

Camouflage that is spot on! Optimization of spot size in prey-background matching

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Abstract Camouflage is a key predation prevention mechanism. The most intuitive camouflage strategy is background matching, where a prey resembles the colour and pattern of its background. Spots (e.g. geometric ‘elements’ that constitute a pattern) are a common feature on the body of prey, but the effect of their size in relation to elements in the background is rarely examined in camouflage studies. Here, we test the survivorship of computer generated prey possessing patterns of elements grouped into eight size classes on backgrounds composed of elements of the same eight size classes. All 64 possible combinations were presented to human volunteers ($n = 10$) acting as ‘predators’ in a computer simulation. As hypothesised, prey survivorship was high when the prey-background element size difference was low. We found significant asymmetry, however, in survivorship pattern: prey morphs with elements larger than those of the backgrounds were harder to detect than morphs with elements smaller than those of the backgrounds. When testing for potential trade-offs we determined that, in a habitat consisting of an equal proportion of two backgrounds with a large element size difference between them, net survivorship of specialist prey morphs (same element size as one of the backgrounds) was similar to that of generalist morphs (intermediate element size). When the two backgrounds were less distinctive, i.e. reduced element size difference between the backgrounds, generalist prey morphs achieved significantly better net survivorship than specialists.

Keywords Camouflage · Computer simulation · Element size · Human predator

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Introduction

Camouflage is one of the most common prey defense mechanisms found in nature (Ruxton et al. 2004; Stevens and Merilaita 2009a, b). To reduce predation risk, many organisms employ one or both of two key detection prevention strategies. One is disruptive colouration, where the organism's outline and shape is hidden by creating the appearance of false edges and boundaries—making it difficult to detect (Cott 1940; Merilaita 1998; Stevens and Merilaita 2009b). A great deal of work has been published on disruptive colouration over the last decade (e.g. Cuthill et al. 2005, 2006; Merilaita and Lind 2005; Stevens et al. 2006, 2009b; Schaefer and Stobbe 2006; Fraser et al. 2007; Dimitrova and Merilaita 2010; Webster et al. 2013, 2015; Espinosa and Cuthill 2014; Kang et al. 2015; Todd et al. 2015; Webster 2015), however, the other principle strategy: resembling or blending into the background, i.e. background matching, is far less studied (Stevens and Merilaita 2011) even though it is arguably more intuitive (Endler 1978; Stevens and Merilaita 2009a).

Early research proposed that a perfect background matching organism should possess colour patterns that “represent a random sample of the background on which it is usually seen by predators” (Endler 1978, p. 321). While it is still generally accepted that the colour pattern should approximate those of the background in a number of aspects including spot (or ‘element’) size, colour, contrast, shape (Endler 1978, 1981, 1984, Stevens and Merilaita 2009b; Merilaita and Stevens 2011), and spatial distribution (Dimitrova and Merilaita 2010, 2012), exactly what role these factors play in optimizing background matching is not yet fully understood despite several theoretical and empirical studies (e.g., Merilaita 1999; Merilaita et al. 2001; Merilaita and Lind 2005; Houston et al. 2007; Sherratt et al. 2007; Todd et al. 2015).

Previous work has demonstrated that some animals patterns match their backgrounds for element size (e.g. Endler 1980, 1984; Kiltie 1992; King 1992) and that background element size can influence the colour patterns of cephalopods (e.g. Hanlon and Messenger 1988; Chiao and Hanlon 2001a, b; Barbosa et al. 2007, 2008). However, a deeper understanding of the role of pattern element size in background matching has only materialised in recent years, with experiments using artificial prey by Merilaita et al. (2001), Sherratt et al. (2007) and Todd et al. (2015). They showed that, while survivorship of prey was mostly (and expectedly) inversely correlated to the morph-background element size difference, other factors also appeared to influence prey survival, for example, prey morphs with pattern elements smaller than the background were more difficult to detect than morphs with pattern elements larger than the background in Merilaita et al. (2001) and Experiment 1 of Todd et al. (2015); the converse, however, was found for Experiment 2 in Todd et al. (2015). Hence, the question “which confers the greater protection—having larger or smaller spots compared to the background?” (assuming that a perfect match is ideal) remains unresolved.

