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Different ways to disappear: transparency extends camouflage beyond background matching in heterogeneous environments

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Abstract

Environmental heterogeneity challenges camouflage because no single phenotype is expected to maximise concealment across all backgrounds. While uniform pigmentation can provide effective background matching on specific substrates, transparency may offer a more generalist camouflage strategy by reducing conspicuousness across different visual backgrounds. However, the relative survival advantages and trade-offs of these alternative strategies, particularly when they coexist within the same species, remain poorly understood. Here, we investigated how camouflage performance varies between solid-coloured and transparent forms of the chameleon prawn (*Hippolyte varians*) across heterogeneous seaweed backgrounds. Using an online visual search experiment, 3,367 participants searched for realistic prawn models presented against photographs of four seaweed species, generating 45,888 prey presentations. Survival analyses revealed strong interactions between prawn colour type and background. Solid-coloured prawns performed as specialists, achieving their highest survival on matching seaweeds, particularly for green and brown individuals. By contrast, transparent prawns maintained relatively high survival across most backgrounds, consistent with a generalist strategy. However, transparency also involved important trade-offs: increasing levels of chromatic and achromatic mismatch made transparent prawns more readily detectable than solid-coloured individuals, while increasing body size had a

negative effect on their survival. These findings reveal complementary advantages and limitations of specialist and generalist camouflage within a single species, suggesting that environmental heterogeneity may create conditions favouring the coexistence of alternative camouflage strategies in natural populations.

Keywords: computer-generated; online game; phenotypic diversity; predator-prey interactions; survival analyses; trade-off

Introduction

Some of the greatest diversity in life on Earth lies in the colours and patterns of animals, plants, and fungi, which serve functions ranging from defence and courtship to protection against harmful ultraviolet radiation^{1,2}. A substantial component of this diversity has evolved through anti-predator coloration, particularly camouflage^{3,4}. Across diverse taxa, colours and patterns reduce the likelihood of detection or recognition by predators or prey^{3,5–7}, making camouflage a classic example of adaptation^{4,8–10}. Despite its seemingly straightforward function, camouflage encompasses diverse strategies that operate through multiple mechanisms closely linked to behaviour, ecology and life history traits^{3,4,11}. One of the most widespread in nature is background matching, whereby an organism resembles the colours, brightness and patterns of its surroundings¹². However, camouflage effectiveness is rarely constant across ecological contexts. Differences among life-history stages, sexes and behavioural strategies, together with spatial and temporal habitat variation, expose animals to multiple visual environments^{13–17}. Consequently, a phenotype providing excellent concealment in one habitat may become ineffective in another, generating trade-offs between camouflage effectiveness and essential activities such as movement, foraging and reproduction^{13,18}.

Animals inhabiting heterogeneous environments can overcome these challenges through alternative camouflage strategies^{4,13}. Specialist phenotypes closely resemble particular substrates¹², substantially reducing detection by visual predators but potentially restricting the use of alternative, colour-mismatching habitats^{19–21}. By contrast, generalist strategies provide acceptable, albeit imperfect, concealment across multiple backgrounds, if this yields higher overall survival than closely matching a single substrate^{17,21}. Transparency offers one possible mechanism for generalist camouflage, as the visual properties of the background are transmitted through transparent body regions, reducing contrast with the surrounding environment^{22,23}. Because

transparency is less dependent on the appearance of a particular substrate than colour-based background matching, it has often been regarded as one of the most effective camouflage strategies in nature^{22–24}.

Despite these potential advantages, transparency involves important trade-offs²⁵. To be transparent animals must sacrifice the use of pigments which would otherwise aid in UV protection and thermoregulation^{24–26}. Meanwhile, partial transparency resulting from opaque elements, such as organs, food and internal pigments may interfere with improvements to background match otherwise provided by transparency^{22,25}. In addition, transparency generally becomes less effective as body size increases because body edges become easier to resolve and internal structures occupy a greater proportion of the visible body^{26,27}. Rather than favouring complete transparency, these trade-offs may instead promote the coexistence of phenotypes with varying levels of transparency and pigmentation within certain species. Such coexistence is commonly observed during ontogenetic shifts²⁸, particularly in benthic crustaceans, where pelagic larvae are generally transparent but become pigmented following metamorphosis. However, the coexistence of both phenotypes within the same life stage, such as the adult phase, is found in some cephalopod and crustacean species^{22,23} and may be underreported. In these animals, coexistence of transparent and fully pigmented phenotypes has been linked to changes in light environment²⁹ or to differences in life-history traits such as movement patterns or trophic resource use^{30,31}. However, the relative survival advantages of these alternative camouflage strategies across heterogeneous environments remain largely unresolved²⁴.

Phenotypic plasticity and behavioural substrate choice provide additional ways for animals to cope with environmental heterogeneity^{32–34}. Colour change occurs over timescales ranging from seconds to days or seasons^{11,35–37}, with rapid physiological changes allowing individuals to track unpredictable environments, whereas slower morphological changes are generally associated with more predictable environmental variation that occurs over longer timescales^{11,13}. Many animals also improve concealment by selecting backgrounds that best match their appearance³⁴, potentially based on visual cues or indirectly through other sensory modalities, such as mechanoreception^{38,39}. The relationship between phenotype and habitat choice may itself depend on the degree of phenotypic plasticity. In species with fixed colour patterns or discrete polymorphisms, such preferences may be genetically determined^{40,41}, whereas in colour-changing species habitat choice is expected to shift plastically alongside changes in phenotype^{33,42}. The success of these strategies, however, will depend not only on the phenotype of the animal, but also on the characteristics of the environment in which it is

82 deployed. Visually or structurally complex habitats can reduce target detectability independently of colour
83 matching^{43,44}, potentially relaxing selection for precise camouflage or strong substrate preferences⁴⁵. Habitat
84 structure may further influence concealment, as structurally complex substrates provide additional opportunities
85 for animals to remain hidden independently of their coloration^{46,47}. Consequently, the benefits of camouflage
86 strategies and associated behaviours are likely to vary with the visual and structural characteristics of the habitats
87 in which they are expressed.

88 The chameleon prawn (*Hippolyte varians*) provides a valuable system for investigating the effectiveness of
89 alternative camouflage strategies because it combines background matching, transparency, colour change and
90 behavioural substrate choice within a naturally heterogeneous environment^{11,42,47,48}. This species inhabits lower
91 intertidal rock pools throughout north-western Europe, associating with seaweeds that differ in colour, structure
92 and seasonal abundance⁴⁹. Individuals occur as fully pigmented green, red and brown forms (hereafter “solid-
93 coloured prawns”) and transparent types exhibiting varying degrees of transparency (hereafter “transparent
94 prawns”) (Figure 1). Solid-coloured prawns closely resemble their host seaweeds and gradually change colour
95 over approximately 1-3 weeks following transfer to a new background^{47,48}, consistent with adaptation to
96 predictable seasonal changes in macroalgal communities or movement into new areas dominated by different
97 algal species⁵⁰. However, this response is too slow to maintain concealment during short-term movements
98 caused by tides or wave action. Instead, prawns preferentially select seaweeds matching their current
99 appearance⁴⁸, with these preferences shifting alongside colour change⁴². By contrast, transparent prawns appear
100 more mobile and exhibit weaker substrate preferences than solid-coloured types (in prep), consistent with
101 observations in the congeneric species *Hippolyte obliquimanus*³⁰. Chameleon prawns can also transition
102 between transparent and fully pigmented forms, although over longer timescales (in prep). Together, these
103 characteristics provide an opportunity to examine the relative benefits of alternative camouflage strategies
104 within a species capable of changing both its appearance and behavioural decisions in a visually complex
105 environment.

