Empirical tests of the role of disruptive coloration in reducing detectability

Stewart Fraser^{1,2}, Alison Callahan¹, Dana Klassen¹ and Thomas N. Sherratt^{1,*}

¹*Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario K1S 5B6, Canada*

²*School of Business Administration, Dalhousie University, 6100 University Avenue, Halifax, Nova Scotia B3H 3J5, Canada*

Disruptive patterning is a potentially universal camouflage technique that is thought to enhance concealment by rendering the detection of body shapes more difficult. In a recent series of field experiments, artificial moths with markings that extended to the edges of their ‘wings’ survived at higher rates than moths with the same edge patterns inwardly displaced. While this result seemingly indicates a benefit to obscuring edges, it is possible that the higher density markings of the inwardly displaced patterns concomitantly reduced their extent of background matching. Likewise, it has been suggested that the mealworm baits placed on the artificial moths could have created differential contrasts with different moth patterns. To address these concerns, we conducted controlled trials in which human subjects searched for computer-generated moth images presented against images of oak trees. Moths with edge-extended disruptive markings survived at higher rates, and took longer to find, than all other moth types, whether presented sequentially or simultaneously. However, moths with no edge markings and reduced interior pattern density survived better than their high-density counterparts, indicating that background matching may have played a so-far unrecognized role in the earlier experiments. Our disruptively patterned non-background-matching moths also had the lowest overall survivorship, indicating that disruptive coloration alone may not provide significant protection from predators. Collectively, our results provide independent support for the survival value of disruptive markings and demonstrate that there are common features in human and avian perception of camouflage.

Keywords: camouflage; crypsis; disruptive coloration; animal coloration; predation

1. INTRODUCTION

Natural prey species are thought to exploit a range of inter-related camouflage techniques to avoid being detected by predators (Ruxton *et al.* 2004; Caro 2005). For example, many prey species have evolved to match their surroundings by adopting colour patterns that represent a more or less random sample of their background (‘background matching’ or ‘crypsis’; Endler 1978, 1984). Other species have evolved a close resemblance to non-random yet inedible elements of their environment, such as leaves or rocks (Allen & Cooper 1985). Intriguingly, many camouflaged prey (including species of mollusc, crustacean, insect, snake, fish, bird and mammal) also exhibit high-contrast markings (‘disruptive patterns’; Thayer 1909; Cott 1940; Silberglied *et al.* 1980; Merilaita 1998; Behrens 2002; Cuthill *et al.* 2005, 2006; Sherratt *et al.* 2005). Following Thayer (1909) and Cott (1940), these markings are thought to create false boundaries and/or obscure existing ones, thereby rendering detection of characteristic shapes more difficult. More recent analyses have confirmed that disruptive markings can indeed make inferences related to prey shape more challenging to observers (Osorio & Srinivasan 1991; Stevens & Cuthill 2006).

Long appreciated by ecologists and artists, the military around the world have also exploited disruptive patterns and other biological solutions to camouflage for

well over a century. Yet despite its widespread application, it is only recently that ecologists and evolutionary biologists have begun to test the effectiveness of disruptive coloration in the field, and to design experiments to distinguish between the benefits of background matching and disruptive coloration *per se* (Cuthill *et al.* 2005; Merilaita & Lind 2005; Schaefer & Stobbe 2006; Stevens *et al.* 2006). In an influential recent paper, Cuthill *et al.* (2005) pinned artificial moth-like prey, baited with mealworms, onto oak trees and evaluated their ‘survivorship’ over 24 h. In their main experiment, five different types of artificial moth were pinned out. Three of these moth types were brown and black, with the two colours and proportions chosen to match the colours of oak when printed onto triangular card (representing the moth’s ‘wings’). An ‘edge’ moth consisted of brown prey with black markings allowed to overlap their triangular border; an ‘inside 1’ moth was similar to edge except the black markings were displaced inwards from the edge, and an ‘inside 2’ moth consisted of prey with randomly selected markings with no edge overlapping; uniform brown and black moths were used as controls. Cuthill *et al.* found that the artificial moths exhibiting markings overlapping their edges (edge moths) survived significantly better than all the other forms, while the inside 2 moths on average survived significantly better than the inside 1 moths. The three bicoloured treatments all possessed life-sized pattern elements more or less