In their natural environment, most prey are likely to be present in an array of different settings and backgrounds; therefore, there is an inevitable trade-off between background matching in one microhabitat versus background matching in another. Merilaita (1999) presented a mathematical model showing that, in a heterogeneous habitat (i.e. two or more visually distinctive microhabitats), an animal morph can either be a ‘specialist’, which closely resembles one microhabitat while being much more conspicuous in other microhabitats, or be a ‘generalist’ (e.g. an intermediate morph) that is a compromise between the background matching requirements of the different microhabitats. The circumstances that

favour a specialist or generalist can be determined by plotting a trade-off curve that relates survivorship (or the probability of not being detected) of a prey morphs on one background with survivorship on another background (Merilaita et al. 2001). Each point on this trade-off curve thus represents the highest level of background matching a species (via its various phenotypes) can attain on Background 2 for a given level of camouflage in Background 1. A concave trade-off, i.e. the net survivorship of a “generalist” prey morph is lower than specialists, results in selection for specialism in a two-background scenario. On the other hand, a convex trade-off, i.e. net survivorship of a “generalist” is higher than a “specialist”, favours generalism. A linear relationship may lead to polymorphism (Fig. 1; Merilaita 1999; Ruxton et al. 2004; Sherratt et al. 2007). In previous studies, trade-offs ranging from concave, linear to slightly convex relationships have been obtained by manipulating sizes, geometries, and contrasts of background and prey elements (Merilaita et al. 2001; Merilaita and Dimitrova 2014; Sherratt et al. 2007). These studies postulated that the more similar the two backgrounds are the less specialism will be favoured—leading to a more convex trade-off (Merilaita 1999; Sherratt et al. 2007), but no tests of this hypothesis have been published to date.

To demonstrate the effects of background element size matching on prey survivorship and to test the hypothesis that a convex trade-off is more likely to occur when the backgrounds in a habitat are less distinct from each other, we conducted a search experiment using computer-based backgrounds and prey with humans as predators. The combination of computer simulations and human predators has been effectively employed in previous studies of background matching (Sherratt et al. 2007; Karpestam et al. 2013; Todd et al. 2015), and disruptive and distractive colouration (Fraser et al. 2007; Cuthill and Szekely 2009; Stevens et al. 2013; Webster et al. 2013, 2015). Further, findings from research employing humans as predators do not vary qualitatively from those of analogous studies using birds (Beatty et al. 2005; Fraser et al. 2007; Cuthill and Szekely 2009; Stevens et al. 2013), the most common non-human predator in camouflage research.

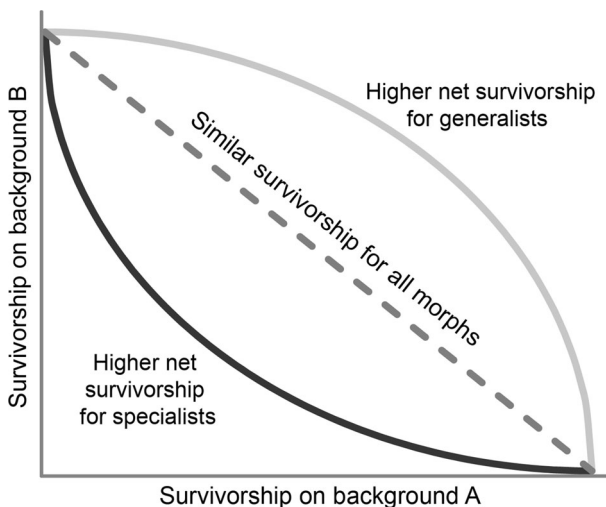


Fig. 1 The three possibilities of (simple) relationship between survivorship of prey patterns on background A and background B and their implication to the evolution of prey colouration. Adapted and modified from Sherratt et al. (2007)

Our experiment used a uniquely wide range of element size classes (ESC) on morphs and backgrounds: eight morphs each with a different ESC and eight backgrounds each with a different ESC. This expanded range of morphs and backgrounds enabled us to test the following hypotheses:

- (a) Survivorship (search time) of a background matching prey decreases as morph-background element size difference increases.
- (b) There exists asymmetry in survivorship. That is, prey with larger elements are harder to detect on backgrounds with smaller elements (or vice versa).
- (c) In a two-background habitat, low element size difference between the two backgrounds will result in a convex trade-off while high element size difference will result in a concave or linear trade-off.

Materials and methods

The use of computer simulations and human predators eliminates potential confounding factors such as non-independence issues (the same predator attacking unknown numbers of study prey items) and erratic predator behaviours. It also provides researchers greater experimental control as every aspect of the prey and background can be manipulated with precision, enabling more nuanced tests and analyses (Todd 2009; Todd et al. 2015). The simulation we designed was presented to volunteers as a game, in which they were requested to find the prey from the background as quickly as possible. The programme was written in JAVA as a Windows application and run on the NetBeans IDE 6.5 platform using Microsoft Window XP computer operating system. Volunteers interacted with the computer through a 19-inch LCD touch-screen monitor (Tyco Elo ET1915L-8CWA-1-G, 1280 × 1024 pixels, 32-bit colour).