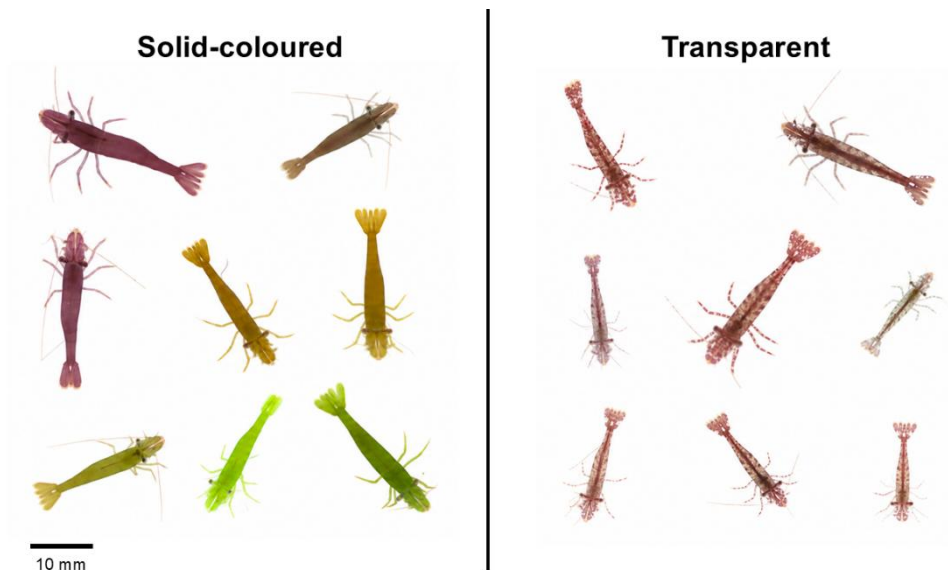


Figure 1. Intraspecific colour variation in the chameleon prawns (*Hippolyte varians*). Individuals exhibit either predominantly uniform body pigmentation (solid-coloured), ranging from red and brown to green tones, or varying degrees of body transparency (transparent), often combined with pigmented stripes and spots. Prawn images were calibrated and converted to human vision for better visualization.

In this study, we developed an interactive, computer-based visual detection experiment to investigate the effectiveness of alternative camouflage strategies in chameleon prawns across heterogeneous environments. By combining realistic digital representations of naturally occurring prawn colour types with photographs of their natural seaweed habitats, our approach recreates key visual features of predator-prey encounters while allowing systematic comparisons across different camouflage and background combinations. Using human players as surrogate predators, an approach supported by previous studies showing strong agreement with detection patterns observed in natural predators^{6,44,51,52}, we tested three predictions based on detection success and detection times. First, we predict that solid-coloured prawns function as camouflage specialists, achieving the highest survival on closely matching seaweeds, whereas transparent individuals act as generalists, maintaining relatively high survival across multiple backgrounds. Second, we predict that the relative importance of chromatic (colour) and achromatic (luminance) matching differs between camouflage strategies. Because transparency depends on transmitting the visual properties of the background, we expect transparent prawns to be more sensitive to changes in both brightness and colour matching than solid-coloured individuals, whose concealment relies primarily on resemblance to a specific substrate. Third, we predict that body size imposes a stronger constraint on transparency than on uniform pigmentation. Specifically, the survival advantage of

transparent individuals should strongly decline with increasing body size, whereas body size should have lower influence on the effectiveness of solid-coloured phenotypes. Altogether, our study evaluates how alternative camouflage mechanisms and environmental heterogeneity influence prey detection, as well as the potential survival advantages associated with intraspecific colour diversity in natural populations.

130

131 **Materials and Methods**

132 **Creation of seaweed backgrounds**

133 The backgrounds used in the game were obtained from digital photographs taken of four different seaweed
134 species where chameleon prawns are commonly found on UK coast, being two native (the red dulse *Palmaria*
135 *palmata* and the green sea lettuce *Ulva lactuca*) and two non-native species (the brown wireweed *Sargassum*
136 *muticum* and the pink harpoon weed *Asparagopsis armata*)^{47,48}. Seaweeds were hand-sampled during low tide
137 from shallow rockpools within the intertidal zone of Gyllyngvase beach, Falmouth, Cornwall, UK (50°08'33"N,
138 05°04'08"W) in May 2023 and transported to the laboratory at the University of Exeter (Penryn). Five clumps
139 of each seaweed species were immersed in a transparent glass tank (45 x 30 x 20 cm) with the bottom covered
140 with natural gravel and filled with seawater, in addition to a scale with a grey standard painted with a waterproof
141 paint of known reflectance (11.80% measured through a spectroradiometer “JETI specbos 1211-UV-2”).
142 Seaweeds were photographed using a Sony Alpha 7 camera mounted on a tripod in an external area of the
143 laboratory under natural illumination and using light diffusers to reduce glare following standard protocols^{53,54}.
144 Seaweed photos were taken in RAW format, with manual white balance and a fixed aperture setting. Images
145 were then equalized (using the grey standard), calibrated to human vision (CIE XYZ visual model) using a
146 colour chart (X-Rite ColorChecker) and finally converted to 24-bit RGB colour images (as png files) using
147 functions available in the MICA-toolbox in ImageJ^{54,55}. Each image was then cropped into three portions (1800
148 x 1300 pixels each) with a minimum overlap between them, resulting in 15 different background replicates. The
149 area of the crop covered by the seaweed was marked as a single region of interest (ROI) to discriminate what
150 regions of the crop represented the seaweed or the gravel substrate. Crops were classified as “seaweed” or
151 “mixed” based on the area covered by the algae, with those with more than 80% of cover being classified in the
152 first group. Finally, a matrix of 48 equidistant circles with a diameter of 10 mm each (which is the approximate

average body size of chameleon prawn models) was set at each crop to determine both the coordinates (i.e., the centre of the circle) where the prawn target could be positioned (using random angles) and if the circle was part of the seaweed or the gravel areas. For this study, only prawn targets positioned within “seaweed” crops were considered for subsequent analyses, whereas those placed on “mixed” substrate were excluded to ensure that all trials involved a consistent and unambiguous seaweed background.

Creation of prawn targets

Given the extensive intraspecific variation in colour patterns and transparency exhibited by chameleon prawns (Figure 1), we used computer-generated prawn targets rather than photos of real individuals. This approach allowed us to closely reproduce the natural appearance of different prawn colour types while minimising uncontrolled variation among individuals (including body positioning), thereby facilitating systematic comparisons of camouflage effectiveness across different seaweed backgrounds. Prawn drawings were created using the GIMP image editor software (<https://www.gimp.org/>) by tracing the body outline of digital photos of real chameleon prawns. Each prawn model resulted from a combination of a maximum of four layers, including a transparent (layer 0) and a solid-coloured (layer 1) layers, as well as two external layers representing the variation in the white longitudinal stripes (layer 2) and spots around the tail (layer 3) that are commonly observed in real chameleon prawns (Figure 1). This layering system resulted in 6 broad prawn types: solid-red, solid-green, solid-brown, transparent-pure, transparent-red, and transparent-brown (Figure 2).

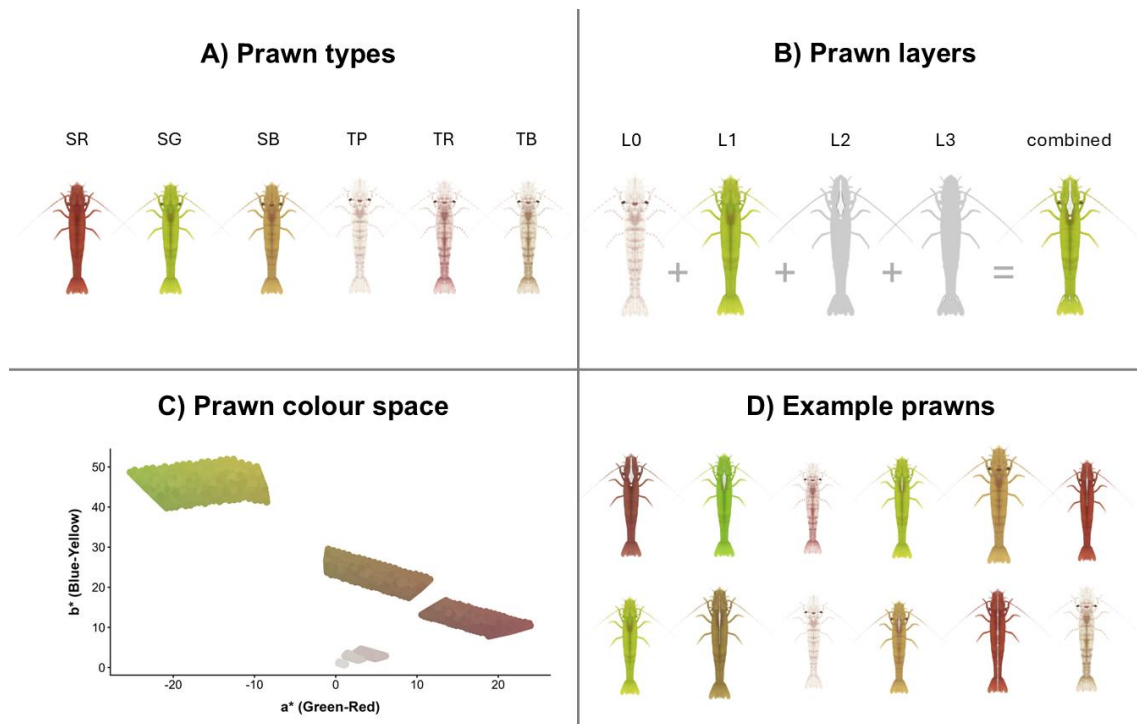


Figure 2. Variations of computer-generated chameleon prawns (*Hippolyte varians*). A) The 6 broad prawn types, solid-red = SR, solid-green = SG, solid-brown = SB, transparent-pure = TP, transparent-red = TR, and transparent-brown = TB. B) Illustration of how the 4 layers were overlayed on top of one another to construct the prawns. Base layer = L0, prawn type = L1, body stripes = L2, and tail stripes and spots = L3. C) Colour variation of prawn L1 when shown on a white background. Colour variants were calculated by varying the hue, saturation and brightness of the prawns, with values being converted back into CIE $L^*a^*b^*$ colour space. D) Example prawns showing variation in size, colour and pattern.