* Author for correspondence (sherratt@ccs.carleton.ca).

randomly sampled from the background, and hence should have been approximately equally cryptic in terms of background pattern matching. However, since edge treatments experienced a higher survival rate, their findings are consistent with the view that patterns help to reduce detection by preventing the recognition of characteristic body shapes, specifically through obscuring edges.

While Cuthill *et al.*'s work is some of the best to date to elucidate the adaptive significance of disruptive coloration, several reservations have been expressed. First, Cuthill *et al.* used colours that effectively matched their backgrounds, so the adaptive value of disruptive coloration is hard to evaluate completely independently of background matching. This limitation has recently been addressed by Merilaita & Lind (2005), Schaefer & Stobbe (2006) and Stevens *et al.* (2006), but, nevertheless, more work needs to be done (Endler 2006). For example, in generating disruptively patterned non-background-matching moths, Stevens *et al.* (2006) varied the lighter colour to create a non-matching treatment, but not the colour of the darker disruptive marks themselves. Moreover, only five different patterns were presented by Schaefer & Stobbe (2006), hence (as the authors note) their results strictly pertain to the specific colour patterns that were evaluated. Second, more importantly, in generating the 'inside' treatments in Cuthill *et al.* (2005) (see also Stevens *et al.* 2006), the density of the interior black patterns was concomitantly increased, raising the possibility that the edge treatments survived better than the inside treatments not because edges were obscured, but because they more closely matched their backgrounds in terms of pattern density. As Stevens *et al.* (2006) observe, 'inside treatments are more likely to have a greater concentration of markings close to the target midline'. Third, since mealworms were placed on top of the artificial moths, there is a possibility that differences in relative contrast between the mealworm and the interior of each moth type played some role in affecting their detectability. Both Cuthill *et al.* (2006) and Schaefer & Stobbe (2006) recognized this problem, and while both considered the effect to be small when compared with the edge effect (Schaefer & Stobbe (2006) had half-concealed their mealworm for this very reason), it remains a potentially confounding factor. Finally, as a field experiment, there was no direct control over the predators and therefore no direct recording of instances in which prey could have potentially been encountered is yet overlooked owing to the difficulty of detecting them. Conceivably, edge moths might be avoided not because they are less readily detected, but because they look more like a co-occurring natural species that has some form of defence.

In this paper, we have addressed each of the above challenges by developing a system in which humans forage for computer-generated moth-like prey. If the findings of Cuthill *et al.* (2005) are robust, then one might expect to uncover similar relationships in this very different system, while avoiding the problems produced by mealworms and being able to strictly control (and measure) the foraging environment. We also set out to introduce new controls with the inside patterns modified to control for pattern density and evaluate the effect of altering the extent of background matching in the darker

rather than the lighter part of the artificial moth. Human predators have frequently been used by researchers in studies of crypsis (e.g. Tucker & Allen 1993; Knill & Allen 1995; Glanville & Allen 1997; Sherratt *et al.* 2007) and good qualitative concordance has been found between the performances of birds and humans when conducting simple discriminative tasks (e.g. Ditttrich *et al.* 1993; Beatty *et al.* 2005). If the validity of the computer-based approach can be broadly established, then it offers a rapid, cheap and ethical way to screen ideas relating to the adaptive significance of camouflage.

2. MATERIAL AND METHODS

A 'Moth Finder' application was developed in JAVA to perform experiments based upon the fieldwork of Cuthill *et al.* (2005). Two different experiments were conducted using the same general protocols.

