Interactions between background matching and disruptive colouration: Experiments using human predators and virtual crabs

Peter A. TODD*, Huijia PHUA, Kok Ben TOH

Experimental Marine Ecology Laboratory, Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Blk S3, #02-05, Singapore 117543

Abstract

Interactions between disruptive colouration and the match between prey and background spot size were manipulated in two experiments that used time taken by human ‘predators’ to find artificial prey (virtual crab morphs) against heterogeneous backgrounds as a measure of the their camouflage. Experiment 1, in which the spots and their placement imitated the arrangement on the crab Carcinus maenas, tested whether high and low contrast spots touching the body outline (disruptive ‘edge’ morphs) made the artificial prey more difficult to detect than when the spots did not touch the outline (non-disruptive ‘inner’ morphs) against three different backgrounds: ‘small’, ‘middle’ and ‘large’ spot size. In Experiment 2, the range of spot sizes and their positions (‘edge’ and ‘inner’) on the crab morphs were varied to determine the most effective combination against the ‘middle’ background. Altogether, 640 volunteers participated in these computer trials, representing a high degree of independent replication. All patterned morphs were significantly harder to detect than plain morphs, indicating that possessing at least some degree of background matching can provide camouflage. Both experiments demonstrated that various morphs, though not having the same spot sizes as the background, had similar or better survivorship as those with matching spot sizes—indicating that optimal camouflage did not come from background matching alone. In Experiment 2, edge-disrupted morphs consistently took longer to find than their non-disruptive counterparts. The relative effects of edge disruption, contrast, and background/prey spot size are clearly context-dependent, highlighting the complexity of prey concealment [Current Zoology 61 (4): 718–728, 2015].

Keywords

Background matching, Camouflage, Carcinus maenas, Crypsis, Disruptive colouration, Predation

Camouflage is a broad term that, in prey, reduces predation by making the organism difficult to find (Stevens and Merilaita, 2009a). Crypsis is a form of camouflage that can be further divided into components that include disruptive colouration (Cott, 1940) and background matching (Endler, 1978). Disruptively-coloured prey possess markings or spots that prevent detection by creating false edges and boundaries (Cott, 1940; Merilaita, 1998; Cuthill et al., 2005; Stevens and Merilaita, 2009b). Such markings are often pattern elements located at the periphery of the animal, fragmenting its shape into several indistinct and separate objects that make it unrecognizable or undetectable (Cott, 1940; Ruxton et al., 2004; Stevens and Merilaita, 2009b; Webster et al., 2013). Highly contrasting spots help to create stronger false edges thus enhancing the disruptive effect (Thayer, 1909; Cott, 1940; Stevens et al., 2006), although they can also make the prey more vulnerable (Stevens et al., 2008; Stobbe and Schaefer, 2008). Disruptive colouration may have evolved because predator edge-detecting neurons are unable to process and register the true form of the organism—instead the neurons detect false boundaries formed by the disruptive components (Oso-rio and Srinivasan, 1991; Stevens and Cuthill, 2006; Troscianko et al., 2009). The disruption does not necessarily have to interfere with the outline of the organism; ‘surface disruption’ (Cott, 1940; Stevens and Merilaita, 2009b), where markings located away from the body periphery create false edges that interfere with predator detection, is also effective (Stevens et al., 2009b). The principles of disruptive colouration have been tested and supported by studies that analysed body colouration of actual animals (e.g. Merilaita, 1998), as well as manipulative experiments that used artificial prey (e.g. Cuthill et al., 2005; Merilaita and Lind, 2005; Stevens et al., 2006; Schaefer and Stobbe, 2006; Stevens et al., 2009b).

Background matching animals avoid detection by adopting patterns, lightness and/or colours that resemble their surroundings, enabling them to ‘blend in’ (Endler,
The visual attributes of the background on which the organism is encountered influence a predator’s ability to detect it, for example, prey in a simple background with few shapes are more easily detected than in a background with many shapes (Dimitrova and Merilaita, 2010). This is a fundamental consideration given that most habitats are heterogeneous. Prey with patterns, such as spots or stripes, matching the luminance of the background have higher survival than those with non-matching patterns (Merilaita et al., 2001; Stevens et al., 2006) and, based on replicating populations of web-based morphs, prey rapidly evolve to match their surroundings when repeatedly presented against a single background (Sherratt et al., 2007). The size of the elements that make up the background may also play a pivotal role in detection, for instance, mean search times can be longer on a background with large spot sizes (relative to those possessed by the prey) compared to a background with small spot sizes (Merilaita et al., 2001). When there are two or more microhabitats characterized by different sized background elements, possessing a pattern of intermediate sized spots can be advantageous (Merilaita et al., 2001).

