettuce for
152 both green and red prawns. Green prawns were significantly more likely to choose green sea lettuce
153 than red dulse (Exact binomial test: *proportion* = 0.80, $n = 41$, $p < 0.001$), while red prawns preferred
154 red dulse instead of green sea lettuce (Exact binomial test: *proportion* = 0.74, $n = 38$, $p = 0.005$).
155 Therefore, prawns show strong behavioural preferences for seaweed matching their current coloration
156 (Fig. 5).

158 **Discussion**

159 Our results show that the coloration of chameleon prawns provides effective visual camouflage to
160 predator vision against their main seaweed substrates. We first quantified the level of *in situ*
161 camouflage between prawns and seaweed using vision models of two fish predators, showing that
162 prawn concealment was closer and more effective against the algal substrate against which they
163 would reside. Next, we show that green and red prawns change colour over time when placed on
164 mismatched seaweed and improve their camouflage on the new substrate. Prawn coloration is
165 therefore highly plastic, with prawns able to switch from red to green and vice versa over a few days
166 and weeks. Finally, we show that individuals actively choose a background based on their current
167 coloration that improves their level of camouflage to predator vision.

168 The capacity to change appearance across species has likely evolved to cope with both spatial
169 and temporal uncertainty over a short time frame, or with predictable changes over a longer time

170 period¹¹. In both cases, it enables animals to change their appearance as they move between patches
171 within their environment (e.g. spatial heterogeneity) or as the composition of environment changes
172 around them over time (e.g. temporal heterogeneity)¹¹. In the case of chameleon prawns, our results
173 indicate that colour change is unlikely to have evolved as response to the spatial heterogeneity of
174 their habitat, as is the case for rapidly changing animals such as chameleons¹⁶ and cuttlefish³².
175 Instead, the slower colour change of chameleon prawns likely allows individuals to maintain their
176 camouflage in response to seasonal variation in the abundance of seaweed species, in accordance
177 with more predictable patterns of environmental variation^{11,13}. In contrast to slow colour change, our
178 results from the behavioural experiment show that the ability of chameleon prawns to select
179 appropriate backgrounds is likely a key strategy for maintaining camouflage in the short term and to
180 cope with the considerable spatial variation in the habitat where individuals live²⁷. Oriented choices
181 will also be important to help prawns dealing with some unique challenges of the intertidal
182 environment, such as wave action dislodging individuals from preferred substrates and tidal changes
183 influencing habitat availability over the day.

184 Our results also indicate that the effectiveness of colour change for camouflage was higher for
185 small green prawns compared to larger individuals. This relationship needs to be properly
186 investigated in future studies but speculatively could indicate that larger green prawns have less
187 selection acting on them due to more effective escape behaviours or by achieving a size-refuge from
188 predators, or due to physiological limitations. Why this occurs only for green prawns is difficult to
189 explain but may be related to the fact that red prawns when changing to green always exhibit lower
190 JNDs compared to the opposite (Fig. 3). This seems to be a physiological constraint, since the red
191 coloration is probably defined by the presence of red-yellow pigments within chromatophore cells,
192 while the green tone is provided by the presence of only the yellow pigment (similar to that observed
193 in the prawns *Heptacarpus pictus* and *H. paludicola*³⁷). Therefore, changing from red to green may be
194 easier and faster than the opposite since both pigments (i.e. red and yellow) are already present
195 within the colour cells of red prawns. On the other hand, green prawns changing to red would need to
196 metabolize red pigments (probably by food ingestion⁴¹) which would take more time, especially for
197 larger individuals, potentially explaining the higher JNDs during the colour change process and the
198 size-effects we observed.