(a) *Creating the backgrounds*

To create backgrounds for our moth targets, 15 digital images of the trunks of different oak trees (*Quercus rubra* and *Quercus alba*) were taken using a Canon Powershot A520 Digital Camera. All the oak trees were photographed from approximately 2 m away, a distance chosen to fill the picture with the tree trunk. To minimize the variation in lighting conditions, all photographs were taken on the same sunny day, and a flash was not used due to ample ambient lighting. Each trunk was relatively uniform in appearance with no branches and minimal lichen. The images were saved as JPEG image files using ADOBE PHOTOSHOP v. 8.0 and cropped to 300 pixels wide $\times$ 400 pixels high, with 50 pixel wide white rectangles framing the image on either side. The 15 background images were vertically flipped and saved as new backgrounds, so that the same background images could be used for a greater number of backgrounds with less chance of the user recognizing repeated backgrounds.

(b) *The test targets*

Our experiment used some of the same target types that Cuthill *et al.* (2005) had used, but a new target type was added. As noted previously, the Cuthill *et al.* (2005) experiment created inside non-disruptive targets by moving the edge markings inwards to the centre. This was intended to reduce disruptive patterning, but had the inevitable and unintended effect of increasing the density of camouflage pattern of the inside targets. Here, we not only used the same high-density interior inside targets, but also added an inside target in which the interior density was controlled to be the same as that of the edge target. In addition, Cuthill *et al.* (2005) determined that high-contrast disruptive coloration was more effective than low-contrast disruptive coloration, but here we evaluated the success of a target type with high-contrast markings in which the markings do not match the surroundings.

The five target types presented were (figure 1):

Disruptive black. A high-contrast disruptive pattern using only the average colour and black, making it a poor background matcher.

Average colour. A poor background pattern matching monochrome target corresponding to the average colour of the background image.

Bicolour with edges (BCE). A disruptive pattern with good background matching.

Figure 1. Examples of the five target types designed for this experiment. A different set of five targets were produced for each of the 15 oak trees photographed (and repeated when the tree images were rotated).

Bicolour no edges with high-density centre (BCNE-high density). A non-disruptive pattern with good background matching.

Bicolour no edges with low-density centre (BCNE-low density). Also a non-disruptive pattern, but with better background matching than (iv) as a consequence of reduced interior density.

Thus, the high-density target had a higher interior density of camouflage pattern than the BCE target, whereas the low-density target had an interior density of camouflage pattern equal to that of the BCE target.

(c) Creating the targets

Five different tailor-made targets were made for each of the 30 images of trees (15 separate background images with two orientations). The average colour of the background was estimated using the histogram function in ADOBE PHOTOSHOP (v. 8.0), which reports the average values for the red, green and blue (RGB) components of the image over any prescribed area. The colour selection tool was then used to manually select the lighter half of the colours from the background image. This was accomplished by setting the colour selection tool to add new selected colours to a cumulative selection until approximately half of the image was selected. Once half the colours were selected, the histogram tool was used to determine the average light colour, as indicated by the average RGB values. The selection was then inverted to select the darker half of the background colours and the histogram tool was used to determine the average dark colour.

Once the average light and dark colours were determined, the background image was modified so that all the dark colours were replaced with the one average dark colour, and all the light colours were replaced with the one average light colour. The resulting image was a bicoloured background template that could be used to excise triangular targets with light–dark patterns that matched their specific backgrounds (see below). The histogram tool was used to ensure that the resulting bicoloured background template had the same averages for each of the colour components as compared to the background image it was created from. If any RGB component deviated from the original mean value by more than two points, the manipulated background template was discarded and the process was restarted.

The background matching targets were created using the bicolour image at a 1 : 1 ratio to obtain the same pattern size as the background. To create targets, a triangular area of the size of the target (38 pixels wide $\times$ 19 pixels high) was excised from a random location within the bicolour background image. To do this, the image surrounding the target was

deleted leaving the background transparent. The resulting target matched the background well and had edge markings that were suitable for the BCE target. The target image was saved as a GIF image, which is able to implement a transparent background. The same pattern was used to create the disruptive black targets by replacing the average light colour with the overall average colour, and replacing the average dark colour with black. The average colour targets were created by filling the entire target area with the average colour of the original background. Luminosity and RGB colour components were all approximately normally distributed, so that the average colours frequently occurred in the background.