Variations in the appearance of each prawn type were achieved by changing (i) the brightness, hue, and saturation of layer 1, (ii) randomising which body and tail stripe options were used for layers 2 and 3, and (iii) randomising the size of the prawn on the screen relative to the background scale (8-12 mm). The base colours for layer 1 were extracted from the CIE $L^*a^*b^*$ values of 45 red and 45 green chameleon prawns photographed using a Nikon D90 camera coupled with 105 mm macro lens in a dark room under the illumination of a UV Arc Lamp (70 W, 6500K Iwasaki Colour Arc Lamp) and calibrated to human vision (as explained above for the seaweeds) using custom-made functions in ImageJ. CIE $L^*a^*b^*$ is a three-dimensional colour model that represents colours based on their human-perceived attributes of lightness (L), and the green-red (a) and blue-yellow (b) colour components. It is designed to be device-independent and encompasses a wide range of colours visible to the human eye⁵⁶. The colour of the layer 1 images was then randomly adjusted within our game with

187 hue being rotated between -10° to $+10^{\circ}$, saturation between 90% to 100% of the original image and brightness
188 between 90% to 105% of the original image. The opacity of each prawn type was defined by the alpha value
189 associated with the combination of the base (L0) and colour (L1) layers, excluding the additional pigmentation
190 patterns in L2 and L3. These values were 0.848 for solid-red, 0.865 for solid-green and solid-brown, 0.231 for
191 transparent-pure, 0.339 for transparent-red, and 0.271 for transparent-brown models, with higher values
192 indicating greater opacity.

193 **Game structure**

194 To test how prawn appearance and seaweed identity influenced chameleon prawn survival we created an online
195 “find the prawn” game using custom Javascript code, adapted from code previously-used in similar citizen
196 science experiments^{20,57}, and made freely available to play on internet browsers ([https://www.visual-](https://www.visual-ecology.com/prawngame)
197 [ecology.com/prawngame](https://www.visual-ecology.com/prawngame); Figure S1). Ethical approval was granted by the University of Exeter Bioscience
198 Ethics Committee (application number 2022/518938), with the players being recruited via social media,
199 scientific magazines, mailing lists and word of mouth. Instructions for playing the game were provided in both
200 English and Brazilian Portuguese.

201 For each trial, the participant was presented with random combinations of 24 images containing a seaweed
202 photo with one of the four distinct species (6 photos of each seaweed species per trial) and a single prawn
203 individual of a random colour pattern (4 models of each prawn type per trial). The participant acted as a surrogate
204 predator and was tasked with finding the prawn as quickly as possible in a maximum of 15 seconds. If the
205 participant found the prawn within the time limit, a green circle appeared around the target and a “successful”
206 ringtone was heard, while when they failed, the position of the missing prawn was marked on the screen with a
207 red circle and the “missing” ring tone played. After that, the next slide was showed, and the same process was
208 repeated for the 24 slides. Before each slide was presented, the participant was tasked with clicking on a circle
209 at the centre of the screen to ensure they were ready and to help standardise cursor location. Participants were
210 free to leave the experiment at any time and no personal or identifying data were collected. Human observers
211 are widely used as surrogate visual predators in camouflage experiments because they rely on many of the same
212 visual search processes involved in prey detection. Previous studies have demonstrated strong agreement
213 between the relative survival or detection patterns obtained from human participants and those measured using

214 natural predators^{6,44,51,52}, indicating that human-based visual search experiments provide a robust proxy for
215 evaluating camouflage effectiveness. Although the experiment is still available to play online, the data used in
216 this study was restricted to the period between 28th June 2023 and 02nd July 2026.

217 At the end of each trial, 58 variables were recorded (check the full dataset in:
218 <https://figshare.com/s/0dff4bb049833bc12a08>), the most important of these being: (i) the date when the
219 participant played; (ii) the device that the participant used (based on the IP number); (iii) the screen scale (which
220 helped us to control for participants using devices with different resolutions); (iv) a binomial variable (yes or
221 no) stating if the participant has undertaken the experiment before so we could control for repeated access of
222 the same person; (v) the type of the prawn target (out of the 6 types described above); (vi) the prawn target size
223 (in mm); (vii) the seaweed species (out of the 4 species); (viii) the capture time of each target (in milliseconds);
224 (ix) the hue, saturation and brightness of the prawn target, which were further converted to L^*a^*b values; and
225 (x) the L^*a^*b mean and standard deviation values of the seaweed area behind the prawn target (defined by a
226 circle with 10 mm of diameter drew around the target). Because participants viewed the stimuli on a wide range
227 of computer screens, absolute colour values could not be assumed to be identical across observers. Instead, we
228 quantified camouflage using relative measures of target-background similarity, which are expected to be more
229 robust to variation among display devices. Screen scale and participant identity were also included in the
230 statistical analyses to account for additional variation associated with display characteristics and repeated
231 observations (see below). Background matching was quantified from CIELAB values by calculating the
232 absolute difference in the L channel ($\text{abs}[L_{\text{prawn}} - L_{\text{background}}]$; LumDiff) as a measure of achromatic similarity,
233 and the Euclidean distance between the a and b channels (ColourDiff) as a measure of chromatic similarity,
234 with lower values indicating greater achromatic and chromatic matching, respectively. To account for
235 differences in transparency among prawn types, both achromatic and chromatic contrasts were weighted by the
236 opacity coefficients (alpha values) defined during target creation, as described above. This correction assumes
237 that the apparent contrast between a prawn and its background decreases proportionally with transparency.

238 **Statistical analyses**

239 All statistical analyses were conducted in R (version 4.5.3)⁵⁸, with the raw data and R scripts available online
240 (<https://figshare.com/s/0dff4bb049833bc12a08>). Before conducting the main analyses, we performed

241 sensitivity analyses to evaluate whether the three transparent prawn categories (transparent-pure, transparent-
242 red, and transparent-brown) differed in their detection probability and survival during the game. Although some
243 statistically significant differences were detected among these categories (Tables S1 and S2), they did not alter
244 the overall pattern of survival across seaweed backgrounds or the contrast between transparent and solid-
245 coloured camouflage strategies (Figure S2). Indeed, the three transparent variants exhibited highly similar
246 survival curves within each seaweed species, differing primarily in the magnitude rather than the direction of
247 their responses. Moreover, these categories were not designed to represent distinct biological colour types or
248 experimental treatments. Instead, they were included solely to capture the natural continuum of appearance
249 observed among transparent chameleon prawns in the wild (Figure 1). Because our hypotheses concerned the
250 ecological differences between transparent and solid-coloured camouflage strategies, rather than variation
251 within transparent individuals, the three transparent categories were pooled into a single “transparent” group for
252 all subsequent analyses.