199 Seasonal variation in animal appearance in response to changes in substrate availability is
200 frequently observed in nature¹¹. Many birds and mammals, for example, change their coat colour from
201 brown in the summer to completely white in the winter as response to the appearance of snow¹¹. In
202 addition, populations of the polymorphic pacific tree frog (*Hyla regilla*) are characterized by both fixed
203 and colour changing morphs and the maintenance of such colour variation in the population is
204 associated with changes in microhabitat use of individuals due to seasonal changes in substrate
205 availability⁵⁰. The assemblage of seaweed species within the intertidal zone varies through the year
206 as a function of both the species' life history and some environmental conditions. The red dulse
207 (*Palmaria palmata*) is a perennial species and, while it undergoes a seasonal burst in growth over the
208 summer months, its holdfasts and fronds provide a 'fixed' habitat over a period of several years⁵¹. On
209 the other hand, the green sea lettuce (*Ulva lactuca*) has a pseudo-perennial life cycle in which the
210 basal portion but not the fronds survive over the years. In this case, seaweed biomass and therefore
211 the habitat availability for algal-dwelling species fluctuates over the year^{51,52}. Sea lettuce exhibits a
212 marked period of rapid growth during the warmer months and, although it may be found throughout
213 the year, it is more susceptible to the effects of harsher winter weather (e.g. lower temperatures,
214 storms and currents) in shallow regions such as rock pools⁵². As such, the combination of slower
215 colour changes and behavioural habitat preferences may enable chameleon prawns to maintain the
216 benefits of cryptic coloration, meanwhile allowing the species to take advantages of seasonal
217 abundances of algal habitats throughout the year. Camouflage through colour change in the carnival
218 prawn (*Hippolyte obliquimanus*), which associates with different seaweeds along the Brazilian coast,
219 is also related to seasonal fluctuations in the cover of its main habitat, the brown algae (*Sargassum*
220 *furcatum*)⁴¹. During the summer, this seaweed dominates the shallow rocky areas in southeast Brazil
221 and brown prawns attain the largest densities⁵³. However, in winter, *Sargassum* cover decreases and
222 the density of the different colour types in the population changes considerably, following the
223 fluctuation of seaweed habitats (Duarte & Flores, in prep). In addition to seasonal changes in
224 substrate, intertidal species may undergo seasonal shifts in predation pressures as fish species move
225 inshore and as juveniles develop, and future work could quantify how the level of crypsis may vary
226 with these predator shifts.

227 Phenotype-environment matching is assumed to be a common outcome of selection for cryptic
228 traits, yet most research to date has shown indirect associations between animal phenotypes and

229 habitats (i.e. has not quantified camouflage itself, but see³⁵). Our work demonstrates that camouflage
230 in chameleon prawns is enhanced on substrates where they live, and that this close association
231 between phenotype and habitat is predicted to be effective to predator vision. Studies investigating
232 associations between the appearance of juvenile shore crabs (*Carcinus maenas*) and that of their
233 habitat substrate composition over a range of spatial scales have demonstrated the strongest
234 associations at the micro scale (<1m-squared)⁵⁴. While camouflage is dependent on the appearance
235 match between individuals and their local habitat, an animal may improve this by either reorienting its
236 body relative to its background or by selecting a more appropriate substrate²⁷. Indeed, many
237 individuals from the same or different species have evolved preferences for habitat patches that
238 enable increased levels of camouflage²⁷. For highly mobile species it is likely that these behavioural
239 preferences allow for the active maintenance of phenotype-environment associations within
240 heterogeneous habitats. For species capable of colour change, we would expect that behavioural
241 preferences for substrates would change in tandem with a change in body coloration to maintain the
242 selective advantages conveyed by visual camouflage²⁷. In addition, we might also expect other
243 processes to come into play for maintaining colour variation, including multiple morph types acting to
244 hinder predator search image formation, and frequency-dependent selection⁵⁵.

245 Changes in behavioural preferences mediated by modifications of body coloration have also been
246 demonstrated in guppies (*Poecilia reticulata*), in which individuals spent significantly more time in
247 black and white habitat zones after being induced to change colour in corresponding black and white
248 tanks⁵⁶. Future work should further consider coloration and camouflage with regards to predator vision
249 and measured attack rates. Another research avenue is to understand how predator cues may affect
250 colour change and cryptic behaviours. For example, in the presence of a perceived predation threat
251 animals may improve their capacity to change colour and select concealing backgrounds, the latter
252 approach especially in slow colour-change species. In salamander larvae, the addition of predator
253 cues in experimental tanks increases larval preference for dark backgrounds followed by a
254 corresponding change in individual coloration³⁴. However, in the absence of predator cues, larvae
255 spend equal time in light and dark habitat zones, adopting a more intermediate colour form³⁴. In the
256 case of chameleon prawns, we would expect that the addition of predator cues may speed up the
257 colour change process and lead to an increase in the proportion of prawns making a choice for
258 concealing substrates.