As they are known to exhibit background matching, disruptive colouration, or both as a defensive strategy, many terrestrial camouflage experiments have used moths, both real and artificial, life-like and abstract, as prey (e.g. Steward, 1977; Endler, 1984; Cuthill et al., 2005; Schaefer and Stobbe, 2006; Stevens et al., 2006). A potential marine counterpart is the relatively well-studied shore crab *Carcinus maenas* (L.), a common intertidal omnivore found throughout Europe (Crothers, 1968; Brian et al., 2006; Stevens et al., 2014a). Adults tend to be monochromatic (Hogarth, 1975) but juvenile *C. maenas* display a wide variety of carapace patterns, usually bold white patches against a darker shade that, >99% of the time, intersect the edge of the animal (Todd et al., 2006). These observations, combined with strong phenotype-environment matching in this species (Todd et al., 2005, 2006; Stevens et al., 2014b), have led researchers to attribute a cryptic function to the shore crab’s spots (Hogarth, 1978; Todd et al., 2006, 2012; Stevens et al., 2014a, b). To explore this further, Todd (2009) printed copies of stylized *C. maenas* morphs and background and used the time taken by human predators to find the morphs as a measure of their camouflage. In the present study, we elaborate on Todd (2009) using a more sophisticated, computer-based, virtual model to better understand the interactions between background matching and disruptive colouration.

The combination of using a virtual environment and humans as ‘predators’ in manipulative studies can be a powerful one, as is evident from previous research into polymorphism (Knill and Allen, 1995; Glanville and Allen, 1997), apostatic selection (Tucker and Allen, 1988, 1991, 1993), aposematism (Sherratt and Beatty, 2003; Sherratt et al., 2004), mimicry (Dill, 1975; Beatty et al., 2004), search rate (Gendron and Staddon, 1984), crypsis (Jackson et al., 2005), background matching (Sheratt et al., 2007; Karpestam et al., 2013), disruptive colouration (Fraser et al., 2007; Cuthill and Székely, 2009) and distractive colouration (Stevens et al., 2013). Humans adopt a similar search pattern to birds, one of the shore crab’s main predators (Crothers, 1968), when looking for prey on a computer screen (Jackson et al., 2005) and have comparable information processing capabilities (Dukas and Ellner, 1993; Dukas and Kamil, 2001; Dukas, 2002). Results from research using humans as predators do not deviate qualitatively from the findings of analogous studies using birds (Cooper, 1984; Knill and Allen, 1995; Beatty et al., 2005; Fraser et al., 2007; Cuthill and Székely, 2009; Stevens et al., 2013), while Karpestam et al. (2013) showed that such methods may provide credible information on the natural selection of pygmy grasshopper’s camouflage in the wild. Furthermore, potential problems associated with camouflage research in natural settings can be circumvented, such as non-independence (the same predator attacking many different study prey items), unpredictable and hard to standardise predator behaviour, or predators carrying over learned behaviour among consecutive trials at the same site. Another advantage when compared to field experiments is that every aspect of the virtual prey and background can be manipulated with precision, facilitating more nuanced tests and analyses (Todd, 2009).

Even though interactions between disruptive colouration and the match between prey and background spot size probably contribute to the effectiveness of an organism’s camouflage, no studies to date have examined these factors together. Here, we use computer-based environments and prey in combination with a touchscreen and human ‘predators’ to identify the relative effects of disruptive colouration and background and prey spot size on search time. In our first experiment (Experiment 1), crab targets with patterns based on *C. maenas* were created to test the following hypotheses:

1. Spots that break up the continuity of the prey margin confer greater protection (longer searching time) than spots displaced inwards.
2. Marginal spots that are highly contrasting enhance
the effect of disruptive colouration.

3. Prey with highly contrasting spots that break the edge of the carapace and also match the size of the background spots are the most difficult to find because the effects of both disruptive colouration and background matching will be maximised.

In our second experiment (Experiment 2), the outline of *C. maenas* was used but the carapace patterns created did not resemble any natural markings found in this species. This series of trials tested the prediction that, against a background of middle-sized spots, a prey morph possessing middle-sized spots that intersect the body outline will be the hardest to detect compared to other spot sizes (larger and smaller) and position arrangements.