The two non-disruptive bicolour no edges (BCNE) target types were created by modifying the BCE target in two different ways. The BCNE-low-density target was created by painting the average light colour over the average dark disruptive markings within a two pixel border from the edge, maintaining the same interior pattern density. The BCNE-high-density target was created by selecting the average dark colour edge markings using the colour wand and moving them inwards, ensuring that they were not moved on top of other average colour dark markings.

On average, therefore, our BCE target comprised 50% light and 50% dark pixels (362 pixels in total). To create the bicolour no edge ‘low’ density (BCNE-low), we simply turned any dark pixels distributed in the 104 pixel edge into light pixels. Therefore, while the *interior* density of the two treatment types was precisely the same (on average 50% light pixels), the BCNE-low had more light pixels *overall* due to the lightened edge (on average 64.4% light pixels). The bicolour no edge ‘high’ density (BCNE-high) involved moving dark pixels on the 104 pixel edge into the interior. In this case, the overall pattern density remained the same as the BCE (on average 50% light pixels), but the interior density had fewer light pixels (on average 29.8% light pixels).

(d) Experiment 1

The first experiment involved presenting human subjects with 60 backgrounds sequentially displayed on the computer screen. Limitations on the speed at which images could be processed into memory in the Applet meant that we had to re-use backgrounds, so that the 15 original and the 15 flipped background images were each shown twice in order to have enough backgrounds to display. A small latency is introduced as the targets are loaded into memory, which would cause flickering if the images were not preloaded. The program therefore loaded each image to be used during an initialization phase. A special background was displayed when all the images had been loaded, informing the test subject that the experiment was ready to commence.

The starting image and the subsequent sequence of backgrounds were pseudo-randomly selected. Of the 60 backgrounds presented, 20 randomly selected backgrounds did not have any target displayed. Eight instances of each of the five target types were presented upon the remaining backgrounds, and they were always placed on the specific background (oak image and orientation) to which they were matched (see below). There was a maximum of one target presented on each displayed background.

In any given foraging trial of 60 backgrounds, each human subject was presented with each of the five target types on four qualitatively different backgrounds over each of the two rounds. To ensure that the same moth image did not appear

in the same location on the background image, one version of the target was placed in the top half of the image and another version was placed in the bottom half (round order decided at random). To ensure independence, if a particular target type was displayed against a given background, then the remaining four target types in the specific series, from which the target was generated, were never displayed to the same human subject. The targets were randomly assigned every time the program was initialized to ensure that each target had an equal chance of being placed on any specific background in any given test.

Experimental data were collected from a total of 81 volunteer test subjects who were either physically present ($n=73$, the majority of whom were visitors to the Page Break Coffee Bar at MacOdrum Library in Carleton University, Canada) or students who participated over the Internet ($n=8$, Carleton students controlled so that no student played more than once). In all the cases, the game was designed to occupy 800×600 pixels regardless of screen resolution. The test subjects selected did not have any particular expertise in the field of crypsis and were not informed as to the hypotheses being tested. Our test subjects were instructed that the objective was to locate triangular 'moth' targets of a described size, that there would be at most one target per background, that some backgrounds might contain no target and that they had 5 s per background to find a target or move on. The test subjects simply clicked the mouse cursor directly over any targets they could see. A pleasant audio clip played if the test subject 'captured' a target, and a more downbeat audio clip played if the test subject clicked in area of background where there was no target. All successful finds were recorded by the computer program. Capture times (in hundredths of a second) for each target were recorded for 41 of the 81 test subjects (capture times for our first 40 subjects were recorded at too low a temporal resolution to be useful). If the user did not see any target, then they could click the 'Next' button bringing them to the next background. At the end of the 5 s time limit, the screen switched to an image informing the user that their time had expired (the vast majority of our subjects regularly moved on before the time limit expired, often erroneously concluding that there was no prey item present). Our test subjects continued foraging for moths until all the 60 backgrounds had been presented and the program informed them that they had finished. To enhance motivation, the program included a scoring system in which each target discovered was worth 10 points—a current score and a list of the current top 10 high scores was continually displayed.