259 In the case of polyphenic species, intra-specific variation in coloration and behaviour may allow
260 different individuals to utilise distinct aspects of visual camouflage to adopt alternative life-histories⁵⁷.
261 Duarte and colleagues⁴¹ demonstrated differences between colour morphs of the 'carnival' prawn
262 (*Hippolyte obliquimanus*) in algal preference, showing morph-specific differences in morphology and
263 mobility which indicate contrasting benthic/pelagic lifestyles⁴¹. Homogenous coloured morphs showed
264 greater habitat fidelity and a stouter body shape, whereas transparent morphs displayed a more
265 streamlined body shape and increased levels of swimming activity⁴¹. In the case of chameleon
266 prawns, besides the homogenous coloured forms we studied here (Fig. 1), there exists an assortment
267 of alternative forms that combine colour patterns (spots or stripes) with some degree of
268 transparency^{13,43}, and these may also reflect different camouflage, behaviour, and life history
269 strategies. In our study, the visual models used are based on colour perception and the spectral
270 sensitivities of ecologically relevant predators available in the literature^{45,46}. However, we do not
271 model the spatial acuity of the predators, which is relevant to pattern matching and something that
272 may be especially relevant to transparent prawn types with their intricate markings.

273 Although our results clearly show that prawns choose backgrounds that improve camouflage, there
274 are many questions regarding what cues control preferences for certain substrates. There is limited
275 information about the existence of colour vision in similar crustaceans, which limits our understanding
276 of whether chameleon prawns are able to identify different seaweeds based on colour cues.
277 Alternatively, caridean prawns living on the pelagic seaweed *Sargassum natans* select appropriate
278 backgrounds based on their shape, with individuals preferring habitats containing structures that best
279 matched their body shape²⁴. Therefore, in some cases, the structure of the habitat allied with a range
280 of behavioural adaptations in the use of that structure may provide better protection from predators
281 than concealing coloration⁵⁸. Since our knowledge of chameleon prawn visual capabilities is limited, it
282 may be that individuals depend upon identifying the structural form of their preferred habitat when
283 making a choice either independently of, or in conjunction with, its coloration. Finally, there is growing
284 evidence about the importance of chemical cues and habitat complexity regulating habitat choices in
285 a wide array of marine organisms, especially for those living on biological substrates (e.g. seaweeds,
286 corals)⁵⁹. Future work could aim to quantify the importance of visual components and other sensory
287 cues that species use when identifying suitable substrates for crypsis.

288 A wide range of mechanisms and evolutionary pressures control appearance and the adaptive
289 benefits of colour forms in polymorphic / polyphenic populations, and the 'fine-tuning' of a species'
290 cryptic stratagem may depend on the integration of morphology, behaviour, and the environment
291 itself^{13,29}. Here, we show that chameleon prawns are able to alter body coloration to improve
292 camouflage against new substrates, potentially allowing prawns to exploit seasonal changes in
293 resource abundance (e.g. food and shelter⁴³). This would allow the exploitation of a wider range of
294 resources within structurally-complex habitats, potentially reducing intra-specific competition⁶⁰ and
295 predation risk⁶¹. Concurrently, behavioural preferences facilitate camouflage over timescales when
296 colour change is too slow. The growing number of studies testing how combinations of chromatic
297 (particularly colour change) and behavioural traits influence crypsis, and the fact that the above-
298 mentioned traits are displayed by a range of phylogenetically and ecologically distinct systems, is
299 indicative of the convergent evolution of these cryptic stratagems and the importance of adaptive
300 benefits conveyed to species in order to maintain crypsis in heterogeneous habitats in wild systems.

301

302 **Methods**

303 ***Prawn and seaweed sampling***

304 Chameleon prawns (*Hippolyte varians*) of varied sex and size, and two seaweed species, green sea
305 lettuce (*Ulva lactuca*) and red dulse (*Palmaria palmata*), were sampled from rocky tide pools during
306 low-tide periods in the intertidal zone of Gyllyngvase beach, Falmouth, Cornwall, UK (50°08'33"N,
307 05°04'08"W). Prawns and algae for the initial camouflage analysis were collected during the spring-
308 summer of 2015, 2016 and 2017, while those for the behavioural trials and colour change experiment
309 were collected in the autumn of 2016. Prawns were obtained by vigorously shaking seaweeds in grey
310 buckets or by dunking buckets adjacent to seaweed patches, after which they were visually classified
311 in green or red colour types (Fig. 1). After sampling, those prawns used in colour change experiments
312 were individually housed inside (2.5"x2.5") white guttering containers with ultra-fine insect mesh
313 netting bases suspended within two indoor tanks with their original seaweed hosts (i.e. green prawns
314 on green sea lettuce and red prawns on red dulse). The water in the tanks was kept at a salinity
315 between 30-35 ppm using Aquarium Systems Instant Ocean sea salt mixture (Swell Ltd, Cheshire,
316 UK) and maintained at a constant temperature (matching local sea temperature ~ 15° C) with a Swell
317 D&D DC300 Refrigerated Cooler (Swell Ltd, Cheshire, UK). The water was pumped and filtered using