1 Materials and Methods

1.1 Prey

The virtual crabs used in Experiment 1 were based on the *C. maenas* ‘3-spot’ morph (one rostrum spot and two hepatic spots), the most common pattern found by Todd et al. (2006). The carapace and pattern outlines of a typical 3-spot example were traced using vector graphics software (Adobe Illustrator CS version 11.0) to produce a virtual crab template of 28 × 20 mm carapace width × height (92 × 66 pixels; visual angle = 9.4°). Using grey-scale tones only, this template was used to create four patterned morphs: ‘high contrast edge’ (HCE), ‘high contrast inner’ (HCI), ‘low contrast edge’ (LCE) and ‘low contrast inner’ (LCI); plus two control morphs: ‘plain 1’ (P1), ‘plain 2’ (P2) (Fig. 1). The carapace for all patterned morphs was shaded 60% black. The spots on high contrast morphs were pure white (0% shading) whereas the spots on low contrast morphs were 45% black. Various combinations of carapace and spot shades were tested during preliminary trials and this final arrangement proved to be the most suitable, i.e. detection of the crabs against the backgrounds was challenging but not impossible. The percentage area occupied by the spots on the carapace of a patterned morph (26.8%) and the spot shades were used to determine the carapace shade of the two plain morphs, i.e. the controls for high and low contrast, as follows: [(area of spot × spot shade) + (area of carapace × carapace shade)]/100.

The prey in Experiment 2 were generated by using a computer program to place randomly a ‘cookie-cutter’ outline of the virtual crab (same shape and size as in Experiment 1) onto one of three different backgrounds: ‘middle’ background (BGM) as used in Experiment 1 (Fig. 2), ‘small’ background (BGS) or ‘large’ background (BGL). Details of the backgrounds are provided in the next section. Whatever fell within the crab outline became the morph; although the spots were rearranged slightly to form edge morphs, i.e. the spots overlapped the margins, and inner morphs, i.e. no spots overlapped the margins. Only whole background spots were included in the prey design as part-elements were not integrated into any aspect of this study. A total of six patterned morph types were produced this way: ‘middle edge’ (ME) and ‘middle inner’ (MI) morphs were filled with a random mixture of ‘middle’ spot sizes, ‘small edge’ (SE) and ‘small inner’ (SI) morphs were filled with spots that were smaller on average, and ‘large edge’ (LE) and ‘large inner’ (LI) morphs were filled with spots that were larger on average (Fig. 3).

![Fig. 1 The six crab morphs used in Experiment 1](image1)

Note the single rostrum spot and two hepatic spots. On the touch screen the morphs were 28 mm wide.

![Fig. 2 Samples of backgrounds used in Experiment 1](image2)

On the touch screen each background was circular and 280 mm in diameter.

![Fig. 3 The morphs used in Experiment 2](image3)

The plain, control, morph (not shown) was identical to these morphs, but minus the spots. Four examples of each morph type were created and used. On screen the morphs were 28 mm wide.
Because not all random samples of a background are necessarily equally cryptic (Merilaita and Lind, 2005), the ‘cookie-cutting’ was repeated to create four edge and four inner morphs per background type (BGL, BGM and BGS). The percentage edge disruption for ‘large edge’, ‘middle edge’ and ‘small edge’ morphs was adjusted to ensure parity (for all morphs the spots intersected approximately 42% of the edge). The mean shading was also calculated; for the large morphs it was ~52% black, the middle morphs ~50%, and the small morphs ~53%, i.e. similar to each other as well as to the overall shading of the background (50% black). Finally, a plain morph (P) filled with 50% black was included as a control.