(e) *Experiment 2*

Although sequential presentation is undoubtedly more realistic, one is not able to compare directly the detectability of the five target types against the same tree at precisely the same moment in time. A second experiment was therefore designed in which we presented the same targets as in the first experiment, except that all the five targets were presented simultaneously at different random locations on the same background. A total of 24 different human subjects (not people drawn from the pool of 81 subjects above) participated. The subjects were instructed to click as many targets as they could see within the 5 s time limit. They were not informed that there would be a total of 5 targets on each background. This experiment presented 15 backgrounds (all

in their original orientation), 12 of which had all the 5 targets, 3 of which had no targets. The survivorship, search times (in hundredths of a second) and the order of predation were recorded for each target presented.

3. RESULTS

(a) *Experiment 1*

A general linear model (GLM) was fitted to the number of targets attacked per target type per human subject, assuming that any potential variation in the cryptic quality of backgrounds would add noise but not confound the results given sufficient replication. The total number of the eight presented targets that were attacked varied significantly among type (fixed factor $F_{4,320}=82.53$, $p<0.0001$) and among human subjects (random factor $F_{80,320}=3.52$, $p<0.0001$). Tukey's HSD *post hoc* tests revealed that all the target types were attacked at significantly different rates from one another (all $p \leq 0.007$; figure 2a). Non-parametric Wilcoxon signed ranked tests (controlling for human subject) likewise confirmed that the attack rates on each target differed significantly from one another (all $p \leq 0.002$). The BCE target experienced the least predation. The bicoloured no edge patterns with a low-density centre (BCNE-low density) exhibited more predation than the BCE target, but less predation than the corresponding high-density version (BCNE-high density). The average colour target experienced high predation, but the disruptive black target experienced the highest predation, preyed upon in nearly every instance it was presented.

We also analysed the search time data from 41 of our 81 test subjects. Figure 2b shows the mean time per human subject (in seconds, ± 1 s.e.) taken to successfully locate and capture each of the target types. Missed targets were necessarily ignored for this analysis, and there were 5 cases out of 205 target–subject combinations, where none of a particular target type were detected by a volunteer. The main effects GLM on the (log transformed to equalize variances) mean detection time per target type again revealed a significant effect of target type (fixed factor $F_{4,155}=37.27$, $p<0.0001$) and human subject (random factor $F_{40,155}=3.75$, $p<0.0001$). Tukey's HSD tests confirmed that BCE target had the significantly longest mean detection time (all $p \leq 0.002$ in pairwise comparisons), while the disruptive black exhibited the shortest detection time (all $p < 0.0001$ in pairwise comparisons). Wilcoxon signed ranked tests on detection times confirmed that BCE had significantly longer, and disruptive black significantly shorter, detection times than all other target types (all relevant $p \leq 0.006$). The differences in detection times between BCNE-low density, BCNE-high density and the average colour target were not statistically significant on the basis of any *post hoc* test (all $p > 0.05$).

(b) *Experiment 2*

The main effects GLM showed that both target type (fixed effect $F_{4,92}=44.41$, $p<0.0001$) and subject (random effect $F_{4,92}=7.42$, $p<0.0001$) influenced the total number of targets of each type attacked (figure 3a). Tukey's HSD tests indicate that the greatest overall attack rates were on disruptive black and average colour target types, which formed a distinct homogeneous subset (all

Figure 2. (a) Mean number of prey items attacked (from eight of each target type presented) per subject ($n=81$ in all cases) and (b) overall mean time to attack a detected prey per item, for each target type in the single target experiment ($n=41, 40, 40, 39$ and 40 subjects for target types 1–5, respectively). Error bars represent ± 1 s.e.