318 an Eheim Classic 350 2215 External Filter (EHEIM GmbH & Co. KG, Germany) and 13 mm aquarium
319 tubing. Each guttering container was fed with oxygenated water from a PVC piping system above the
320 tank. Natural lighting was simulated using two GroBeam 600 Ultima ND Natural Daylight and one
321 AquaBeam 600 Ultima NUV (Tropical Marine Centre, Hertfordshire, UK). These lights were set to a
322 12-light cycle from 07:30–19:30. Different sets of prawns and seaweed were used for the three
323 different procedures we carried out, which included: (i) calculating camouflage of wild prawns against
324 seaweed to test whether prawns are better concealed to the backgrounds they are found, and
325 performing (ii) colour change experiments and (iii) behavioural choice trials to test whether prawns are
326 capable to change colour and/or choose backgrounds to improve their concealment and camouflage.

327 ***Photography***

328 We used digital image analysis to obtain colour estimates of prawns and seaweed in all the different
329 experimental procedures we carried out. Pieces of both green sea lettuce and red dulse, as well as
330 living chameleon prawns of both green and red colour types, were photographed in a dark room in a
331 custom made acrylic chamber (5 x 5 cm) using cameras converted to full spectrum sensitivity by
332 removal of the UV and IR blocking filter (Advanced Camera Services Limited, Norfolk, UK). Initial
333 camouflage images were taken using a Nikon D7000 digital camera fitted with a Coastal Optic 60 mm
334 lens, and images for the colour change experiment were taken using a Nikon D90 SLR camera fitted
335 with a 105 mm Nikkor lens. Human-visible spectrum photographs were obtained through a Baader
336 UV-IR blocking filter (Baader Planetarium, Mammendorf, Germany), permitting only visible spectrum
337 light (420 to 680 nm), and UV photographs were taken with a Baader UV pass filter allowing
338 ultraviolet light (320 to 380 nm). Following initial imaging, UV photographs were not taken of prawns
339 during the colour change experiment to speed up proceedings, since both predator visual systems do
340 not have UV sensitive vision^{45,46} and prawn/seaweed general coloration is low in UV reflectance.
341 Illumination was provided by one human visible Arc Lamp (70W, 6500K Iwasaki Colour Arc Lamp)
342 with a modified bulb in order to remove its UV filter enabling UV photography. We also placed a PTFE
343 (polytetrafluoroethylene) diffuser cylinder around the photography chamber in order to ensure even
344 lighting conditions and reduce light reflection. All images were taken in RAW format, with manual
345 white balancing and fixed aperture settings, to avoid overexposed areas⁴⁷ and included a black and a
346 white Spectralon reflectance standards (Labsphere - 8.5% and 95% for the initial camouflage data,
347 and 7% and 93% for the colour change data) and a scale bar. After capture, images were linearised

348 using curves modelled from eight Spectralon reflectance standards with reflectance values ranging
349 from 2 to 99% in order to correct for camera non-linear responses to light intensity^{47,48}. Each
350 photograph was also equalised for any changes in light conditions using the two Spectralon standards
351 and saved as 32-bit multispectral images. All these routines were performed by a series of
352 customized functions implemented in the ImageJ software⁴⁸.