1.2 Backgrounds

Backgrounds were inspired by the poly-luminous mussel-beds and shell-hash that juvenile C. maenas use as nursery habitats. The ‘middle’ (BGM) background consisted of a circle filled with 50% black. Its diameter was set at 280 mm (1000 × 1000 pixels; Visual angle = 29.2°); effectively spanning the height of the touch-screen used throughout these experiments. So that the effect of shape-matching could be controlled for in subsequent analyses, the elements superimposed on this circular background were shapes identical to the ‘rostrum’ and ‘hepatic’ spots of the ‘3-spot’ morph used in Experiment 1. The spots varied in both size and shading. Sizes ranged from 70% to 130% (in 10% increments) of those found on the virtual crabs. Shades ranged from 0% to 100% black (omitting 50% black, which would be invisible), also in 10% increments (Fig. 4). Thus, there were a total of seven different spot sizes and ten different spot shades. To avoid overlap, the background spots were distributed manually, but placed and rotated haphazardly. An equal number of spots of each size and shading were positioned to create an overall mean of 50% black shading. For the ‘middle’ background, a total of 840 hepatic spots (10 shades × 7 sizes × 2 spots × 6 duplicates) and 420 rostrum spots (10 shades × 7 sizes × 6 duplicates) were placed in the circle. As Experiment 2 focused on testing the effects of spot sizes of morphs on a standardised background, the BGM background was the only one used in Experiment 2.

For Experiment 1, ‘small’ (BGS) and ‘large’ (BGL) spot-size backgrounds were also created. Both BGS and BGL started with the same 50% black circular template. BGS was filled with a range of elements sizes of which the largest was the middle spot size of the middle background. BGL was also filled with a range of elements sizes of which the smallest was the middle spot size of the ‘middle’ background (Fig. 2, Fig. 4). Size increments remained at 10% and there were a total of seven sizes; the range of spot shades remained as per the ‘middle’ background. For BGS, there were 10 duplicate spots of every shading and size, making a total of 2,100 spots whereas for BGL had three duplicate spots of every shade and size, resulting in a total of 630 spots. The area not covered by the spots was similar, ranging between 29.4% and 34.1%. All three backgrounds (BGS, BGM and BGL) were used for Experiment 1.

1.3 Experimental procedure

The simulation was presented to human volunteers as a computer game in which they were instructed to find hidden crabs as quickly as possible. The program was written in JAVA™ as a Windows application and run on Windows XP operating system in high graphics mode (1,280 × 1,024 pixels, 32 bit colour quality). Prey were deleted by touch on a 480 mm touch-sensitive screen (Elo Touchsystems) linked to a Maxston processor. Although the trials could have been conducted using a standard mouse, our earlier tests revealed that the touch-screen method was more intuitive and reliable.

Trials were carried out in January and February 2007 on campus by 640 student volunteers from the National University of Singapore (NUS). To avoid problems with age-related eyesight deterioration in older humans younger participants were encouraged, thus, the mean age of the volunteers was 21.98 y (S.E.± 0.003) for Experiment 1 and 23.54 y (S.E. ± 0.006) for Experiment 2. No volunteer undertook the experiment more than once, nor did they have any prior knowledge of the details of the study. Volunteers performed each trial alone in a cotton tent (2 m × 1.7 m × 1 m; length × height × width) lined with blackout cloth and lit by a single 40 W fluorescent bulb. Distance from the viewer to screen was ~50 cm.

For Experiment 1, there were 18 combinations of backgrounds and crab morphs (three different back-
grounds \times six crab morphs) and 20 valid trials per crab-background combination were conducted, whereas, in Experiment 2, 40 trials for each of the seven morphs were completed (as only the ‘middle’ background was used). All of the 360 trials for Experiment 1 and 280 trials for Experiment 2 were unique, i.e. undertaken by different human subjects. One trial was treated as one replicate for analysis.

For both Experiments 1 and 2, at the beginning of each trial, volunteers were asked to type their age and state (yes/no) whether they had performed the experiment before or had any prior knowledge of the details of the experiment. When volunteers chose ‘Yes’ to the second question, rather than not letting them continue, their trial data was automatically invalidated and that particular crab-background combination was made available to a different volunteer.

After filling in their details, volunteers were presented with an instructions screen describing the aim of the experiment, i.e. to locate and delete (by touching) the crab morph as fast as possible (by careful searching, not trial and error). It was made clear to them that they would be presented with a certain number of screens and each screen contained one prey only. Only one prey was generated per screen because pilot tests showed that subjects tended to use multiple fingers simultaneously if there was more than one prey at a time on the screen. To familiarise the subjects with the set-up, a training screen was generated with a black oval object as the ‘prey’ against a blank circle. Prior to the actual trial, the program provided a series of instructions which included screens that displayed the target crab followed by an example background for five seconds each.