Backgrounds

Eight different background types were generated based on eight element size classes (ESC). Each background comprised four types of elements: (a) $X \times X$ squares, (b) $X/2 \times 2X$ rectangles, (c) isosceles triangles with a base of X and a height of X , and (d) isosceles triangles with a base of $X/2$ and a height of $2X$. X was a random number from a normal distribution with standard deviation of 1.5 pixels (px; 1 px was approximately 0.3×0.3 mm on screen). ESC 1 had the smallest mean value for X , i.e. 10.5 px, while each subsequent ESC was 1.5 px larger than the previous one with ESC 8 having the largest X at 21 px. ‘Background 1’ was constructed by elements with ESC of 1, ‘Background 2’ with ESC of 2, and so on. To generate a background, first a 50% black (i.e. mid-gray) circle with a diameter of 850 pixels was drawn by the program. Four main elements were then picked, colored with 0, 20, 40, 60, 80 or 100% black, and placed onto the circle randomly. The process was repeated (with the criteria that no element overlapped another) until the circle was saturated with elements, i.e. the programme could not find sufficient space to place more elements. The background generated was then transferred to Adobe Photoshop CS2 and stored in GIF format. Ten backgrounds were created for each element size class, resulting in total of 80 backgrounds (Fig. 2).

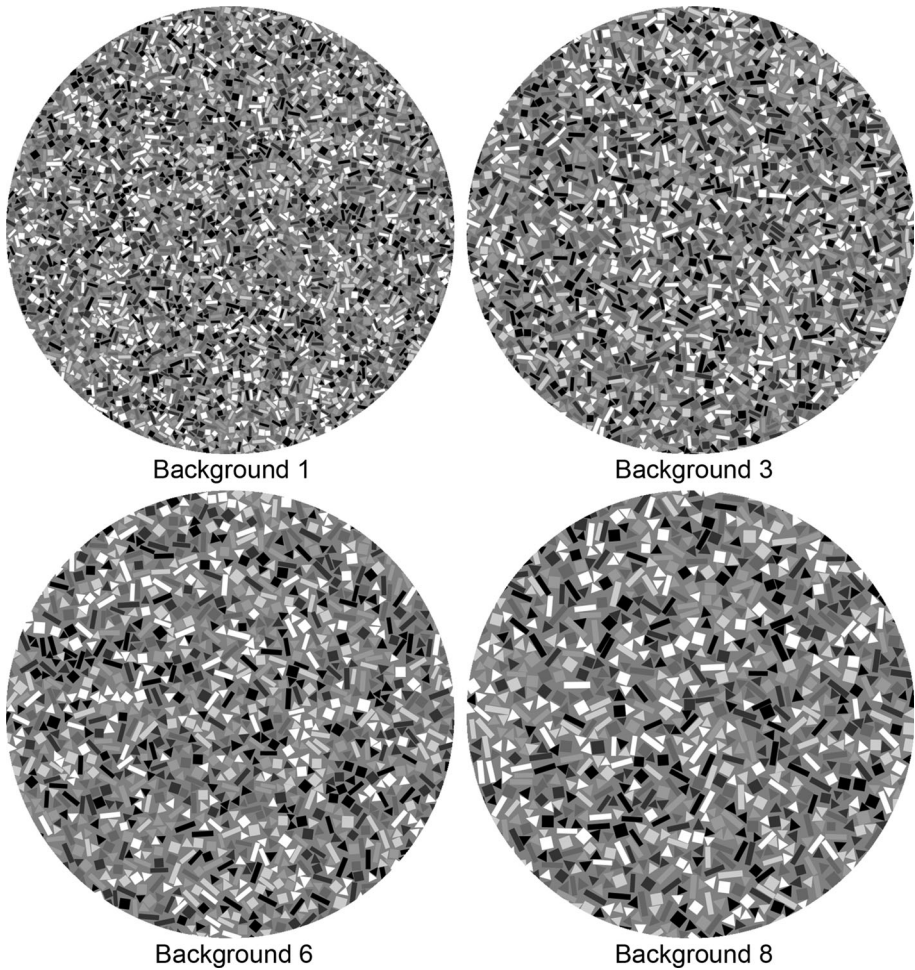


Fig. 2 Examples of backgrounds (not actual scale) used in the experiment. Background 1 had the smallest element size while Background 8 had the largest

Prey morphs

To create a prey morph, a $79 \text{ px} \times 79 \text{ px}$ octagon ‘mask’ was placed randomly onto a background using Adobe Photoshop CS2 and ‘cut’ out. Background elements that were bisected by the margin of the mask were manually removed or shifted inwards such that no element was $<40\%$ of its original size. Each prey morph generated was stored in GIF format.