353 ***Visual modelling***

354 In our study, we choose fish as our model predators as they are a common group associated with
355 intertidal areas either in association with seaweed and seagrasses or as opportunistic visitors coming
356 from deeper areas during high tide periods. Since the assemblage of fish species in a certain area will
357 vary depending on different factors, including local depth, turbidity, and tidal conditions, we decided to
358 utilise two disparate types of fish visual system with known spectral sensitivities that are known to
359 have chameleon prawns (or similar prawn species) in their diet^{62,63}. Fish exhibit a range of variation in
360 their visual capabilities⁶⁴, and so testing prawn camouflage using both dichromatic (i.e. possessing
361 cones sensitive to short and medium wavelengths) and trichromatic (i.e. possessing cones sensitive
362 to short, medium and long wavelengths) systems is important to account for camouflage perception to
363 different receivers. Therefore, we map the digital images of prawns and seaweeds to corresponding
364 models of predator vision^{47,48}, using the spectral sensitivity data found in the literature of two potential
365 prawn predators: (i) the dichromatic pollack (*Pollachius pollachius*), which has spectral peaks for
366 single cones at 436 nm (shortwave sensitivity - SWS) and for double cones (paired cells with a similar
367 morphology) at 521 nm (mediumwave sensitivity - MWS)⁴⁵, and (ii) the trichromatic two-spotted goby
368 (*Gobiusculus flavescens*), which has spectral peaks for single cones at 456 nm (SWS) and for double
369 cones at 531 nm (MWS) and 553 nm (longwave sensitivity - LWS)⁴⁶. Here, we propose that colour
370 vision in pollack and goby is encoded by both single and double cones, but for the latter, we assumed
371 that each double cone component works independently, as has been already reported for other fish
372 species⁶⁵. In addition, we incorporated 50% light transmission cut-off at 410 nm for both species^{45,46}
373 and used a D65 standard irradiance spectrum as a measure of incident illumination. Although this is
374 not the precise light conditions under which natural predation would occur, water clarity is normally
375 high in shallow tide pools (maximum 1.5 m deep) where prawns and seaweed were sampled.

376 We used a polynomial mapping function to convert prawn and seaweed images from the camera
377 colour space to fish vision^{47,48}, generating values of pollack and goby cone catches. This is a widely

378 used procedure for visual modelling and results in cone catch values that are in close accordance
379 with data derived from spectrometry approaches^{48,66,67}. We have previously characterized the spectral
380 sensitivity of our camera in combination with the lens and filters^{48,67}. Visual modelling resulted in
381 multispectral images, which were used to estimate photon catches values for each colour channel in
382 the regions of interest (ROIs) we selected. For the initial camouflage analysis, prawn ROIs consisted
383 of the prawn carapace and abdomen from the area behind the eyes to the end of the third abdominal
384 somite, avoiding the stomach area. For the colour change analysis, prawn's ROI consisted of the
385 entire prawn carapace and abdomen from the area behind the eyes to the end of the sixth abdominal
386 somite where it reaches the telson. ROIs were also selected on images of green sea lettuce and red
387 dulse, consisting on the entire fronds of small seaweed pieces.

388 ***Quantification of prawn camouflage in the field***

389 In order to first predict whether the existing colour differences between wild prawns and seaweeds
390 are perceived by fish predators, we used the widely implemented noise model for colour
391 discrimination of Vorobyev and Osorio⁴⁹, which predicts chromatic signal discriminability as units of
392 "just noticeable differences" (JNDs). Weber fractions were calculated based on the specific cone
393 ratios of each visual model (shortest to longest wavelength; pollack 0.70: 1⁴⁵; goby 0.72 : 1 : 0.60⁴⁶)
394 and a noise-to-signal ratio of 0.05 was used for the most abundant cone type in each species⁶⁸. JNDs
395 lower than 1 indicate that two colours cannot be discriminated by the receiver, while values higher
396 than 1 would indicate a higher probability of prey detection by predators⁴⁹. Using this model, we
397 calculated colour differences (expressed as JNDs) between freshly sampled prawn types ($n = 64$ for
398 both green and red colour types) and a single randomly selected image from a pool of 64 photos of
399 both the green sea lettuce and red dulse, resulting in 64 JND values for each comparison. We predict
400 that each prawn type would exhibit lower colour contrasts and be better camouflaged against the
401 seaweed they are found mostly in nature, i.e. green chameleon prawns will be better concealed to
402 green sea lettuce while red individuals to the red dulse.