When the volunteers were ready and pressed a button to start the actual trial, the program presented a sequence of different screens—but all with the same morph-background combination; the mean time to find the morph was then used as a replicate in subsequent analyses. For each of the screens, the same crab morph was repositioned and rotated randomly; simultaneously, the same background was also rotated randomly (to circumvent volunteers learning its configuration). Six screens were generated for Experiment 1 and four screens for Experiment 2 as pilot tests indicated that volunteers had a tendency to give up if presented with more screens than this. A counter showed the number of screens left and a picture of the target crab morph was always present at the bottom right corner (again, because without this, the trials took too long and the students gave up). Subjects were not allowed to skip screens. Upon completion of the trial the program thanked the subject, gave their timing and rank for their particular crab morph and background type and were asked not to reveal details of their experiment to their peers.

1.4 Data recording

The program recorded the following details and stored all data in MySQL™ tables (1) the test type—Experiment 1 or 2; (2) whether the test was completed; (3) the identity of the crab morph; (4) the type of background; (5) the time taken per screen; (6) the number of touches per screen; and (7) whether the test was valid.

There were four ways by which data could be rendered invalid: (a) if the test was not completed (e.g. the application was closed before the trial was completed); (b) if the program recorded more than a maximum number of touches per screen (15 for Experiment 1 and 25 for Experiment 2) as this suggested a trial and error approach by the volunteer; (c) if subjects stated that they had already taken the experiment before; and (d) if the researcher decided to manually invalidate the data upon his or her discretion. For example, it was necessary to invalidate the trial when participants asked for help or when they were deemed to have been distracted (such as a call to their mobile telephone). Invalid trials were excluded from analysis but, to maintain a balanced statistical design, the morph-background combination of the discarded trial was made available to another volunteer. The program automatically calculated the time taken to find each morph and the mean value was taken to represent the level of camouflage that particular morph afforded on that background (Merilaita et al. 2001; Merilaita and Lind, 2005). Data were extracted to Microsoft Excel 2000 tables using PHP script (version 4.4) running on an APACHE (version 2.0) server.

1.5 Statistical analyses

Differences in the time taken to find each morph in Experiment 1 were first tested with a three-factor (high/low contrast \times edge/inner \times small/middle/large background types) ANOVA with plain morphs excluded from the analysis. For each individual factor that contributed significantly to the three-factor ANOVA, single-factor ANOVAs and post hoc Student-Newman-Keuls (SNK) test were conducted to compare the search time. If there was a significant interaction between factors, single-factor ANOVAs and post hoc Student-Newman-Keuls (SNK) tests were conducted to investigate the effect of one factor in each level of the other factor. Subsequently, a two-factor ANOVA (6 morphs with plain morphs included \times 3 background types) was
conducted to compare search time of plain morphs with patterned morphs.

For Experiment 2, a two-factor ANOVA (edge/inner × small/middle/large spot size) was used to determine the differences in the time taken to find the morphs (plain morph excluded). For each individual factor that contributed significantly to the two-factor ANOVA, single-factor ANOVAs and post hoc Student-Newman-Keuls (SNK) tests were conducted to compare the search time. A single-factor ANOVA was then performed to compare search time of the plain morphs with the patterned morphs.

Where necessary, data were log transformed in order to meet the assumptions of ANOVA. All tests were performed using SPSS Statistics 17.0.

2 Results

For Experiment 1, search time varied significantly between morphs with different contrasts and among backgrounds, but not between edge and inner morphs (Table 1). Overall, mean search time for high contrast morphs were higher than low contrast morphs, and search time on the large background was higher than on the middle background, which was in turn higher than on the small background. There were significant interactions between morph contrast and background. On small and middle backgrounds, mean search times were significantly longer for both high contrast edge (BGS: 2.99 ± 0.26 s; BGM: 5.21 ± 0.62 s; all values are Mean ± SE) and high contrast inner morphs (BGS: 3.27 ± 0.31 s; BGM: 5.25 ± 0.51 s) compared to low contrast edge (BGS: 2.10 ± 0.26 s; BGM: 3.01 ± 0.23 s) and low contrast inner morphs (BGS: 2.15 ± 0.19 s; BGM: 2.57 ± 0.30 s). On the large background, high contrast morphs (Edge: 7.06 ± 0.94 s; Inner: 4.60 ± 0.45 s) were not significantly harder to find than low contrast morphs (Edge: 4.79 ± 0.50 s; Inner: 4.31 ± 0.49 s). The plain morphs were significantly easier to detect than all other morphs on all backgrounds (Table 1; Fig. 5).