253 The probability that a participant failed to find the prawn target within the allocated time (15 s) was analysed
254 using generalized linear mixed-effects models (GLMMs) implemented with the function ‘glmmTMB’ from the
255 “glmmTMB” package. Models were fitted using a beta-binomial distribution and a logit link function,
256 considering “TimeOut” as a binary response variable (coded 0 when the target was found and 1 when it was
257 missed). Fixed effects included the factors “prawnColourType” (solid-red, solid-green, solid-brown, and
258 transparent) and “SeaweedSpecies” (red dulse, green sea lettuce, pink harpoon weed, and brown wireweed),
259 including their interaction, “playedBefore” (yes or no), to test whether previous experience affected the
260 probability of missing the target, “screenScaleCat” (i.e., the screen size scaling factor, which was categorized
261 into three groups, namely low (0.132,0.428], medium (0.428,0.723] and high (0.723,1.020] resolution, to speed
262 up computer processing), to account for variation associated with device characteristics, and “Slide” (i.e., the
263 ID of the images presented to the participant across the trials), to account for learning effects over the session
264 time. To account for variation associated with repeated measurements within each trial session, “UniquePlay”
265 (i.e., a factor combining the participant’s device based on IP address and the date of play) was included as a
266 random effect. Model assumptions, including potential overdispersion and residual distribution, were evaluated
267 using functions from the “DHARMA” package. The model was defined as:

268 `glmmTMB(TimeOut ~ prawnColourType * SeaweedSpecies + playedBefore + screenScaleCat + Slide +`
269 `(1|UniquePlay), data)`

270 To analyse the capture time of chameleon prawns, we used mixed-effects survival models to evaluate how
271 prawn colour and seaweed species, achromatic and chromatic contrasts against the substrate, and prawn size,
272 affected detection by participants. These models allowed the inclusion of prawns that were not found within 15
273 seconds as censored observations (i.e., surviving up to that time limit). Because the same participant captured
274 prawns across a sequence of 24 slides and could undertake multiple sessions, we fitted Cox proportional hazards
275 mixed models using the function “coxme” from the “coxme” package⁵⁹, including “UniquePlay” as a random
276 effect to account for repeated measurements. Four survival models were built to test specific hypothesis:

277 The first model tested the effects of prawn colour type and seaweed species on prawn survival, including
278 “playedBefore” (yes/no), “screenScaleCat” (three categories of screen size) and “Slide” (the image identity,
279 from 1 to 24) as fixed effects,” and “UniquePlay” as a random term. An example of the survival model is:

280 `coxme(Surv(CaptureTime, TimeOut) ~ prawnColourType * SeaweedSpecies + playedBefore +`
281 `screenScaleCat + Slide + (1|UniquePlay), data)`

282 The second and third models tested the effects of achromatic (LumDiff) and chromatic (ColourDiff)
283 contrasts, respectively, between each prawn and the surrounding seaweed (within a 10 mm radius), as well as
284 their interactions with prawn colour type. Seaweed species was included as an additive fixed effect to account
285 for differences in background features that could influence contrast independently of the measured achromatic
286 and chromatic differences. Both models included the same random effect (“UniquePlay”) and fixed covariates
287 (“playedBefore”, “screenScaleCat”, and “Slide”) as the previous model. Finally, the fourth model tested the
288 effect of prawn size (mm) and its interaction with prawn colour type, using the same random and fixed-effect
289 structure. For this last analysis, solid-red, solid-green, and solid-brown prawns were pooled into a single “solid-
290 coloured” category and contrasted with transparent prawns. For all timeout and survival models, the significance
291 of fixed effects and interactions was assessed using likelihood-ratio tests (LRTs). When appropriate, pairwise
292 comparisons among factor levels and estimated marginal trends for continuous predictors were obtained using
293 the “emmeans” package in R⁶⁰.

294

295 Results

296 *Camouflage effectiveness varies strongly with seaweed background*

297 We received 3,367 individual experimental trials, resulting in 45,888 unique prawn presentations. Of these,
 298 2,215 participants reported that they had not undertaken the experiment before. Across all trials, 1,882 timeout
 299 events occurred, indicating that participants failed to detect the prawn within the 15-s time limit in 4.10% of
 300 presentations. Timeout probability was strongly influenced by the interaction between prawn colour type and
 301 seaweed species (GLMM, likelihood-ratio test – LRT: $\chi^2_9 = 856.34$; $p < 0.0001$). Overall, 45.70% of all timeout
 302 events occurred on the brown wireweed *Sargassum muticum*, followed by the pink harpoon weed *Asparagopsis*
 303 *armata* (21.25%), the red dulse *Palmaria palmata* (20.56%), and the green sea lettuce *Ulva lactuca* (12.49%).
 304 However, the prawn colour type associated with the highest timeout probability differed among seaweed species
 305 (Table 1). Brown prawns showed the highest timeout probability on brown wireweed, transparent prawns on
 306 red dulse, transparent and brown prawns performed similarly on pink harpoon weed, and green prawns showed
 307 the highest timeout probability on green sea lettuce (Table 1). Pairwise comparisons supported these patterns
 308 (Table S3). On brown wireweed, brown prawns were significantly more likely to remain undetected than all
 309 other colour types, followed by transparent, red, and green prawns, with significant differences across all level
 310 comparisons. On red dulse, transparent prawns had significantly higher timeout probabilities than all solid-
 311 coloured phenotypes. On pink harpoon weed, transparent and brown prawns did not differ significantly from
 312 one another but were both significantly more likely to remain undetected than green prawns. Conversely, on
 313 green sea lettuce, green prawns exhibited the highest timeout probability and were significantly more likely to
 314 escape detection than all remaining colour types.

315 **Table 1.** Summary of the online "Find the Prawn" game showing the number of chameleon prawn (*Hippolyte varians*)
 316 model presentations, timeout events (participants failed to detect the target within the 15-s time limit), and the
 317 corresponding percentage of timeouts for each combination of seaweed species and prawn colour type.

Seaweed	Prawn type	Presentations	Timeouts	% of timeouts
Dulse (<i>Palmaria palmata</i>)	Red	2037	36	1.77%
	Green	2052	10	0.49%
	Brown	2133	17	0.80%
	Transparent	6096	324	5.31%
Sea lettuce (<i>Ulva lactuca</i>)	Red	2526	21	0.83%
	Green	2411	125	5.18%

	Brown	2616	16	0.61%
	Transparent	7872	73	0.93%
Harpoon weed (<i>Asparagopsis armata</i>)	Red	1746	47	2.69%
	Green	1778	14	0.79%
	Brown	1828	71	3.88%
	Transparent	5319	268	5.04%
Wireweed (<i>Sargassum muticum</i>)	Red	1300	25	1.92%
	Green	1288	5	0.39%
	Brown	1229	296	24.1%
	Transparent	3657	534	14.6%

Across all trials, the probability of prawn capture by participants was influenced not only by prawn colour type and seaweed species, but also by participants' previous experience, device's screen scale, and slide order (Table 2). Participants who had previously completed the experiment exhibited a significantly higher probability of detecting prawns (estimated hazard = 1.17, lower CI 95% = 1.12, upper CI 95% = 1.22) than first-time participants (estimated hazard = 0.86, lower CI 95% = 0.83, upper CI 95% = 0.88), indicating a learning effect. Screen scale also affected detection likelihood, with medium-resolution displays producing significantly higher capture probabilities (estimated hazard = 1.15, lower CI 95% = 1.13, upper CI 95% = 1.17) than low- (estimated hazard = 0.95, lower CI 95% = 0.92, upper CI 95% = 0.98) and high-resolution displays (estimated hazard = 0.93, lower CI 95% = 0.85, upper CI 95% = 1.01), whereas high- and low-resolution screens did not differ significantly. Likewise, capture probability changed significantly throughout the sequence of slides, indicating that detection performance increased over the course of the trial session. Considering the entire seaweed colour space, prawn colour types occupied regions that differed markedly in visual similarity to the available backgrounds (Figure 3A). These differences were reflected in spatial variation in capture likelihood across the colour space (Figure 3B), with transparent and brown types generally exhibiting lower capture probabilities across broader portions of the available backgrounds than red or green prawns. Consequently, capture probability depended strongly on the interaction between prawn colour type and seaweed species (LRT: $\chi^2_9 = 9809.90$, $p < 0.0001$; Table 2).

Table 2. Summary of likelihood-ratio tests (LRTs) from Cox mixed-effects survival models testing the effects of different predictors on the probability of detection of artificial chameleon prawn (*Hippolyte varians*) models by human participants in an online experiment. Model 1 (a) tested the interaction between prawn colour type ("prawnColourType": red, green, brown and transparent) and seaweed species ("SeaweedSpecies": dulse, sea lettuce, harpoon weed and wireweed). Models 2 (b) and 3 (c) tested the effects of achromatic ("LumDiff") and chromatic ("ColourDiff") contrasts between each prawn