$p \leq 0.036$ in pairwise comparisons with other target types). Similarly, the lowest attack rates were on BCE and BCNE-low density which themselves formed a homogenous subset (all comparisons with other types $p \leq 0.001$). The high-density BCNE targets were attacked at a statistically distinct (all $p \leq 0.036$) intermediate rate. Wilcoxon signed rank tests (controlling for subject) support this general conclusion (here, $p \leq 0.03$ from all pairwise comparisons).

The mean attack time for detected targets varied significantly among the target types (GLM, target fixed factor $F_{4,92}=34.68$, $p < 0.0001$) and subject (random factor $F_{23,92}=2.33$, $p < 0.003$; figure 3b). Tukey's HSD tests indicate that, when detected, disruptive black targets had the shortest mean attack times than all other targets (all pairwise comparisons $p < 0.0001$) and that average colour targets had shorter mean attack times than all other targets

Figure 3. (a) Mean number of prey items attacked (from 12 of each target type presented) per subject ($n=24$ in all cases) and (b) overall mean time to attack detected prey per item, for each target type in the multiple target experiment ($n=24$ in all cases). Error bars represent ± 1 s.e.

besides the former (all $p \leq 0.01$). Wilcoxon signed rank tests support this interpretation (all $p \leq 0.0002$ in pairwise comparisons with disruptive black targets; all $p \leq 0.002$ in pairwise comparisons with average colour targets).

4. DISCUSSION

Our results provide independent support for the contention that obscuring edges in prey reduce the overall detectability of prey items. This result was obtained using two-dimensional target moths without the potentially confounding effects of centrally placed mealworms which are challenging to eliminate in field experiments. Furthermore, through our control of the foraging environment, we were able to directly confirm that the result arose simply because subjects did not detect the target type as readily as other types and not owing to any post-detection preferences. These insights were possible

through the use of human subjects in our investigations, and an implication is that disruptive camouflage is not a consequence of any special feature of avian vision.

The mean total number of prey items of a given target type attacked was negatively (and approximately linearly) correlated to the time taken to successfully detect them (test whether the median of the distribution of correlation coefficients per subject differed from 0; experiment 1: Wilcoxon's $Z = -4.957$, $n = 41$, $p < 0.0001$; experiment 2: $Z = -3.829$, $n = 24$, $p < 0.0002$). This indicates that even among the subset of prey items that were successfully attacked, certain types were still harder to detect than others. Furthermore, the fact that experiments 1 and 2 produced parallel results in terms of the number of prey of each type attacked and the times taken to successfully detect each target type further emphasizes the robustness of these findings to variation in the way prey are presented.

The higher survivorship of our BCNE-low-density targets compared with the BCNE-high-density targets suggests that part of the reason why Cuthill *et al.*'s inside 1 treatment was vulnerable was its poorer interior background matching. However, by the same token, it is possible that our edge (BCE) targets may have been overall more difficult to detect than either of the two no edge targets, because the margins of the former matched their background more effectively. Cuthill *et al.* (2005) themselves carefully controlled for this possibility by including the inside 2 treatment (randomly placed markings that did not overlap with edges), explicitly recognizing that their inside 1 treatments (equivalent to our BCNE-high-density targets) could have created pattern elements with straight lines that enhance conspicuousness. While inside 1 moths had significantly lower survivorship than inside 2 moths in their experiments, both moth types had significantly lower survivorship than the edge moths (equivalent to our BCE targets). Combining insights from this experiment and ours leads us to suggest that inside 1 (BCNE-high density) targets were detected more readily than edge (BCE) targets in part owing to their less effective background matching in both their interior and margins, but that edge-disruptive markings provide an additional benefit above and beyond background matching.

