Original Article

Revealed by conspicuousness: distractive markings reduce camouflage

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Animal camouflage is a textbook example of natural selection. Despite substantial progress, one historical theory remains controversial: that conspicuous "distractive" markings draw predator attention away from the prey outline, preventing detection. Here, we present evidence from 4 experiments to resolve this controversy. In field experiments, we measured bird predation on artificial cryptic prey that were either unmarked or had distractive markings of various attributes (number, color, and location). Prey with 3 high-contrast distractive markings, and with markings located away from the body outline, suffered reduced survival compared with unmarked controls or prey with low-contrast markings. There was no effect of small single markings with different colors on the survival of targets. In 2 computer-based experiments with human subjects searching for hidden targets, distractive markings of various types (number, size, and location) reduced detection times compared with controls. This effect was greatest for targets that had large or 3 markings. In addition, small and centrally placed markings facilitated faster learning. Therefore, these 2 experimental approaches show that distractive markings are detrimental to camouflage, both facilitating initial detection and increasing the speed of predator learning. Our experiments also suggest that learning of camouflaged prey is dependent on the type of camouflage present. Contrary to current and historical discussion, conspicuous markings are more likely to impair camouflage than enhance it, presenting important implications for the optimization of prey coloration in general. *Key words:* camouflage, conspicuousness, distraction, learning, predation, vision. *[Behav Ecol]*

INTRODUCTION

Camouflage has long been a classical textbook example of natural selection (Cott 1940; Stevens and Merilaita 2011), and a recent resurgence of interest in the subject has used camouflage as an important model system to test the molecular basis of adaptation (e.g., Rosenblum et al. 2004; Steiner et al. 2007; Manceau et al. 2011) and to understand mechanisms of visual perception (e.g., Kelman et al. 2007; Stevens 2007; Zylinski et al. 2009). In addition, substantial work over the last decade has sought to determine the survival advantage of different camouflage types and the attributes they require to work effectively (reviewed in Stevens and Merilaita 2009b, 2011). These experiments have found support for a number of previously untested hypotheses, such as disruptive coloration, self-shadow concealment and obliterative shading (via countershading), and motion dazzle (e.g., Hanlon and Messenger 1988; Cuthill et al. 2005; Merilaita and Lind 2005; Schaefer and Stobbe 2006; Stevens et al. 2006, 2008d, 2009b, 2011; Fraser et al. 2007; Kelman et al. 2007; Rowland et al. 2007, 2008; Zylinski et al. 2010; Scott-Samuel et al. 2011; Marples and Kelly 1999; Marples et al. 1998).

Background matching (where the animal matches the general appearance of the background; Stevens and Merilaita 2009b; Merilaita and Stevens 2011) probably provides the fundamental basis of camouflage in most animals. However, it has a crucial limitation; it leaves the outline and shape of the body intact, which presents salient cues for predator detection. It is, therefore, important to break up the appearance of the body outline. Perhaps, the most widespread means of doing so, and certainly the most effectively studied to date, is disruptive coloration. This consists of high-contrast patterns touching the body edge that break up the outline, and various experiments have shown that disruption is an important means of camouflage (reviewed by Stevens and Merilaita 2009a). An additional suggestion of Thayer (1909) to hide body edges concerns so-called distractive markings that "direct the 'attention' or gaze of the receiver from traits that would give away the animal (such as the outline)" (Stevens and Merilaita 2009b). Thayer (1909) suggested that small, conspicuous markings located away from the body edge conceal prey by drawing and holding ("distracting") predators' attention (e.g., pp. 151–152). Although distractive markings were once associated with disruptive camouflage and dazzle coloration (Cott 1940), they are now considered distinct strategies (Stevens and Merilaita 2009b). A key defining feature of distractive markings is that they comprise colors not found in the background or have contrasts in excess of features of the background; that is, they are conspicuous and are not markings that are a form of background matching (Stevens et al. 2008a). It is possible that some background-matching markings could promote distraction, but this seems unlikely because the key aim of background matching is to prevent rather than to encourage detection.