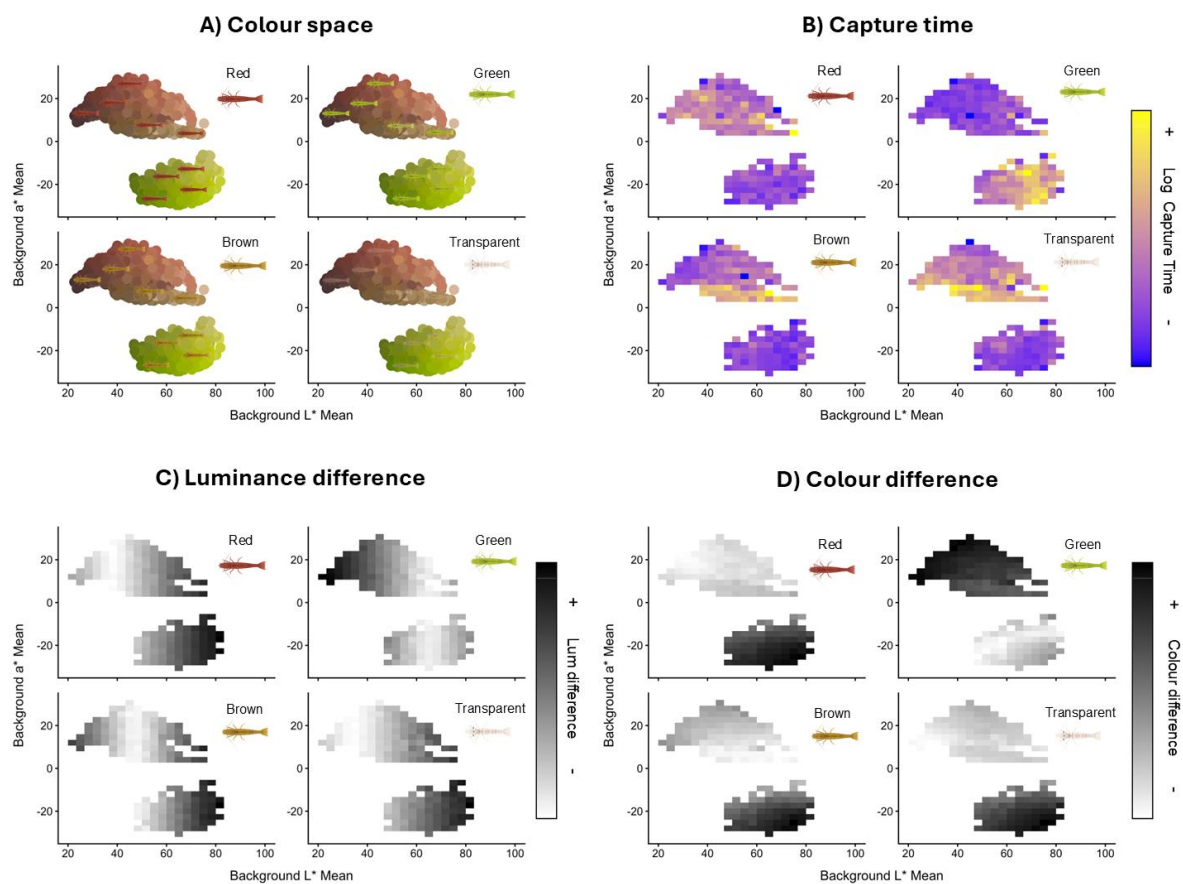
341 and the surrounding seaweed, respectively, and their interactions with prawn colour type. Model 4 (d) tested the effect of
 342 prawn size and its interaction with camouflage strategy (solid-coloured versus transparent prawns). All models included
 343 “playedBefore”, “screenScaleCat” and “Slide” as additive fixed covariates, and “UniquePlay” as a random effect. Models
 344 2–4 additionally included seaweed species as an additive fixed effect.

a) Model 1: Prawn colour type × seaweed species			
Predictors	LRT χ^2	Δdf	<i>p</i>
prawnColourType x SeaweedSpecies	9806.90	9	< 0.0001
playedBefore	141.36	1	< 0.0001
ScreenScaleCat	74.51	2	< 0.0001
Slide	1709.5	1	< 0.0001
b) Model 2: Achromatic contrast (LumDiff)			
Predictors	LRT χ^2	Δdf	<i>p</i>
LumDiff x prawnColourType	989.18	3	< 0.0001
SeaweedSpecies	3562.60	3	< 0.0001
playedBefore	145.33	1	< 0.0001
ScreenScaleCat	80.82	2	< 0.0001
Slide	1364.70	1	< 0.0001
c) Model 3: Chromatic contrast (ColourDiff)			
Predictors	LRT χ^2	Δdf	<i>p</i>
ColourDiff x prawnColourType	3347.50	3	< 0.0001
SeaweedSpecies	2017.30	3	< 0.0001
playedBefore	146.10	1	< 0.0001
ScreenScaleCat	79.10	2	< 0.0001
Slide	1625.80	1	< 0.0001
d) Model 4: Body size			
Predictors	LRT χ^2	Δdf	<i>p</i>
prawnSize x prawnColourType	11.14	1	0.0008
SeaweedSpecies	4929.90	3	< 0.0001
playedBefore	150.25	1	< 0.0001
ScreenScaleCat	66.24	2	< 0.0001
Slide	1101.80	1	< 0.0001

345

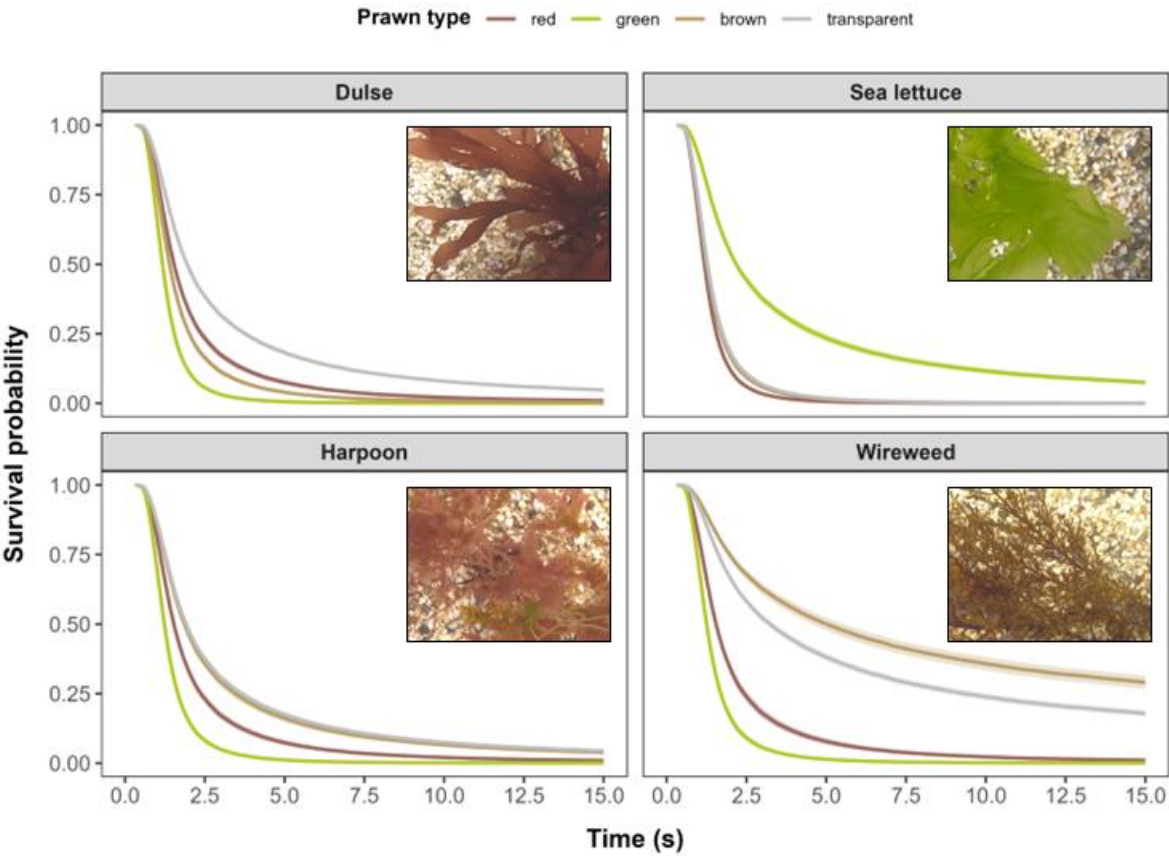
346 On red dulse, transparent prawns exhibited the lowest capture likelihood of all colour types, followed by
 347 brown and red individuals, whereas green prawns consistently showed the highest probability of capture, with
 348 significant differences across all level comparisons (Figure 4, Table S4). Transparent and brown prawns
 349 exhibited similarly low capture probabilities and did not differ significantly from one another on pink harpoon

350 weed. In this seaweed, both colour types were significantly less likely to be detected than red prawns, whereas
 351 green prawns showed the highest capture likelihood (Figure 4, Table S4). On brown wireweed, brown prawns
 352 experienced by far the lowest capture probability, followed by transparent individuals. Red and especially green
 353 prawns showed substantially higher probabilities of capture, indicating poor concealment on this background
 354 (Figure 4, Table S4). Conversely, on green sea lettuce, green prawns exhibited the lowest capture likelihood,
 355 whereas red, brown and transparent colour types all showed substantially higher probabilities of capture and did
 356 not differ greatly from one another.