Each background was used to produce a prey morph, i.e. 80 morphs were created using 80 backgrounds. The morphs were likewise categorized into 8 groups according to their ESC. For example, prey morphs that were generated from Background 1 (produced with elements of ESC of 1) were termed ‘Morph 1’, and so on (Fig. 3). Each morph group therefore had 10 replicates. This was to ensure that the pool of morphs was large enough to

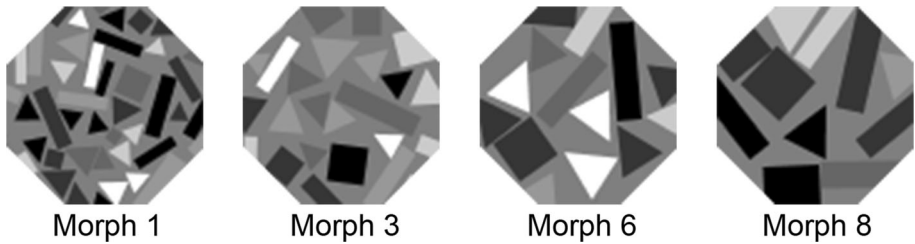


Fig. 3 Examples of virtual prey used in the experiment. The morphs are random samples of the backgrounds

reduce the possibility that not all random samples of a background were equally cryptic, as shown by Merilaita and Lind (2005).

Experimental setup and volunteer trials

The computer trials were conducted on campus with 640 student volunteers from the National University of Singapore (NUS). As our preliminary tests suggested that older volunteers (25–50 years old) tended to perform more erratically (greater variation around mean times), only volunteers between the ages of 18 and 25 were used in this study. If a volunteer responded at the beginning of the trial that he/she had participated in this experiment previously, the data collected from that particular trial was considered invalid.

Volunteers performed the computer trial alone in a cotton tent (2 m × 1.7 m × 1 m; length × width × height) lined with blackout cloth. A small fan was placed behind the chair to provide ventilation. The volunteers were requested to rest their head onto a padded restraint which fixed the distance between him/her and the monitor screen to 50 cm. The tent was zipped down once the volunteers started the test to ensure minimum disturbance. At the beginning of each trial, the volunteers were asked to fill in the following details:

- (a) Age
- (b) Gender
- (c) Whether they needed to wear glasses or contact lens
- (d) Whether they were wearing them at that point of time
- (e) Whether they had any visual impairment such as color blindness
- (f) Whether they had participated in the experiment before

The volunteers were then presented with an instruction screen describing the flow of the experiment. The volunteers were requested to search for the camouflaged prey on the complex background as quickly as possible.

The computer simulation randomly assigned a background and prey morph category for each volunteer (from a total of 64, i.e. 8 × 8, combinations). One of the ten replicates within the assigned morph group, and one from the assigned background group, would then be chosen and used in all of the following screens. If the trial was subsequently deemed valid, both the morph and background replicates would not be used in any future trials that had the same background-morph group combination. Combinations that had 10 successful trials (i.e. the number of replicates required by the experimental design) would not be allocated to new volunteers.

The volunteer was first presented an example screen with instructions to find the prey morph from the background within 90 s. The example screen consisted of a generic background and morph that were not used in the actual trial. They were then asked to press

the “Start” button to initiate the actual trial. The programme randomly rotated the background, and randomly placed the morph onto the background. The volunteer was reminded to search and tap on the morph as quickly as possible. A “well done” message appeared if the volunteer managed to locate the morph, while a “sorry” message would appear if the volunteer could not find the morph within 90 s. Nothing happened if the volunteer pointed at the wrong location, but the programme recorded the number of incorrect taps. The volunteers were then instructed to tap the “Next” button to start a new round of searching. Each volunteer was presented with a total of four background/morph screens for that background/morph combination. The mean time for these four screens was used as the input data (the replicate) in the analysis.

After the last (4th) round of searching, the programme thanked the volunteers and showed them their time-score and rank of their performance compared to the other volunteers who were also assigned that combination.

The following details were recorded and stored in mySQL server 5.1, which was running on an Apache server 2.2.11:

- (a) The volunteer’s personal details (as described previously)
- (b) The allocated background and morph
- (c) The time taken in each round of searching
- (d) The number of taps (attempts) per round,
- (e) Whether the test was successfully completed
- (f) Whether the test was valid.

A test was deemed as invalid if (a) the test was not completed, e.g. the volunteer left the trial without completing all the searches, and (b) the volunteer responded that he/she had done the experiment before. It was also possible for us to manually delete the data, for instance, if the volunteer was talking on their phone during the trial.

Data analyses

All data analyses were conducted using R 2.13.1 unless otherwise stated. Mean search time, calculated by averaging the search time for the four screens within a trial, was used as a measure of survivorship of a prey morph (i.e. higher mean search time indicated higher survivorship). To reduce the possibility that volunteers were blind guessing the morph location, replicates with an average number of >25 taps across the four rounds were excluded from the analyses. Impact of such exclusion was minimal as the average number of replicates excluded for each morph-background combination was 0.64 (6.4%) and not more than two replicates were excluded in each combination.