Earlier studies have found that disruptively patterned prey items with close resemblance to the background survived better than parallel examples of cryptic prey that exactly matched the background but did not have their edges obscured (Merilaita & Lind 2005). Here, we find an opposite situation in which a moderate background matcher survived at a higher rate than the non-matching but disruptively patterned form. In our case, the lower survival of the high-contrast (disruptive black) edge treatment compared with the monocolour average clearly indicates that a reasonable degree of background matching of both component colours must also be involved if disruptive coloration is to provide a camouflage effect. Although both Schaefer & Stobbe (2006) and Stevens *et al.* (2006) proposed on the basis of their results that disruptive patterns are still effective even when some of the pattern elements do not match the background, the current results indicate that it is important to consider the specific degree to which pattern elements differ from their background. To take an extreme, if disruptive markings are highly conspicuous, then subtle differences

in where they are placed is likely to have little effect on the survivorship of the prey. Stevens *et al.* (2006) argued precisely this when they proposed that 'it does appear that disruptive patterns are maximally effective when all components match elements present in the background'. Therefore, although they are two fundamentally different processes (Ruxton *et al.* 2004), background matching and disruption may have an important yet asymmetrical inter-relationship; background matching can be effective in the absence of disruption, but disruption is only effective if there is at least some background matching.

The similarity of our results to Cuthill *et al.* (2005) not only supports the importance of disruptive markings in enhancing camouflage, but also suggests that human subjects are useful models in the screening of basic hypotheses related to camouflage. In some ways, this conclusion is not surprising, given the ubiquitous use of disruptive patterns by the military, hunters and artists. Future work might address whether disruptive patterning allows its carrier to exploit a greater range of habitats than an organism with only background matching, and whether search images for disruptively patterned prey can be developed by predators. A computer-based system such as the one employed here not only enables close control over the foraging environment, but it also potentially allows camouflage solutions to evolve when subjected to selection (see also Bond & Kamil 2002, 2006; Sherratt *et al.* 2007). If disruptive pattern solutions were introduced to this general approach, then we would have a unique set of tools for designing and identifying effective camouflage strategies in a wide range of contexts.

We thank the numerous volunteers at the Carleton University for their participation and happy smiles. The research was approved by the Carleton University Research Ethics Committee and conducted according to the guidelines set out in the Tri-Council Policy Statement on the Ethical Conduct for Research Involving Humans. We wish to thank Innes Cuthill and an anonymous referee for their extremely helpful critiques, while Graeme Ruxton and David Wilkinson also provided feedback on an earlier draft. Our research was facilitated by grants to T.N.S. from the Natural Sciences and Engineering Research Council of Canada, the Canada Foundation for Innovation and the Ontario Innovation Trust.

REFERENCES

- Allen, J. A. & Cooper, J. M. 1985 Crypsis and masquerade. *J. Biol. Educ.* **9**, 268–270.
- Beatty, C. D., Bain, R. S. & Sherratt, T. N. 2005 The evolution of aggregation in profitable and unprofitable prey. *Anim. Behav.* **70**, 199–208. (doi:10.1016/j.anbehav.2004.09.023)
- Behrens, R. R. 2002 *False colors: art, design and modern camouflage*. Dysart, IA: Bobolink Books.
- Bond, A. B. & Kamil, A. C. 2002 Visual predators select for crypticity and polymorphism in virtual prey. *Nature* **415**, 609–613. (doi:10.1038/415609a)
- Bond, A. B. & Kamil, A. C. 2006 Spatial heterogeneity, predator cognition, and the evolution of color polymorphism in virtual prey. *Proc. Natl Acad. Sci. USA* **103**, 3214–3219. (doi:10.1073/pnas.0509963103)
- Caro, T. 2005 *Antipredator defenses in birds and mammals*. Chicago, IL: University of Chicago Press.
- Cott, H. B. 1940 *Adaptive coloration in animals*. London, UK: Methuen.