357
 358 **Figure 3.** Visualization of the CIE $L^*a^*b^*$ colour space for the seaweed backgrounds used in the experiment (A) and
 359 associated heatmaps showing variation in prawn capture time (B), and prawn-background luminance (C) and colour (D)
 360 differences for red, green, brown, and transparent chameleon prawn models (*Hippolyte varians*). (A) Colour space plots
 361 illustrate the distribution of background lightness (Background L*Mean) and chromatic variation along the red-green axis
 362 (Background a*Mean) with overlaid examples of prawn models. (B) Capture time heatmaps indicate regions of the
 363 background colour space where each prawn model was located more slowly (yellow) or more quickly (blue) by players.
 364 Heatmaps of luminance (C) and colour (D) difference show the corresponding regions where prawn models exhibited

365 higher (dark shading) or lower (light shading) achromatic and chromatic contrasts, respectively, against seaweed
 366 backgrounds.

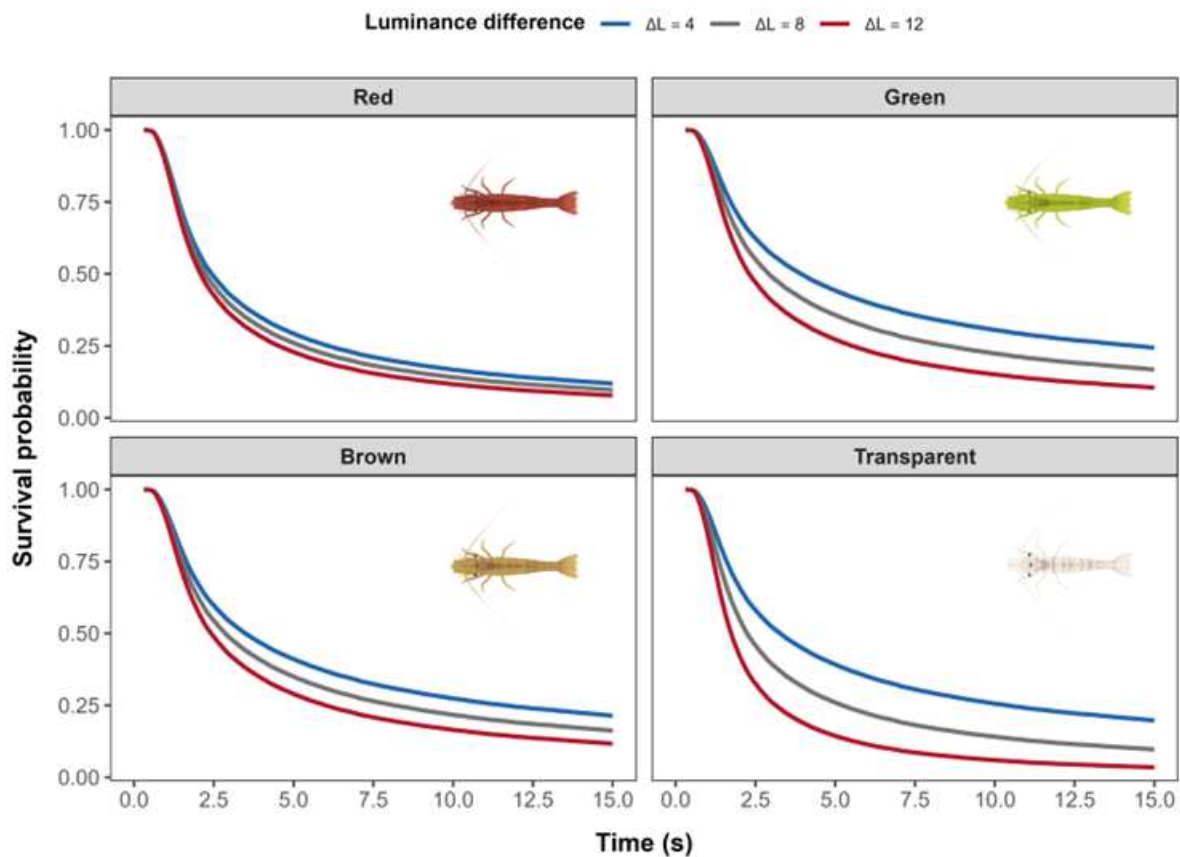


367
 368 **Figure 4.** Survival curves showing the probability of remaining undetected over time for red, green, brown, and transparent
 369 chameleon prawn (*Hippolyte varians*) models presented against four seaweed backgrounds: red dulse (*Palmaria palmata*),
 370 green sea lettuce (*Ulva lactuca*), pink harpoon weed (*Asparagopsis armata*), and brown wireweed (*Sargassum muticum*)
 371 to human participants in an online game. Differences among curves reflect variation in the probability of detection of each
 372 prawn colour type across seaweed backgrounds. Shaded areas represent 95% confidence intervals, based on 45,888 prawn
 373 presentations from 3,367 participants.

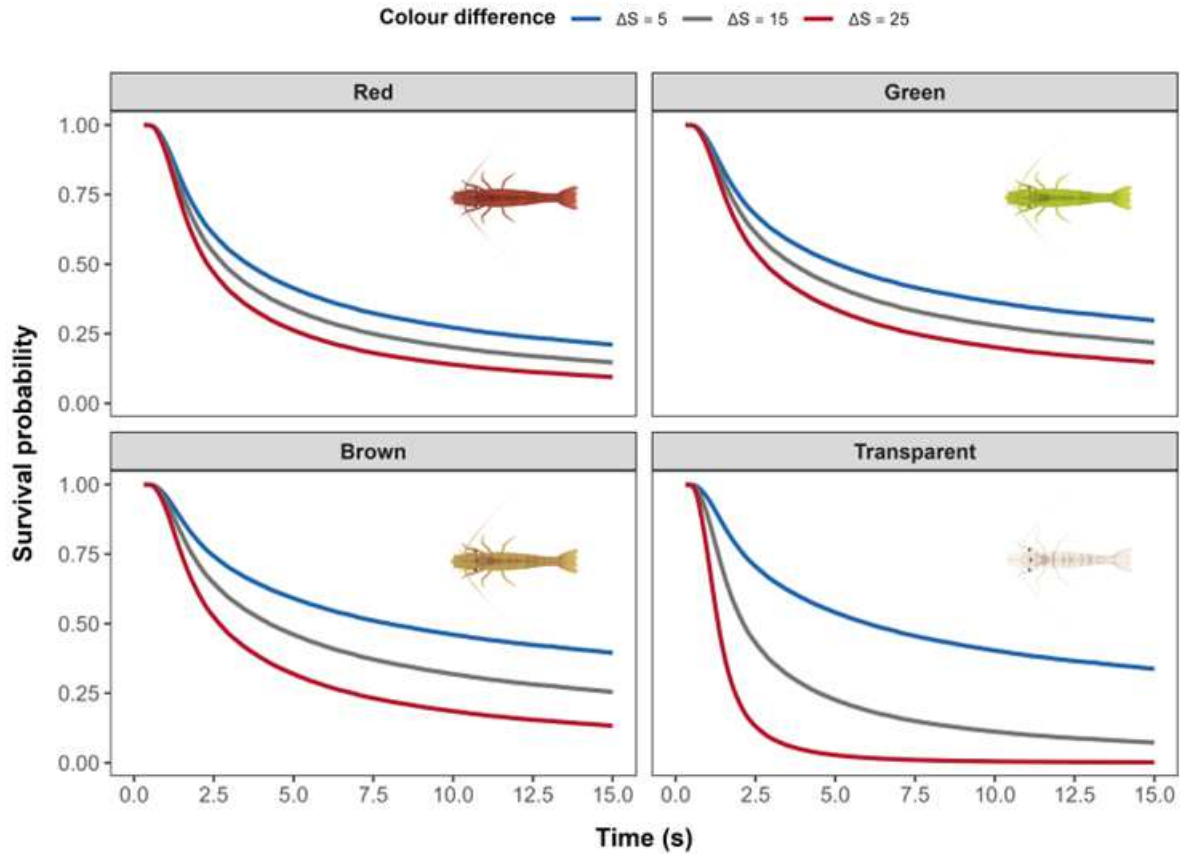
374 ***Differences in achromatic and chromatic contrasts between prawns and seaweeds predict survival***

375 Prawn models exhibited substantial variation in both achromatic and chromatic contrasts across the seaweed
 376 colour space (Figures 3C, 3D). Red, brown, and transparent colour types generally exhibited low achromatic
 377 contrast against darker regions of the colour space, whereas green prawns showed the lowest achromatic contrast
 378 against lighter backgrounds (Figure 3C). A similar pattern emerged for chromatic contrast, with red, brown and
 379 transparent prawns exhibiting reduced colour differences against red and brown regions of the colour space,

380 whereas green prawns showed the closest chromatic match to green backgrounds (Figure 3D). Increasing both
 381 achromatic and chromatic mismatch significantly increased the probability of detection, although the magnitude
 382 of these effects differed among prawn colour types (LRT: $\chi^2_3 = 989.18$ and 3347.50 , respectively, both $p <$
 383 0.0001 ; Table 2). Transparent prawns were by far the most sensitive to changes in both luminance and colour
 384 matching, showing the steepest increase in detection likelihood with increasing achromatic (slope $\pm$ SE = 0.091
 385 ± 0.002) and chromatic contrast (0.113 ± 0.002). Green prawns showed the second strongest response ($0.062 \pm$
 386 0.001 and 0.033 ± 0.001), followed by brown (0.041 ± 0.002 and 0.049 ± 0.001) and red colour types ($0.025 \pm$
 387 0.001 and 0.027 ± 0.001) (Table S5). Predicted survival curves confirmed these patterns, with increasing
 388 achromatic or chromatic mismatch resulting in progressively lower probabilities of remaining undetected across
 389 all colour types, but with substantially steeper declines for transparent prawns (Figure 5, Figure 6).