For Experiment 2, mean search time among morph element size and between edge and inner morphs was significantly different (Table 2). There was no interaction between edge disruption and morph spot size. In general large (Edge: 32.15 ± 5.94 s; Inner: 14.72 ± 2.99 s) and medium spotted morphs (Edge: 25.20 ± 3.16 s; Inner: 10.68 ± 2.06 s) took a significantly longer time to find compared to the small-spotted morphs (Edge: 13.77 ± 2.02 s; Inner: 10.16 ± 3.77 s). Mean search time for edge morphs were longer than inner morphs. The plain morph (1.31 ± 0.08 s) was the easiest to detect (Table 2; Fig. 6).

3 Discussion

The two experiments conducted here were, in part, similar to previous crypsis studies. For example, to test for disruptive colouration, Schaefer and Stobbe (2006)

| Table 1 | a) Three-factor ANOVA and post-hoc Student-Newman-Keuls tests comparing mean search time among crab morphs patterns (‘contrast’: HC = high contrast, LC = low contrast; ‘edge’: edge = outline disrupted by spots, inside = spots placed away from outline) and ‘backgrounds’ of different element sizes; b) Two-factor ANOVA and post-hoc Student-Newman-Keuls tests comparing mean search time among all six crab ‘morphs’ on ‘backgrounds’ of different element sizes
| Experiment 1 | a) 3-way ANOVA (plain morphs excluded) | df | F | P |
| | contrast | 1 | 43.90 | <0.001 |
| | edge | 1 | 2.19 | 0.14 |
| | background | 2 | 37.38 | <0.001 |
| | contrast × edge | 1 | 0.019 | 0.89 |
| | contrast × background | 2 | 3.90 | 0.02 |
| | edge × background | 2 | 1.99 | 0.14 |
| | contrast × edge × background | 2 | 1.04 | 0.36 |
| | residual | 228 | | |
| | mean search time | overall contrast | HC = LC |
| | overall background | BGL > BGM > BGS |
| | Interaction between contrast and background | background | large | HC = LC |
| | | medium | HC > LC |
| | | small | HC > LC |
| | contrast | high | BGL = BGM > BGS |
| | low | BGL > BGM > BGS |
| b) 2-way ANOVA (plain morphs included) | df | F | P |
| morph | 5 | 58.65 | <0.001 |
| background | 2 | 54.72 | <0.001 |
| morph × background | 10 | 1.69 | 0.083 |
| residual | 342 | | |
| mean search time | overall morph | HCE = HCE > LCE = LCI > P1 = P2 |
| overall background | BGL > BGM > BGS |
Fig. 5 Mean search time for six different morphs on three different backgrounds \((n = 20)\)
Error bars indicate SE.

Table 2 a) Two-factor ANOVA and post-hoc Student-Newman-Keuls tests comparing mean search time among crab morphs patterns (‘edge’: edge = outline disrupted by spots, inside = spots placed away from outline) and ‘backgrounds’ of different element sizes; b) Single-factor ANOVA and post-hoc Student-Newman-Keuls tests comparing mean search time among all seven crab ‘morphs’

Experiment 2

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<th></th>
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<tr>
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<tr>
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<td>65.78</td>
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<td>background × edge</td>
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mean search time

overall background BGL = BGM > BGS
overall edge edge > inside

b) 1-way ANOVA (plain morphs included)

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</tbody>
</table>

mean search time

overall morph LE = ME > SE = LI = MI > SI > P

produced paper copies of naturally-occurring moths; we based our virtual morphs in Experiment 1 on real crabs. To test background matching and disruptive coloration, Merilaita and Lind (2005) used samples of a background to create completely artificial prey/background scenarios; we did the same in Experiment 2. However, both our experiments included an important additional factor: the size of background and crab spots. To our knowledge, only two studies have tested the effects of spot size in the context of background matching (i.e. Merilaita et al., 2001; Sheratt et al., 2007), and none have also included disruptive colouration.