The effect of absolute ESC difference between prey morph and background (‘ESC difference’) on log-transformed mean search time was determined using a weighted least square regression. Samples were weighted using the variance of search time, grouped according to ESC difference. Two additional co-factors were added to the regression model to control for the human factors: (a) Total number of wrong taps/attempts (Tap) and (b) Whether the volunteer who needed to wear glasses wore glasses or contact lens during the experiment (Glasses, 0 = No, 1 = Yes, or the volunteer did not need to wear glasses). The assumption of homoscedasticity of the model was examined by plotting the residuals against the fitted values.

To test whether there was symmetry between survivorship of prey with large ESC on small ESC background versus small ESC on ESC large background, a morph-background combination with morph ESC > background ESC was paired with its counterpart (e.g.

morph-background combinations of 3–1 and 4–2 were paired with 1–3 and 2–4 respectively). Combinations with the same morph and background ESC were excluded from this analysis. Average survivorship of each morph-background combination was represented by a number: the mean of the mean search time. Average survivorship between combinations with morph ESC > background ESC was compared with combinations with background ESC > morph ESC using a paired *t* test.

To compare the trade-off of prey morph survivorship when presented against two highly distinctive backgrounds and two less distinctive backgrounds, two trade-off curves were plotted: (a) mean search time of each morph type (Morph 1 to Morph 8) on Background 1 (x-axis) and Background 8 (y-axis), (b) mean search time of Morph 3–6 on Background 3 (x-axis) and Background 6 (y-axis). Specialist morphs matched one of the background's ESC, i.e. Morph 1 and 8 in the first trade-off and Morph 3 and 6 in the second trade-off; a generalist morph's ESC laid in between the background's ESCs, i.e. Morph 2–7 in the first trade-off and Morph 4 and 5 in the second trade-off. On the trade-off plot each morph type was represented by a point, and the straight line with a slope of -1 that intersected this point represented a set of points that shared same net survivorship, i.e. probability of detection in the whole habitat comprising 50% of each background, as the morph type. Any point that was located above this straight line had higher net survivorship compared to the morph type and vice versa. The concavity (or convexity) of the trade-off relationship was determined using a similar method as Merilaita et al. (2001). We first determined the equation of the straight line that passes through the points representing the mean search time of the 'specialist' morphs. Subsequently, we calculated the shortest distance to the line for each of the point representing a morph replicate. Points below the line were assigned a negative value. A convex trade-off would result in the distances being larger than zero, as determined by a single sample *t*-test.

Results

Of the 640 individual trials, 599 were included in the analysis. The remaining 41 were excluded due to excessive number of taps. The mean age of the volunteers was 21.02 years ± 2.20 (\pm SD). There was no significant bias in volunteer gender (Binomial test: $p > 0.10$). Volunteers who needed glasses/contact lens but did not wear them did not perform differently from volunteers who wore glasses or did not need glasses/contact lens (Weighted linear model with ESC difference and number of wrong attempts as a co-factor: $F_{1,595} = 0.06$, $p = 0.81$). Hence, there was no need to exclude any trials due to the 'glasses/contact lens' factor.

Survivorship for prey morph-background combinations

The longest mean search time (57.87 ± 23.32 s, mean \pm SD), i.e. the hardest morph to find, was Morph 1 on Background 1. The shortest mean search time (1.39 ± 0.39 s, mean \pm SD) was recorded for Morph 8 on Background 1 (Figs. 2, 3). Combinations with less absolute difference between morph ESC and background ESC (i.e. 'ESC difference') generally took longer to find (Fig. 4). Standard deviations for most of the combinations were high (20–30 s) with the exception of combinations with very high (e.g. 6 or 7) ESC difference (Fig. 4).