390
 391 **Figure 5.** Survival curves showing the probability of remaining undetected over time for red, green, brown, and transparent
 392 chameleon prawn (*Hippolyte varians*) models as a function of achromatic mismatch (ΔL) with the surrounding seaweed.
 393 Higher ΔL values indicate greater luminance differences between the prawn and the background. Shaded areas represent
 394 95% confidence intervals based on 45,888 prawn presentations from 3,367 participants.

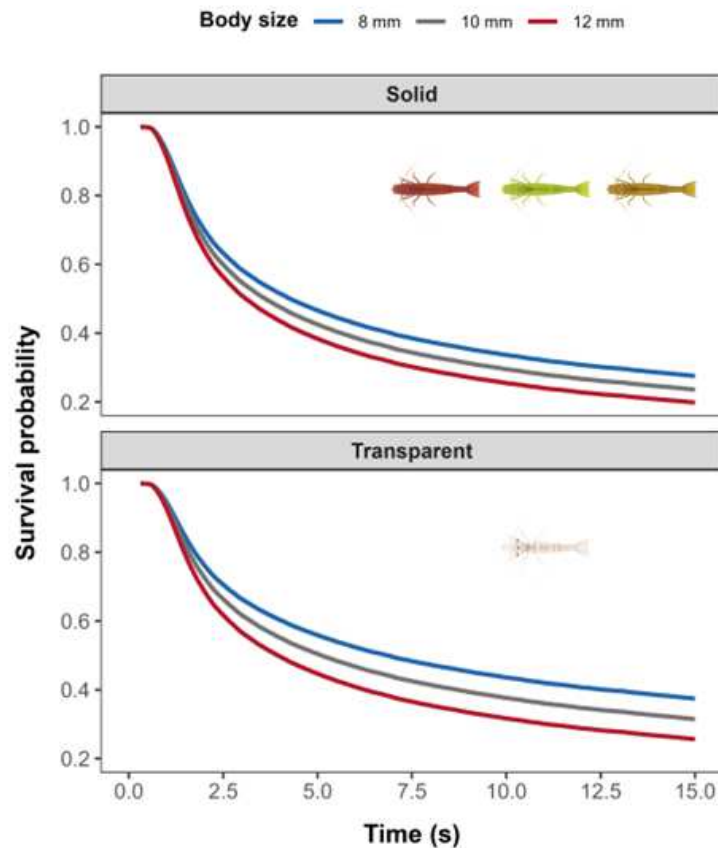


395

396 **Figure 6.** Survival curves showing the probability of remaining undetected over time for red, green, brown, and transparent
 397 chameleon prawn (*Hippolyte varians*) models as a function of chromatic mismatch (ΔS) with the surrounding seaweed.
 398 Higher ΔS values indicate greater colour differences between the prawn and the background. Shaded areas represent 95%
 399 confidence intervals based on 45,888 prawn presentations from 3,367 participants.

400 ***Size variation has a greater effect on the survival of transparent than solid-coloured prawn models***

401 Increasing prawn body size significantly increased the probability of detection by human participants, but the
 402 magnitude of this effect differed between transparent and solid-coloured prawn models (prawn size $\times$ colour
 403 type interaction: LRT: $\chi^2_1 = 11.14$, $p = 0.0008$; Table 2). Although larger individuals of both colour groups were
 404 more likely to be detected, the increase in detection likelihood was substantially steeper for transparent than for
 405 solid-coloured prawns (Figure 7). The estimated effect of body size on detection probability was approximately
 406 39% greater in transparent individuals (slope $\pm$ SE = 1.044 ± 0.062) than in solid-coloured individuals ($0.751 \pm$
 407 0.062), indicating that the survival advantage conferred by transparency declined more rapidly with increasing
 408 body size.



409

410 **Figure 7.** Survival curves showing the probability of remaining undetected over time for solid-coloured (pooled red, green,
 411 and brown) and transparent chameleon prawn (*Hippolyte varians*) models as a function of body size. Curves compare
 412 individuals spanning the range of body sizes used in the experiment, illustrating the stronger increase in detection hazard
 413 with increasing size for transparent than for solid-coloured prawns. Shaded areas represent 95% confidence intervals based
 414 on 45,888 prawn presentations from 3,367 participants.

415

416 Discussion

417 Our findings demonstrate how alternative camouflage strategies within the same species can provide distinct
 418 survival advantages in heterogeneous environments. Transparent and solid-coloured chameleon prawns
 419 (*Hippolyte varians*) differed consistently in how their survival depended on background identity, chromatic and
 420 achromatic matching, and body size. As predicted, solid-coloured prawns acted as camouflage specialists,
 421 achieving their highest survival on matching seaweeds, whereas transparent individuals maintained consistently
 422 high survival across most backgrounds, consistent with a generalist strategy. Notably, green prawns substantially
 423 outperformed transparent individuals on green sea lettuce, demonstrating that precise background matching can

424 provide superior protection on particular substrates. Transparency therefore appears to reduce the costs of
425 habitat heterogeneity by providing broadly effective, although not always optimal, camouflage. This advantage,
426 however, is constrained by greater sensitivity to visual chromatic and achromatic mismatch and increasing body
427 size. Together, our findings suggest that environmental heterogeneity may favour the coexistence of alternative
428 camouflage strategies within populations, potentially contributing to the persistence of colour variants in
429 nature⁶¹.

430 Demonstrating the adaptive value of camouflage under ecologically realistic conditions remains an important
431 challenge in evolutionary ecology. Although the theoretical links between camouflage and reduced detection
432 are well established^{4,16}, empirical tests involving natural predators and prey remain relatively uncommon.
433 Previous approaches have included laboratory experiments with trained predators^{62–64}, field experiments using
434 tethered prey⁶⁵, and correlational evidence of field predation rates⁶⁶. Studies using artificial prey exposed to
435 natural or “human” predators in the field^{41,44,67,68}, or computer-generated stimuli presented under controlled
436 conditions^{57,69,70}, have also been instrumental in testing camouflage principles. Our approach builds on these
437 methods by combining realistic digital representations of naturally occurring chameleon prawn colour types
438 with calibrated photographs of their natural seaweed habitats. This enabled controlled comparisons of
439 camouflage effectiveness across natural backgrounds while preserving key visual characteristics of the study
440 system. Nevertheless, our two-dimensional stimuli were restricted to a single viewing angle, simplifying the
441 three-dimensional nature of predator-prey interactions. Moreover, static images could not reproduce natural
442 variation in underwater illumination, including dynamic shadows and light fluctuations caused by water
443 movement. Despite these limitations, our study provides one of the first direct empirical tests comparing the
444 adaptive value of transparency and fully-pigmented camouflage strategies within the same species across
445 multiple natural backgrounds varying in colour and visual complexity.

446 The contrasting survival patterns of solid-coloured and transparent prawns support the prediction that
447 alternative colour types occupy different positions along a specialist-generalist camouflage continuum¹⁷. Green
448 prawns achieved exceptionally high survival on green sea lettuce but were more readily detected on other
449 substrates, whereas brown individuals performed best on brown wireweed. These patterns are consistent with
450 conceptual predictions that specialist camouflage provides substantial benefits on matching backgrounds at the
451 cost of reduced survival elsewhere^{45,71}. By contrast, transparent prawns maintained relatively high survival

452 across most seaweeds without consistently outperforming the best-matched solid-coloured individuals. Thus,
453 transparency appears to provide a generalist alternative to precise background matching, reducing dependence
454 on any single substrate^{17,22}.