3.1 Experiment 1

Overall, the virtual crabs were harder to find on the large background (BGL) compared to the middle background (BGM) which, in turn, provided more protection than the small background (BGS) (Table 1a). Merilaita et al. (2001) varied the size of spots on artificial prey and also found that mean search times were longer on large-patterned backgrounds, and suggested they could be a “more difficult visual environment for the searcher” (Pg 1928). It is also possible, however, that the substantial area (73.2%) of solid-shaded carapace on each patterned morph simply became less noticeable with increasing background spot size. The fact that both plain morphs (P1 and P2) also took significantly longer to find on larger backgrounds supports this supposition.
numerous visual predators (Crothers, 1968), the fact that ‘three spot’ is the most common pattern (Todd et al., 2006) suggests this arrangement provides some fitness benefit in natural populations—possibly by protecting it under a variety of common backgrounds or, as suggested by Todd et al. (2006), because *C. maenas* tends to peer out from under rocks and hence its anterior is more exposed to attack. Plain morphs were relatively easy to find in this experiment—suggesting they should be selected against; nonetheless, they are common on the shores where they are found. Plain *C. maenas* probably survive due to the wider range of habitats available under natural conditions. Due to the hypotheses being tested, the present study is highly artificial and the backgrounds limited. In real life, many microhabitats exist where being plain should provide camouflage, for example, within beds of macro algae or in shaded crevices.

We found no significant difference between inner and edge morphs on all backgrounds. These results are contrary to those of previous studies (e.g. Cuthill et al., 2005; Stevens et al., 2006; Fraser et al., 2007), and Experiment 2 here, where edge morphs survived longer than inner morphs. We can only speculate that different experimental setups account for this unexpected outcome. For instance, although the morph spots could be found on the backgrounds, the large area of homogeneous carapace meant that the overall geometric match was generally poor, which may have negatively influenced the disruptive effect (Wilkinson and Sherratt, 2008). In addition, the degree of edge disruption in Experiment 1’s edge morphs was relatively low at ~23%, compared to ~37% in Cuthill et al. (2005), ~52% in Stevens et al. (2006), and ~42% in Experiment 2 of the present study. Unlike Cuthill et al. (2005) and Stevens et al. (2006), the spots on the crab morphs were uniform and symmetrically positioned, which can also influence detection (Cuthill et al., 2006). Furthermore, in our experiment, the ‘template’ shade of the carapace was an exact match to the ‘template’ shade of the background (both were 50% black). This is different to the field experiments by Cuthill et al. (2005) and Stevens et al. (2006) where the match to the natural tree bark was based on average values. A perfect match may make spots touching the margin of the prey less necessary, because the edge coloration will very likely blend into some substrate patches and hence break up the outline even if the prey spots do not disrupt it (Stevens and Merilaita, 2009b). Finally, in Experiment 1 there was no variation within each morph type; that is, for a morph such as “high contrast inner”, only one artificial morph was created. Hence, it is possible our results are due to artefacts peculiar to each unique design, and not findings that can be extrapolated to a general population (Stevens et al., 2013).

High contrast morphs were harder to find than low contrast morphs on the medium and small patterned backgrounds, and were equally effective on the large background. This could be due to disruptive contrast being maximised while still maintaining a high level of background matching (Stevens and Merilaita, 2009b). However, as edge disruption was not demonstrated (see previous paragraph), the difference in overall “greyness” between high contrast morphs and low contrast morphs may also contribute to the results. Based on the hexadecimal colour scale (where 0 = 100% black and 255 = 100% white) the grey value for the background was ~112, while the mean values (spots and carapace together) for the high and low contrast morphs were ~126 and ~90, respectively. Overall morph-background difference was therefore higher for the low contrast morph than the high contrast morph, potentially causing the low contrast morph to be detected more easily. Additionally, the lower tone range in the low contrast morph could be a disadvantage in backgrounds with a full range of tones as visually homogeneous morphs can be more conspicuous in a heterogeneous background, as found for the plain morphs of the present and previous studies (Cuthill et al., 2005; Stevens et al., 2006, 2009a, 2009b; Fraser et al., 2007). Even though there remains the possibility that our low contrast morphs were easier to see because that particular spot shading (45%) was not present in the background, 40% and 50% spots were included and, from our experience, a 5% difference is very hard to detect in the environments we created.

### 3.2 Experiment 2

As only the middle background was used in Experiment 2 we expected that virtual crabs with middle spots would be the hardest to find. However, for both inner and edge morphs, the trend in search time was identical, i.e. large = middle > small, indicating that patterns with spots larger than the background can provide a similar
level of protection as a those that are a close match. Stevens and Merilaita (2009a,b) highlight how difficult it is to control for background matching when testing for disruptive coloration. The converse is equally true, i.e. differential levels of disruptive coloration may also confound efforts to focus in on the effects of background matching. But, as detailed in the Materials and Methods, the mean shading for all morphs was between 50% and 53% black, and the percentage disruption for all edge morphs was approximately 42%. It is possible that surface disruption may also have played a role in this experiment (Cott, 1940; Stevens and Merilaita, 2009), and that the degree of this type of disruption varied among the three spot sizes—with it perhaps being less pronounced in the small-spotted morphs. This is, however, speculative as no work to date has examined the effects of element size on the efficacy of surface disruption.