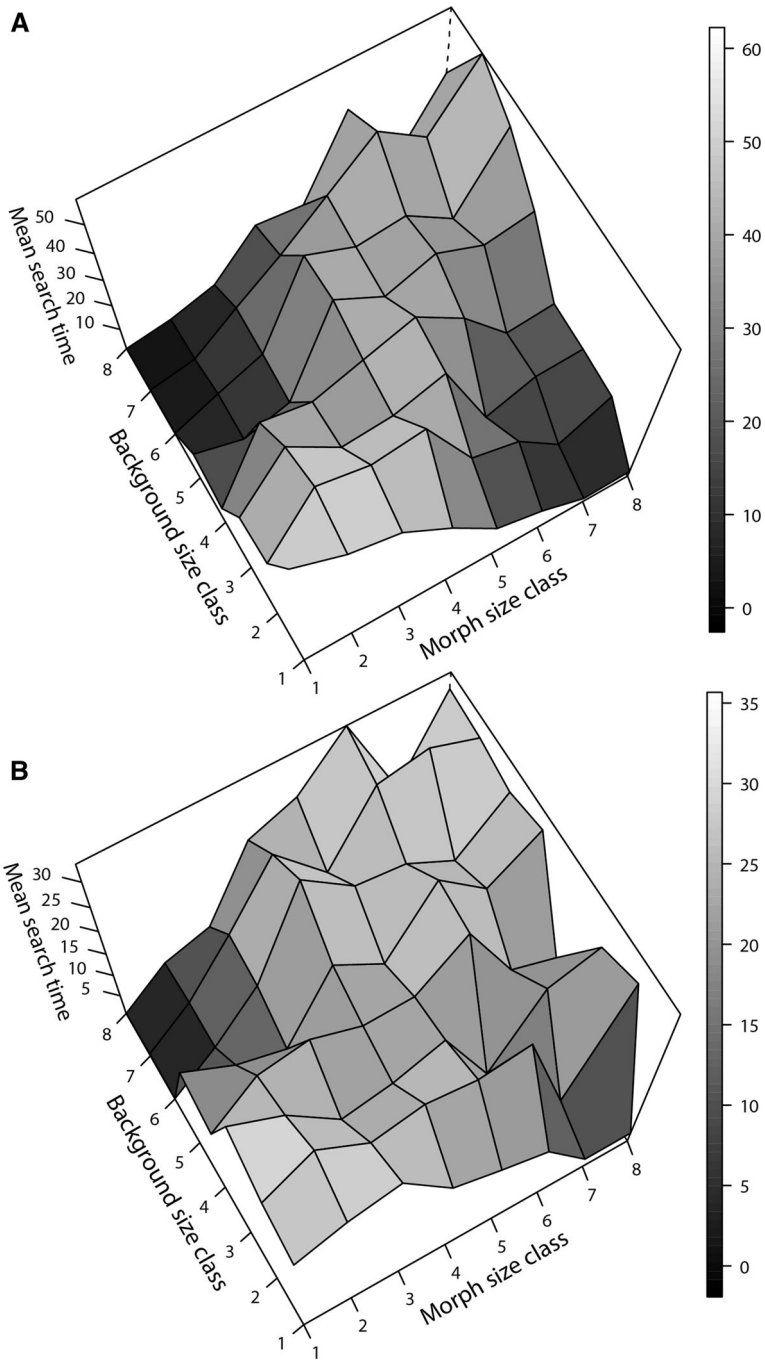


Fig. 4 Mean search time in seconds (*top*) and standard deviation of the search time (*bottom*) of each prey and background combination

Mean search time for combinations where the morph element size was larger than the background element size was significantly longer (paired *t*-test; $t = 3.11$, $df = 27$, $p < 0.01$) than for their counterparts, i.e. where the morph element size was smaller than the background element size (Fig. 5). In 22 of the 28 combination pairs, morph ESC > background ESC combinations had higher search times.

Both ESC difference between morph and background and total number of wrong taps/attempts were highly significantly associated with survivorship of a prey item (mean search time). The mean search time was negatively associated with ESC difference ($F_{1,595} = 560$, $p < 0.0001$); positively associated number of wrong taps/attempts ($F_{1,595} = 81.9$, $p < 0.0001$). The weighted least square regression model had limited data points when the fitted value was high, but the Breusch–Pagan test indicates the error variance was not significantly different among the fitted values ($p > 0.05$).

Net survivorship

The trade-off relationship was approximately linear when all morphs were presented against two highly distinctive backgrounds, i.e. Background 1 and Background 8 (largest ESC). The equation of the line passing through the mean search time of Morph 1 and Morph 8 was $y = -1.42x + 59.84$. The distances to this line of expectation for all generalists (Morph 2–7) averaged +2.25 and were not significantly different from zero ($t = 0.79$, $df = 57$, $p > 0.05$).

Conversely, the trade-off curve was convex when the morphs were presented against two backgrounds with a narrower element size difference, e.g. Backgrounds 3 and 6 (Fig. 6b). Intermediate morphs (Morph 4 and 5) had higher net survivorship compared to