403 ***Colour change trials***

404 This experiment was conducted to test the ability of chameleon prawns to change colour to improve
405 their level of camouflage in response to non-matching algal substrates. Prawns ($n = 25$ of each green
406 and red colour types) of similar size (here defined as the distance between the region behind the eyes

407 and the junction between the sixth abdominal somite and the telson - green = 7.67 mm \pm 0.34 [mean
408 \pm SE] , red = 8.34 mm \pm 0.41 , $t_{(48)} = 1.28$, $p = 0.21$) were photographed in the field (day 0) and then
409 were acclimatised to laboratory conditions for 24 hours on matching algal substrates (green prawns
410 on green sea lettuce, red prawns on red dulse). Prawns were then switched to algal substrates of
411 contrasting coloration (green on red dulse, red on green sea lettuce). Photographs were then taken
412 on days 5, 10, 15, 20, 25 and 30 to analyse the colour change process. During the first 10 days, when
413 colour change was most abrupt (see Fig. 3), prawn survival was 100% for both colour types. 92% of
414 green and 88% of red prawns survived to day 20, after which we experienced an increased die off
415 leaving us with 56% of green and 60% red prawns surviving to the end of the experiment. Missing
416 values (i.e. data for prawns that died before the end of the experiment) were controlled using the
417 option 'na.omit' of the 'lmer' function (see below), which allowed the inclusion of data from dead
418 prawns in the model but keeping only those from the time periods they were alive.

419 In order to evaluate the capacity of colour change in prawns along the experiment, we calculated a
420 colour metric (= hue) using two different approaches based on each fish visual system. For pollack,
421 hue was simple defined as the SWS/ LWS ratio, since only these two colour channels are responsible
422 for colour vision in this species⁴⁵. For goby vision, we conducted a principal component analysis
423 (PCA) to determine the main axis of colour variation that exists in prawn types and used this to
424 determine a logical colour channel¹⁴. PCA was applied on a covariance matrix of the standardized
425 cone catch data from the three reflectance channels and hue was further defined as the ratio
426 [SWS/(MWS+LWS)], which is a simple measurement of short-wavelength versus medium-longwave
427 reflectance, broadly analogous to an opponent colour channel¹⁴. Similarly, in order to quantify how
428 this change in colour relates to changes in camouflage, we used the same JNDs⁴⁹ procedure from the
429 perspective of pollack⁴⁵ and goby⁴⁶ vision. To calculate these colour differences, each prawn image,
430 for each day, was randomly paired with an image from a pool of 26 images of both green sea lettuce
431 and red dulse (green prawns vs. red dulse, red prawns vs. green sea lettuce), allowing for comparison
432 between prawn and seaweed ROIs over the experiment.

433 ***Behavioural choice trials***

434 Behavioural observations were concentrated around low tide periods under a range of lighting
435 conditions at Gyllyngvase Beach using custom made Y-choice decision chamber to test whether
436 green and red prawns actively choose an algal substrate that improved camouflage. Each individual

437 was first acclimatised to the chamber for one minute before the opaque divider was removed allowing
438 the prawn to access the two arms of the y-choice chamber. For each trial lasting a maximum of 10
439 minutes, we recorded if the prawn individual made a choice and what substrate was chosen. Prawn
440 decision within the allotted time was observed in 79 of 180 trials and did not differ between the two
441 colour types ($X^2 = 0.22$, $df = 1$, $p = 0.64$).

442 **Statistical analysis**

443 All statistical analysis were undertaken using the software R [v. 3.3.0]⁶⁹ (the supporting data are
444 available online as Supplementary Data 1 and the R scripts used for the statistical analysis can be
445 assessed in <https://github.com/rafaduarte87/chameleon-prawn-camouflage>). Regardless of the visual
446 model, a linear mixed-effects model was performed on colour JNDs for wild prawns, with both 'prawn
447 types' (green or red) and 'seaweed species' (green sea lettuce or red dulse) as fixed between-
448 subjects factors, and 'individual' as a random factor to control for repeated measurements on the
449 same individual, since each prawn was compared to both seaweed species. Similarly, for the colour
450 change experiment, prawn hue and prawn JND were analysed separately for each colour type and
451 visual model using a linear mixed effect model, in which 'day' was included as a fixed factor with
452 seven levels (0, 5, 10, 15, 20, 25 and 30 days), 'size' as a co-variate in order to control for possible
453 colour changes due to prawn size, and 'individual' as a random factor to account for repeated
454 measurements in the same prawn individual across days. All linear models were fitted using the 'lmer'
455 function in the 'lme4' package⁷⁰. Model residuals were checked for the homogeneity of variances and
456 normal error distribution, for which colour JND data for green prawns in the colour change experiment
457 needed a log transformation to meet model assumptions. In the case of significant effects, the Tukey
458 post hoc test was applied to compare mean differences between factor levels using the 'lsmeans'
459 function from the 'lsmeans' package⁷⁰. Finally, for the behavioural-choice trial, the decisions of green
460 and red prawns were analysed separately using an exact binomial test ('binom.test' function from the
461 'stats' package in R), specifying the number of successful choices (green - green sea lettuce, red -
462 red dulse) and the total sample size.