Similar to the results of Cuthill et al. (2005), Stevens et al. (2006) and Fraser et al. (2007), it took longer to find the large, middle and small edge morphs than their corresponding inside morphs, suggesting a positive effect of disruptive coloration. Cuthill et al. (2005) noted that the margin or ‘line’ formed by moving the elements inwards can make inside morphs more conspicuous. Such an effect could have occurred here, but might have been weakened because the line was irregular, and the inter-spot spaces of the background themselves often created line-like shapes. In addition, the process of aggregating the spots to create the inner morphs slightly increased their density and thus potentially lessened their background matching (Fraser et al., 2007) which may have made them more conspicuous. But, as the density within the background also varied slightly, and the morphs were placed randomly upon it, it is unlikely this had a significant effect.

3.3 Conclusions

All patterned morphs were significantly harder to detect than plain morphs, indicating that possessing at least some degree of background matching can provide camouflage. Both experiments also showed that various morphs, though not having the same spot sizes as the background, had similar or better survivorship as those with matching spot sizes. Results from Experiment 2, that indicated large-spotted morphs were as hard to find as middle-spotted morphs on the middle background, were particularly clear and robust. Together with the findings reported by Merilaïta et al. (2001), there is mounting evidence that the ‘closest match is the most effective’ model does not always hold true.

The fact that disruptive edges worked in Experiment 2 but not in Experiment 1 is probably explained by the poor background match in Experiment 1 ‘overriding’ any disruptive effect, which resulted in very short search time compared to Experiment 2. The greater length of edge disruption in Experiment 2 (~42% vs ~23%) may also have contributed to this result. In Experiment 2, regardless of whether the edge-disrupted morphs were small, middle or large, they always took longer to find than their inner counterparts (which had a quite defined marginal ‘line’ when the posts were moved inwards). While disruptive markings did not confer any advantage to the virtual crabs in Experiment 1, morphs possessing high contrast spots might have had better background contrast and colour range matching and hence achieved better concealment on middle and small backgrounds. This suggests that, background matching of even one aspect of colour pattern can still be advantageous to the morphs.

Even though there have been some recent crypsis studies on real prey (e.g. Todd et al., 2009; Defrize et al., 2010; Miller and Hollander, 2010), especially cephalopods (e.g. Allen et al., 2010; Chiao et al., 2010), there are many more that use some form of artificial system. There now exist numerous models that should be possible to test in the field with natural predators and prey. Certainly, it is viable to make direct comparisons between the characteristics of juvenile C. maenas spots and the background elements of their mussel-bed nurseries; and also test whether altering the features of the carapace or habitat affects survival. Due to their abundance, diversity of phenotypes, and ease of handling, arthropods probably offer some of the best opportunities for crypsis fieldwork, as well as being excellent subjects for manipulative research based on prey that are artificial (e.g. Cuthill et al., 2005) or fully virtual (as here).

Some cephalopods studies have examined body patterns in relation to background matching and disruptive colouration by manipulating background (a checkerboard design) square size and contrast (e.g. Chiao and Hanlon, 2001; Chiao et al., 2007; Barbosa et al., 2008). But the present study is the first to test the effect of disruption, background and prey spot size on ‘predator’ search time. Stevens and Merilaïta (2009b, Pg 486) state “background matching is purely about correspondence between the prey markings and the background …for background matching, the animal markings are expected to match the distribution of the background markings.” The results here, however, suggest that a match between prey spots and background spots does not nece-
ssarily confer the greatest protection. Interestingly, while previous research has shown that benefits attributed to edge disruption were contingent on the type of contrast (achromatic or chromatic) (Schaefer and Stobbe, 2006) or luminance differences between the background and the prey (Stevens et al., 2006), spot size had no effect on the effectiveness of edge disruption in Experiment 2. As discussed by others (e.g. Dimitrova and Merilaita, 2010) the relative effects of disruption, contrast, and background/prey spot size appear to be context-dependent.

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