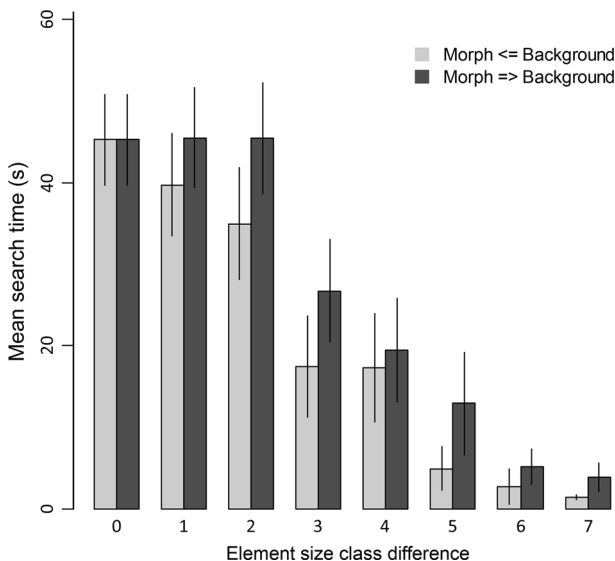


Fig. 5 Mean search time $\pm 95\%$ CI of combinations with element size class difference of 0–7. Combinations with prey element size class larger than the background's were separated from those with background element size class larger than the prey's. As background and prey morph element size for the group with 0 element size class difference were the same, the two bars (Morph \leq Background and Morph \geq Background) are identical

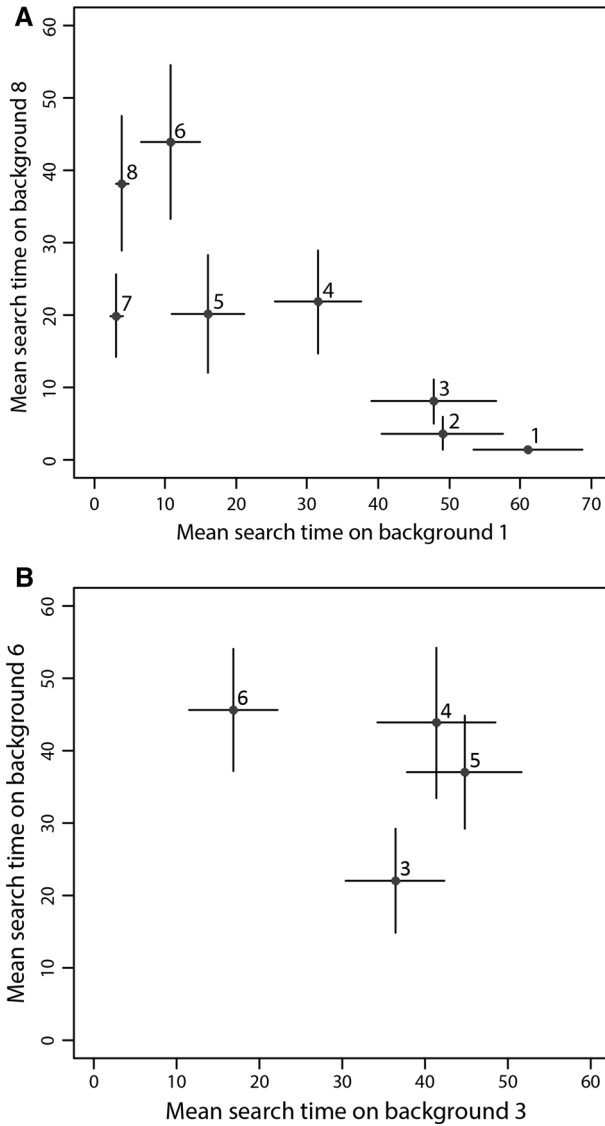


Fig. 6 **a** Mean search time \pm SE of prey morph types 1–8 when presented against Backgrounds 1 and (on separate occasions) Backgrounds 8. **b** Mean search time \pm SE of prey types 3–6 when presented against Backgrounds 3 and (on separate occasions) Backgrounds 6. Numbers beside the points refer to the prey morph type

specialist morphs (Morphs 3 and 6). The equation of the line passing through the mean search time of Morph 3 and Morph 6 was $y = -0.98x + 50.93$. The distances to this line of expectation for all generalists (Morph 4 and 5) averaged +24 and were significantly larger than zero ($t = 4.2, df = 15, p < 0.001$), indicating the convex shape.

Discussion

Spot (or element) size is one of the major determinants of background matching (Endler 1978, 1981, 1984), but it is not well studied. We show that prey survivorship decreases steadily as the background-morph element size class (ESC) difference increases (Fig. 4). Furthermore, similar to previous research (but see Sherratt et al. 2007), there is an asymmetry in detection time (Fig. 5). Finally, and most importantly, we demonstrate that some prey with ‘compromised’ element sizes perform better than ‘specialists’ in two-background systems, and that this depends on the range of element sizes in the two backgrounds (Fig. 6).

That prey survivorship is high when the prey-background spot size difference is low is an intuitive result and has been demonstrated by others (e.g. Merilaita et al. 2001; Sherratt et al. 2007; Todd et al. 2015). Our experiment, however, tested a wider range of prey-background combinations than attempted previously and hence can show in detail the degrees by which prey become easier to find (Fig. 4). For example, while the relationship is generally linear, there is a clear drop in search time between ESC differences of 2 and 3 (Fig. 5) when the pattern on the prey morph is bigger than that of the background. It is apparent that not all patterns are equal: some can achieve near-optimal protection despite matching their background imperfectly, while others cannot.