463 **Data availability**

464 All data generated or analysed during this study are available in Supplementary Data 1. The R scripts
465 for statistical analysis can be assessed in [https://github.com/rafaduarte87/chameleon-prawn-](https://github.com/rafaduarte87/chameleon-prawn-camouflage)
466 [camouflage](https://github.com/rafaduarte87/chameleon-prawn-camouflage).

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624

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630 Mynott and Jim Galloway for providing additional images of prawns and seaweeds for the initial
631 camouflage analysis.

632

633 **Author contributions**

634 S.D.G., R.C.D. and M.S. designed the experiment. R.C.D. collected initial camouflage data. S.D.G.,
635 E.K. and N.A. collected behavioural data, S.D.G. collected colour change data, R.C. D. and S.D.G.
636 performed all image and statistical analysis. S.D.G., R.C.D. and M.S. contributed to the writing of the
637 manuscript.

638 **Competing interests**

639 The authors declare there are no competing interests.

640 **Ethical Compliance**

641 Work was approved by University of Exeter Bioscience ethics committee (code: 2017/1568).

642 **Figure Legends**

643 **Fig. 1 *Hippolyte varians* seaweed habitats and colour types.** Chameleon prawns (*H. varians*) are
644 found in a variety of colour forms which, subjectively, show a close resemblance to the seaweed
645 species on which they are found. **(a)** The heterogeneous nature of intertidal rock pool habitats in UK
646 shores including the green algae sea lettuce (*Ulva lactuca* - sl) and the red algae dulse (*Palmaria*
647 *palmata* - d). **(b)** The green and red colour types of chameleon prawns used in this study. Prawn
648 images provided by Dr Cyril Bennett.

649 **Fig. 2 Coloration provides adaptive camouflage against natural substrates.** Pollack (upper
650 panel) and goby (lower panel) vision discrimination (as 'just noticeable differences'; JNDs) of green (n
651 = 64) and red ($n = 64$) prawn types against green sea lettuce (*Ulva lactuca*) and red dulse (*Palmaria*
652 *palmata*) habitats. Boxes display medians and inter-quartile ranges (IQRs), whiskers represent lowest
653 and highest values within $1.5 \times$ IQRs, and black filled circles represent outliers. The dashed line
654 (JND=1) indicates the threshold for predicted visual discrimination of prawns by fish predators.

655 **Fig. 3 Colour change improves camouflage match in response to mismatched substrates.**
656 Changes in hue (mean \pm SE) of green ($n = 25$) and red ($n = 25$) prawns when placed against
657 seaweed of opposing coloration over 30 days to the vision of both pollack **(a)** and goby **(b)**. A
658 crossover pattern can be observed between the two colour types as hue in green prawns increases
659 due to an increase in the relative proportion of shortwave reflectance whereas hue for red prawns
660 decreases due to the reduction of reflectance in this channel. Changes in JNDs (mean \pm SE) over
661 time for green and red prawns to the modelled perspectives of **(c)** pollack and **(d)** goby,

662 demonstrating that both colour types are able to alter their coloration in response to new substrates
663 and that this change increases the level of camouflage (lower JNDs) when perceived by ecologically
664 relevant predators.

665 **Fig. 4 Colour change in chameleon prawns.** Changes in the body coloration of green and red
666 chameleon prawns (*Hippolyte varians*) in response to colour mismatching seaweed over 30 days of
667 experiment. For the purposes of display here, images were linearized and equalized but not
668 converted to predator vision.

669 **Fig. 5 Behavioural substrate choices facilitate crypsis.** Percentages of choices ($n = 79$) made by
670 green and red chameleon prawns (*Hippolyte varians*) between two seaweed species, green sea
671 lettuce (*Ulva lactuca*) and red dulse (*Palmaria palmata*). When given a choice, each colour type
672 clearly chooses the substrate of corresponding coloration (e.g. green – green sea lettuce; red – red
673 dulse).

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