455 Transparency nevertheless involves important ecological trade-offs. Despite performing well across multiple
456 backgrounds, transparent prawns were more sensitive than solid-coloured individuals to increasing chromatic
457 and achromatic mismatch and body size. This suggests that transparency, although less dependent on substrate
458 identity, remains sensitive to the visual contrast between an individual and its surroundings. Unlike background
459 matching through uniform pigmentation, transparency reduces conspicuousness by transmitting the visual
460 properties of the background through the body^{22,23}, potentially making concealment more vulnerable to changes
461 in background colour and luminance. The importance of optical conditions to camouflage effectiveness was
462 experimentally tested for the mesopelagic cephalopods *Japetella heathi* and *Onychoteuthis banksii*, which can
463 rapidly switch from transparent to darkly pigmented states in response to direct illumination²⁹. While
464 transparency provides concealment under the predominantly downwelling light of their deep-water habitats,
465 exposure to directed light, such as that produced by bioluminescent searchlights used by predators, can trigger
466 a rapid transition to red or black pigmentation, facilitating camouflage under these conditions²⁹. Beyond
467 illumination, body size represents another potential constraint on transparency. The stronger negative effect of
468 body size on transparent prawn models is consistent with theoretical predictions that transparency becomes
469 progressively less effective in larger organisms, as body outlines become easier to resolve and internal structures
470 occupy a greater proportion of the visible body^{26,27}.

471 The context-dependent benefits of transparency are also evident in terrestrial vertebrates and insects. In glass
472 frogs, transparency allows body luminance to vary with the underlying background, reducing detectability and
473 improving survival through a mechanism known as edge diffusion, which softens the visual boundary between
474 the animal and its surroundings⁷². Experiments manipulating butterfly wing transparency have similarly shown
475 that transparent individuals experience greater reductions in concealment than opaque butterflies with increasing
476 background luminance and body size²⁶. Together, these examples illustrate how the effectiveness of
477 transparency-based strategies depends on optical conditions, physiological mechanisms and morphological
478 constraints across distantly related taxa²³. The relationship between transparency and body size may also interact
479 with sex-specific morphology and behaviour. In carnival prawns (*H. obliquimanus*), transparent individuals are

480 predominantly males, which are generally smaller than females⁷³, a pattern also reported in other caridean
481 prawns⁷⁴. Larger transparent females may become more conspicuous when carrying pigmented eggs, whereas
482 smaller males may benefit from transparency while moving among differently coloured substrates in search of
483 mates^{74,75}. Such trade-offs may help explain why transparency does not universally replace uniformly pigment-
484 based camouflage and may instead contribute to the coexistence of specialist and generalist strategies within
485 some populations^{14,17}. Their relative advantages may also change across ontogeny as body size, habitat use and
486 environmental conditions change, potentially contributing to the widespread transition from transparent to
487 pigmented forms during development in benthic invertebrates^{23,28}.

488 Red chameleon prawns were the principal exception to the specialist-generalist pattern. Although they were
489 among the least detectable colour types on red seaweeds, they did not show the same level of pronounced
490 specialist advantage observed for green and brown individuals. This contrasts with previous visual modelling
491 predicting close resemblance between red prawns and red macroalgae as perceived by fish predators^{47,48}, and
492 with experimental evidence from *H. obliquimanus* showing that visual matching predicts fish predation risk¹⁹.
493 One possible explanation is that red and transparent prawns form a more continuous range of appearances than
494 our models represented. Many red individuals exhibit some transparency, while transparent prawns often
495 possess fine red markings resembling filamentous red algae. By treating these forms as distinct categories, our
496 digital models may have simplified biologically relevant variation. Differences between human and fish vision,
497 as well as incomplete representation of natural variation in brightness, saturation and translucency, despite our
498 efforts to reproduce the appearance of naturally occurring prawns, may also have influenced the results. In
499 particular, our red models may have appeared darker and more conspicuous than natural individuals, potentially
500 underestimating their survival advantage. Future studies using calibrated photographs that capture the full range
501 of natural colour variation of chameleon prawns, together with predator-specific visual modelling and
502 comparable detection experiments, could help establish whether the patterns observed here persist when
503 evaluated through the visual systems of natural predators. Complementary predation experiments using real
504 predators and live prawns with previously quantified colour characteristics could then determine whether these
505 differences in detectability translate into survival advantages under natural predator-prey interactions.

506 The heterogeneous seaweed communities inhabited by chameleon prawns provide an ecological context for
507 the coexistence of alternative colour types in the species. Seaweeds differ in colour, structural complexity and

508 seasonal persistence, creating habitats with distinct opportunities for concealment⁴⁷. Green sea lettuce (*Ulva*
509 *lactuca*) provides a relatively simple background but is highly seasonal, with most of its frond dying back during
510 winter when only the basal portion of the seaweed remains alive⁵⁰. By contrast, brown wireweed (*Sargassum*
511 *muticum*) and harpoon weed (*Asparagopsis armata*) can persist for much of the year, despite some seasonal
512 changes in their cover^{76,77}, are structurally more complex than sea lettuce and red dulse (*Palmaria palmata*).
513 Previous field studies with chameleon and carnival prawns have shown that green, brown, and red prawns are
514 strongly associated with their corresponding seaweeds, whereas transparent individuals occur across a wider
515 range of substrates^{47,48,73}. Our experimental results are consistent with these observations: green prawns
516 achieved by far their highest survival on sea lettuce, suggesting that this habitat exerts particularly strong
517 selection for precise background matching, while transparent individuals performed relatively well across the
518 remaining seaweeds, consistent with a strategy adapted to cope with greater environmental heterogeneity.
519 Brown wireweed is particularly interesting because it supports the greatest diversity of prawn colour types in
520 the field despite relatively poor overall background matching⁴⁷ and had the highest timeout probability among
521 all seaweeds in our experiment. Its structural complexity may reduce the importance of precise colour matching
522 by providing additional concealment among branches and fronds^{43,44}. Alternatively, its seasonal persistence may
523 allow it to function as a refuge when other seaweeds decline⁴⁷. Both mechanisms could reduce dependence on
524 precise background matching and help explain the diversity of colour types associated with this habitat. Future
525 studies should examine how seasonal changes in seaweed communities influence the distribution and frequency
526 of prawn colour types in the field, whether transparent individuals are indeed less constrained by fluctuations
527 in the availability of matching substrates, and how colour change facilitates transitions between seasonal
528 habitats. Such research would provide a more mechanistic understanding of how environmental heterogeneity,
529 phenotypic plasticity, and alternative camouflage strategies interact to maintain phenotypic diversity in natural
530 populations.

531 The biology of chameleon prawns closely parallels that of the congeneric “carnival prawn”, *Hippolyte*
532 *obliquimanus*, from Brazil, which also exhibits colour change, behavioural substrate choice, and the coexistence
533 of solid-coloured and transparent forms^{19,30,73}. In both species, camouflage effectiveness depends not only on
534 colour matching, but also on habitat structure. Individuals achieve their closest background matching and
535 experience the strongest selection for camouflage on visually simple seaweeds, whereas more structurally

complex seaweeds support a greater diversity of colour types, lower overall colour matching, and weaker colour change responses. Experimental predation trials with *H. obliquimanus* further demonstrated substrate-dependent differences in predation risk: pink prawns experienced fewer attacks on pink than brown seaweeds, while brown individuals showed similar attack rates across both habitats¹⁹. Behavioural studies also revealed that transparent carnival prawns have lower substrate fidelity, spend more time swimming and move more frequently among seaweeds than solid-coloured individuals, suggesting that transparency is associated with a more mobile lifestyle³⁰. Although comparable behavioural evidence remains limited for *H. varians*, these similarities suggest that alternative camouflage strategies may be associated with differences in habitat use and mobility. More broadly, the coexistence of transparent and solid-coloured forms may reflect complementary combinations of camouflage, behaviour and life-history traits favoured under different ecological contexts.

Conclusion

Our study demonstrates that alternative camouflage strategies can provide complementary survival advantages in heterogeneous environments, with specialist and generalist colour types performing differently across ecological contexts. Rather than favouring a single optimal phenotype, environmental heterogeneity may contribute to the persistence of multiple camouflage strategies through interactions among coloration, behaviour and phenotypic plasticity. Importantly, our findings highlight transparency as an underappreciated form of generalist camouflage, providing relatively high survival across diverse backgrounds but subject to important constraints imposed by visual mismatch and body size. Future studies combining predation experiments with natural predators, behavioural observations and long-term field surveys will be essential to establish how these strategies influence lifetime fitness, habitat use and population dynamics. More broadly, our findings suggest that understanding the maintenance of phenotypic diversity requires considering not only the effectiveness of individual traits, but also the ecological conditions under which alternative strategies provide complementary advantages.

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571

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