Although distraction may seem like a paradoxical idea, it may not be as illogical as it first appears because high-contrast markings have been shown to promote disruptive camouflage (Cuthill et al. 2005; Stevens et al. 2009b). The major caveat, however, is that disruptive markings seem to work best when

the level of pattern contrast does not exceed that found in the background (Stevens et al. 2006; Fraser et al. 2007), whereas distractive markings should have marking colors or contrasts that are not found in the general environment. Two mechanisms have been suggested by which distractive markings could work. First, Stevens (2007) suggested that distractive markings could work by a process akin to "crowding" or contour inhibition. Here, markings or "distractors" placed close to but not overlapping with a stimulus edge can interfere with processes such as lateral inhibition and where there is neuronal overlap between the target and the distractor, being especially effective when the distractors are of high contrast (Chung et al. 2001; Wertheim et al. 2006). This mechanism would favor distractive markings placed near (but not touching) the body margins. Alternatively, distractive markings may work by drawing predator attention ("attention" loosely defined) away from the body margins so that the predator does not detect the prey outline because its gaze is drawn to a small marking away from the body edges (Thayer 1909; Stevens et al. 2008a; Stevens and Merilaita 2009b). This mechanism would predict markings to be most effective when found nearer the centre of the object. Although no studies have investigated the potential presence of distractive markings in real animals, suggestions for candidate species include Lepidoptera, such as the bright streak on the camouflaged ventral wing surface of the comma butterfly (*Polygonia c-album*), the markings on the silver Y moth (*Autographa gamma*) (Dimitrova et al. 2009), the gold spangle (*Autographa bractea*), crescent moth (*Celaena* spp.), and the crescent dart moth (*Agrotis trux lunigera*). Caro (2011) suggests that the white tail tips frequently found in carnivorous mammalian grassland predators may act as distractive markings to reduce the preys' recognition of the stalking predator's main body. Numerous fish species display candidates for distractive markings as their names often allude to, such as the spot croaker (*Leiostomus xanthurus*), three spot gourami (*Trichopodus trichopterus*), the ticto barb (*Puntius ticto*), and the threespot dascyllus (*Dascyllus trimaculatus*). A possible reptilian candidate would be the black spot behind the eye of the green crested lizard (*Bronchocela cristatella*). Generally, potential distractive markings include isolated bright high-contrast spots or blotches (but generally not "eyespots," which are involved in deflecting or halting attacks that have already started; Stevens 2005), located away from the body edge and low in number, on otherwise background-matching bodies.

To date, only 2 experimental studies have tested distractive markings in camouflage, providing conflicting results. Stevens et al. (2008a) measured predation by wild birds on artificial camouflaged prey (printed triangles with an edible mealworm larva, *Tenebrio molitor*) pinned to trees in woodland. Prey targets with distractive markings survived worse than the unmarked controls, an effect that was exacerbated by increasing levels of marking contrast. These findings suggest that distractive markings are actually detrimental to survival.

Dimitrova et al. (2009) used captive blue tits (*Cyanistes caeruleus*) that were trained to search for artificial prey items on backgrounds with either high- or low-contrast patterns. Two prey types matched either the high- or low-contrast background patterns, and one prey type was a "generalist" pattern that matched both backgrounds. The blue tits found high-contrast prey items harder to detect than both the low-contrast and generalist targets, with all target types being harder to detect on the high-contrast background than the low-contrast background. The authors conclude that distractive markings on both prey and backgrounds facilitate concealment from predators.

These conflicting findings may have arisen through the different experimental approaches. Dimitrova et al.'s (2009) experiment was conducted under controlled conditions but did not replicate ecologically relevant viewing distances, search areas, or light conditions. However, there are additional problems with their experimental design that we consider here. First, all 3 prey treatments apparently had exactly the same geometrical pattern, with only the contrast of 2 shapes altered, so each subject was presented with just 3 targets. This pseudoreplication means we cannot extrapolate the results of their study to a treatment effect because any differences between the prey types could simply reflect something unique about the specific limited set of prey patterns used (Hurlbert 1984). Second, the training of blue tits during the study with all treatment types presented simultaneously could have led them to disregard contrast information entirely because it was not a salient predictor of the presence of a reward. Third, the patterns and contrasts used in their treatments violate the key defining features of distractive markings; 1) their markings did not exceed the contrast found in the background, and 2) they were of an identical shape and size to those found in the background; that is, their markings were essentially background matching (Stevens 2007; Stevens et al. 2008a). Fourth, Dimitrova et al. constructed their backgrounds by positioning geometric shapes, of which there were only 6 types used, all of a roughly uniform size, in a homogenous fashion. Thus, the low-contrast background is a good example of underdispersion in both spatial frequencies and contrast, which would rarely be found in a real-world foraging environment. This pattern choice means that the blue tits could have used a search strategy that was independent of the patterns and contrast on the triangular cardboard "prey," instead allowing them to search for any of these 6 standardized background shapes that were disrupted by the edge of the overlapping cardboard. Under this strategy, an increase in background contrast could effectively increase the number of background pattern types that must be compared for the detection of disrupted patterns.