- Cuthill, I. C., Stevens, M., Sheppard, J., Maddocks, T., Parraga, C. A. & Troscianko, T. S. 2005 Disruptive coloration and background pattern matching. *Nature* **434**, 72–74. (doi:10.1038/nature03312)
- Cuthill, I. C., Stevens, M., Windsor, A. M. M. & Walker, H. J. 2006 The effects of pattern symmetry on detection of disruptive and background-matching coloration. *Behav. Ecol.* **17**, 828–832. (doi:10.1093/beheco/arl015)
- Dittrich, W., Gilbert, F., Green, P., McGregor, P. & Grewcock, D. 1993 Imperfect mimicry—a pigeon's perspective. *Proc. R. Soc. B* **251**, 195–200. (doi:10.1098/rspb.1993.0029)
- Endler, J. A. 1978 A predator's view of animal color patterns. *Evol. Biol.* **11**, 319–364.
- Endler, J. A. 1984 Progressive background matching in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc.* **22**, 187–231.
- Endler, J. A. 2006 Commentary—disruptive and cryptic coloration. *Proc. R. Soc. B* **273**, 2425–2426. (doi:10.1098/rspb.2006.3650)
- Glanville, P. W. & Allen, J. A. 1997 Protective polymorphism in populations of computer-simulated moth-like prey. *Oikos* **80**, 565–571. (doi:10.2307/3546630)
- Knill, R. & Allen, J. A. 1995 Does polymorphism protect? An experiment with human “predators”. *Ethology* **99**, 127–138.
- Merilaita, S. 1998 Crypsis through disruptive coloration in an isopod. *Proc. R. Soc. B* **265**, 1059–1064. (doi:10.1098/rspb.1998.0399)
- Merilaita, S. & Lind, J. 2005 Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proc. R. Soc. B* **272**, 665–670. (doi:10.1098/rspb.2004.3000)
- Osorio, D. & Srinivasan, M. V. 1991 Camouflage by edge enhancement in animal coloration patterns and its implications for visual mechanisms. *Proc. R. Soc. B* **244**, 81–85. (doi:10.1098/rspb.1991.0054)
- Ruxton, G. D., Sherratt, T. N. & Speed, M. P. 2004 *Avoiding attack: the evolutionary ecology of crypsis, warning signals and mimicry*. Oxford, UK: Oxford University Press.
- Schaefer, H. M. & Stobbe, N. 2006 Disruptive coloration provides camouflage independent of background matching. *Proc. R. Soc. B* **273**, 2427–2432. (doi:10.1098/rspb.2006.3615)
- Sherratt, T. N., Rashed, A. & Beatty, C. D. 2005 Hiding in plain sight. *Trends Ecol. Evol.* **20**, 414–416. (doi:10.1016/j.tree.2005.05.010)
- Sherratt, T. N., Pollitt, D. & Wilkinson, D. M. 2007 The evolution of crypsis in replicating populations of web-based prey. *Oikos* **116**, 449–460. (doi:10.1111/j.2006.0030-1299.15521.x)
- Silberglied, R. E., Aiello, A. & Windsor, D. M. 1980 Disruptive coloration in butterflies: lack of support in *Anartia fatima*. *Science* **209**, 617–619. (doi:10.1126/science.209.4456.617)
- Stevens, M. & Cuthill, I. C. 2006 Disruptive coloration, crypsis and edge detection in early visual processing. *Proc. R. Soc. B* **273**, 2141–2147. (doi:10.1098/rspb.2006.3556)
- Stevens, M., Cuthill, I. C., Windsor, A. M. M. & Walker, H. J. 2006 Disruptive contrast in animal camouflage. *Proc. R. Soc. B* **273**, 2433–2438. (doi:10.1098/rspb.2006.3614)
- Thayer, G. H. 1909 *Concealing coloration in the animal kingdom; an exposition of the laws of disguise through color and pattern; being a summary of Abbott H. Thayer's disclosures by Gerald H. Thayer with an introductory essay by A. H. Thayer*. New York, NY: MacMillan.
- Tucker, G. M. & Allen, J. A. 1993 The behavioural basis of apostatic selection by humans searching for computer-generated cryptic “prey”. *Anim. Behav.* **46**, 713–719. (doi:10.1006/anbe.1993.1248)