The asymmetry in detection time suggests that other visual factors that are specific to the experimental design may be important to prey survivorship. We found that larger-patterned morphs on smaller-patterned background are significantly more difficult to detect compared to proportionately smaller-patterned morphs on larger-patterned backgrounds (Fig. 5). This finding aligns with Experiment 2 of Todd et al. (2015) but not with Merilaita et al. (2001) and Experiment 1 of Todd et al. (2015), who found the reverse, i.e. smaller-patterned morphs on larger-patterned backgrounds have higher mean search times than their counterparts. The inconsistency among studies suggests that having larger or smaller element sizes than the background *per se* does not confer greater protection. Instead, experiment-specific visual factors, such as background complexity or disruptive colouration, are likely to play a role. It is possible that the sheer number of elements in the smaller backgrounds of our study might have increased the background complexity, which can make prey detection more difficult (Gordon 1968; Farmer and Taylor 1980; Merilaita 2003; Dimitrova and Merilaita 2010, 2012; Espinosa and Cuthill 2014). Alternatively, larger body elements on the prey are more likely to create false edges as well as boundaries away from the body outline, protecting the prey through disruptive colouration and/or surface disruption (Cott 1940; Stevens and Merilaita 2009b; Stevens et al. 2009). If these hypotheses are indeed true, they would have broad ecological implications: prey can be expected to favour complex backgrounds and larger-patterned prey should survive well in greater range of backgrounds. Also, the existence of these additional visual factors means that it is not possible to predict the survival of an animal based solely on the extent of its background matching.

As the natural environment is unlikely to comprise a single type of background, we determined the net survivorship of a range of prey in a hypothetical two-background habitat using trade-off curves. The first trade-off curve (Background 1 and 8; Fig. 6a) indicates that net survivorship of both specialists and generalists are comparable. Elements in Background 8 are more than double the size of those in Background 1 and hence the background-matching prey survived extremely well in one background but poorly in the other. On the other hand, mean search time for the generalist morphs (Morphs 2–7) falls

gradually on Background 1 but rises steadily on Background 8 as the element size class grows. Therefore, their net survivorships are similar to the specialists, forming a linear trade-off relationship analogous to that in Sherratt et al. (2007).

The second trade-off (Fig. 6b) provides empirical support for the hypothesis that a convex trade-off is more likely to occur in a two-background habitat when the difference between the two backgrounds is narrowed (Merilaita 1999; Sherratt et al. 2007). When the element size class difference between the two backgrounds is decreased from 7 to 3 (i.e. from Backgrounds 1 and 8 to Backgrounds 3 and 6), generalists (Morphs 4 and 5) exhibit better overall survivorship than the specialists (Morphs 3 and 6), producing a convex survivorship curve as also seen in Merilaita et al. (2001). A convex trade-off is possible here in part because survivorship of size-mismatched prey do not drop markedly. It may be harder to obtain such trade-offs by manipulating other aspects of colour pattern. For example, the survivorship of colour contrast mismatched prey tends to fall steeply, producing a concave trade-off (Sherratt et al. 2007). In addition, in our study, some elements on a morph or in a background could also be found in the morphs and backgrounds of ± 2 ESC difference. Therefore, the generalist morphs, which had ESC differences of 1 and 2 to each background, are relatively well matched to the background, while the specialist morphs have very little to no common elements with one of the backgrounds.

Unlike previous camouflage experiments using humans as predators (e.g. Fraser et al. 2007; Sherratt et al. 2007; Cuthill and Szekely 2009; Hall et al. 2013; Webster et al. 2013; Espinosa and Cuthill 2014, with the exception of Todd et al. 2015), we utilised hundreds of volunteers, each of whom was presented with only one combination of morph and background. Even though this resulted in high variation in search time due to varying ability among participants to find the cryptic prey, our study presents robust evidence that survivorship of a background matching prey is affected by the degree of mismatch of pattern element size between itself and the background. The survivorship pattern is asymmetrical with larger element morphs on smaller element backgrounds being harder to find higher than the smaller element morphs on larger element backgrounds. Asymmetry patterns are not consistent among studies, suggesting that other visual factors interact with background matching and this is an area requiring additional research. In accordance with previous research (e.g. Merilaita et al. 2001; Sherratt et al. 2007), our findings indicate the evolutionary advantage of ‘generalist’ prey with compromised pattern size matching in a two-background habitat, as they performed similarly or better than specialised size matching prey. The advantage is especially pronounced when the range of pattern element sizes in the two backgrounds narrows. Together, our results suggest that, while it is important to match the background element sizes closely, perfect size matching is not necessarily the optimum strategy for prey survival. Instead, a generalist prey that uses visual factors beyond background matching may prevail.

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