To resolve this ongoing debate, we present findings from both field and computer-based experiments to test whether distractive markings are effective in concealment, and which factors influence their value. In 2 field experiments, similar to Stevens et al. (2008a), we tested the influence of distractive markings on "survival" of artificial prey items detected by wild birds. We tested the effect of marking color, proximity to the target edge, and contrast on survival. Comparing the survival of targets with distractive markings placed either near the body edge or near the centre also enabled us to distinguish between the 2 potential mechanisms for how distraction could work (see above).

Computer-based experiments tested the effect of distractive marking size, location, and number on both detection times and on the speed of predator learning (decrease in detection times across trials). Provided humans are not used to test the coloration of real species that have nonhuman predators, experiments conducted with human subjects offer a useful route to test general principles of antipredator coloration (e.g., motion dazzle; Stevens et al. 2008d, 2011; Scott-Samuel et al. 2011). In particular, work has confirmed the generality of results from field studies by using human subjects searching for similar camouflaged stimuli on computer screens (e.g., Fraser et al. 2007; Cuthill and Székely 2009). Dimitrova et al. (2009) criticized Stevens et al.'s (2008a) experiments on the basis that "birds were not familiar with the triangles and hence did not associate them with the mealworm." However, it is difficult to understand how their criticism is relevant because if the birds did not associate the mealworms as part of the camouflaged targets, then this would specifically predict that there would be no difference in survival between any of

the treatments (i.e., no difference in predation rate on the mealworms associated with the different target types). That Stevens et al. did find a difference between the treatments (as have numerous other similar studies; e.g., Cuthill et al. 2005; Schaefer and Stobbe 2006; Stevens et al. 2006, 2009b; Stobbe and Schaefer 2008) renders this criticism invalid. Nonetheless, a computer approach also offers a means to address this criticism because in computer experiments, no mealworm is needed and the subjects search solely for hidden targets.

Computer experiments also allow another major aspect of camouflage to be tested. To the best of our knowledge, learning effects have never been explored with regards to different types of camouflage before (e.g., background matching, disruption, distraction). Even though experiments have investigated search image formation and prey polymorphism (e.g., Bond and Kamil 2006), we are aware of no experiment addressing whether different types of camouflage facilitate or inhibit predator learning rates. All work so far investigating the relative value of different camouflage types has focused on initial detection; yet, if different types of camouflage markings are learnt at different rates, then this could have a major impact on the types of camouflage that evolve in the wild. We suggest that because distractive markings are inherently conspicuous, they may afford the observer a salient and reliable cue that would assist predator learning. We, therefore, suggest that distractive targets, even if beneficial or neutral regarding initial detection by naïve subjects, will be learnt more quickly and suffer a reduction in detection times over a sequence of trials with the same subjects. To test this, we compared detection times of both distractive and background-matching prey types and also the speed of learning (i.e., how detection times change for each treatment type over a series of trials).

MATERIALS AND METHODS

Field experiments

The methods followed previous field experiments investigating camouflage (e.g., Cuthill et al. 2005; Stevens et al. 2008a). Artificial prey targets were randomly pinned to ash trees (*Fraxinus excelsior*) at a height of 1–2 m in the mixed deciduous University of Cambridge Madingley Woods, Cambridgeshire, UK (0°3.2'E, 52°12.9'N). Artificial prey were triangular targets made from waterproof paper (HP LaserJet Tough Paper) printed with patterns designed in Adobe Photoshop Elements v.5 (Adobe Systems Inc., San Jose, CA) on a Hewlett Packard LaserJet 2605dn color printer at 300 dpi. A mealworm larva was pinned underneath each prey, partly projecting out (as Schaefer and Stobbe 2006), as an edible component. Both experiments comprised a randomized block design. Targets were pinned along nonlinear transects (i.e., not running in a straight line) approximately 1–8 m wide and 1–2 km long, in different regions of the wood for each block and using less than 5% of the available trees to minimize the risk of predation on more than one target by the same bird (Cuthill et al. 2005). The woodland has a range of avian species that attack such targets, but especially great tits (*Parus major*; see Stevens et al. 2008b). The targets were checked at an interval of 2, 4, 6, 24, 29 and 48h. Bird predation was classified as complete disappearance of the mealworm or when half or more than half of the mealworm was taken. Censored data (i.e., data where the target was removed from the study for reasons other than avian predation, but which can still be included in survival analysis up to the point of censorship; Cuthill et al. 2005) included surviving targets at 48h, complete target disappearance, and nonavian predation (spiders and harvestmen left an exoskeleton "shell," slugs left slime trails, and ants

were seen eating the mealworm). Experiments took place in July and August 2011.

Experiment 1: does the color of distractive markings influence survival?

Experiment 1 tested the role of distractive marking color on prey survival. As in Stevens et al. (2008a), prey targets (5.5 cm wide, 2.8 cm high) were made from random triangular sections of digital photographs (uncompressed TIFF files) of ash tree bark images taken with a Fuji Finepix S7000 camera in the same woodland at 1:1 reproduction. The printed stimuli were calibrated by taking reflectance spectra of the printed stimuli and irradiance spectra taken in the study site (using an Ocean Optics USB2000+ spectrometer with illumination by a PX-2 pulsed Xenon lamp), followed by modeling the photon catches of a blue tit's single and double cones (Hart et al. 2000). The criterion was simply that the modeled bird cone responses for the experimental stimuli were within the range of values measured from reflectance spectra of ash bark samples found in the study site ($n = 30$) (Cuthill et al. 2005). Neither the lichen-free tree backgrounds to which the targets were pinned or the artificial stimuli reflect much ultraviolet light (Cuthill et al. 2005).

There were 5 treatments, 4 of which had a 2 mm wide circular marking placed randomly but not touching the edge of the triangle (to avoid making the markings disruptive): red (R), blue (B), green (G), white (W), and an unmarked control (C) (Figure 1; see Supplementary Figure 1). The markings were slightly smaller than those used in Stevens et al. (2008a) (3 mm) because we sought to test not only if certain colors work in distraction but also if smaller markings to those used in previous work would have the same effect on survival. As with previous work, for each replicate set of targets, we used a different background sample and placed the distractive marking in a different location. The experiment comprised 8 blocks each with 10 targets per treatment (80 replicates per treatment, 400 stimuli in total).

Experiment 2: do marking contrast and location influence survival?

Experiment 2 tested the effect of distractive marking contrast and proximity to the target edge on prey survival. Prey targets were slightly larger than in experiment 1 (6.3 cm wide, 3.1 cm high) to allow enough space for 3 widely spaced markings. We aimed to test whether higher numbers of distractive markings could enhance camouflage by drawing and holding predator attention, or through a crowding effect (see INTRODUCTION). There were 6 treatments, 4 of which were marked, plus 2 unmarked controls: low-contrast marginal (LM), low-contrast centre (LC), high-contrast marginal (HM), high-contrast centre (HC), high-contrast control (CH), and low-contrast control (CL) (Figure 2a; see Supplementary Figure 3a).
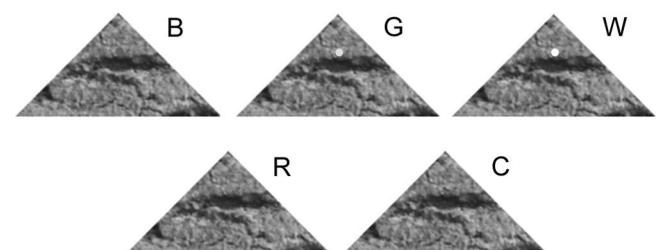

Figure 1
An example set of the 5 target types used in experiment 1. Control (C) and targets with red (R), green (G), white (W), or blue (B) distractive markings. See Supplementary Material for color version.
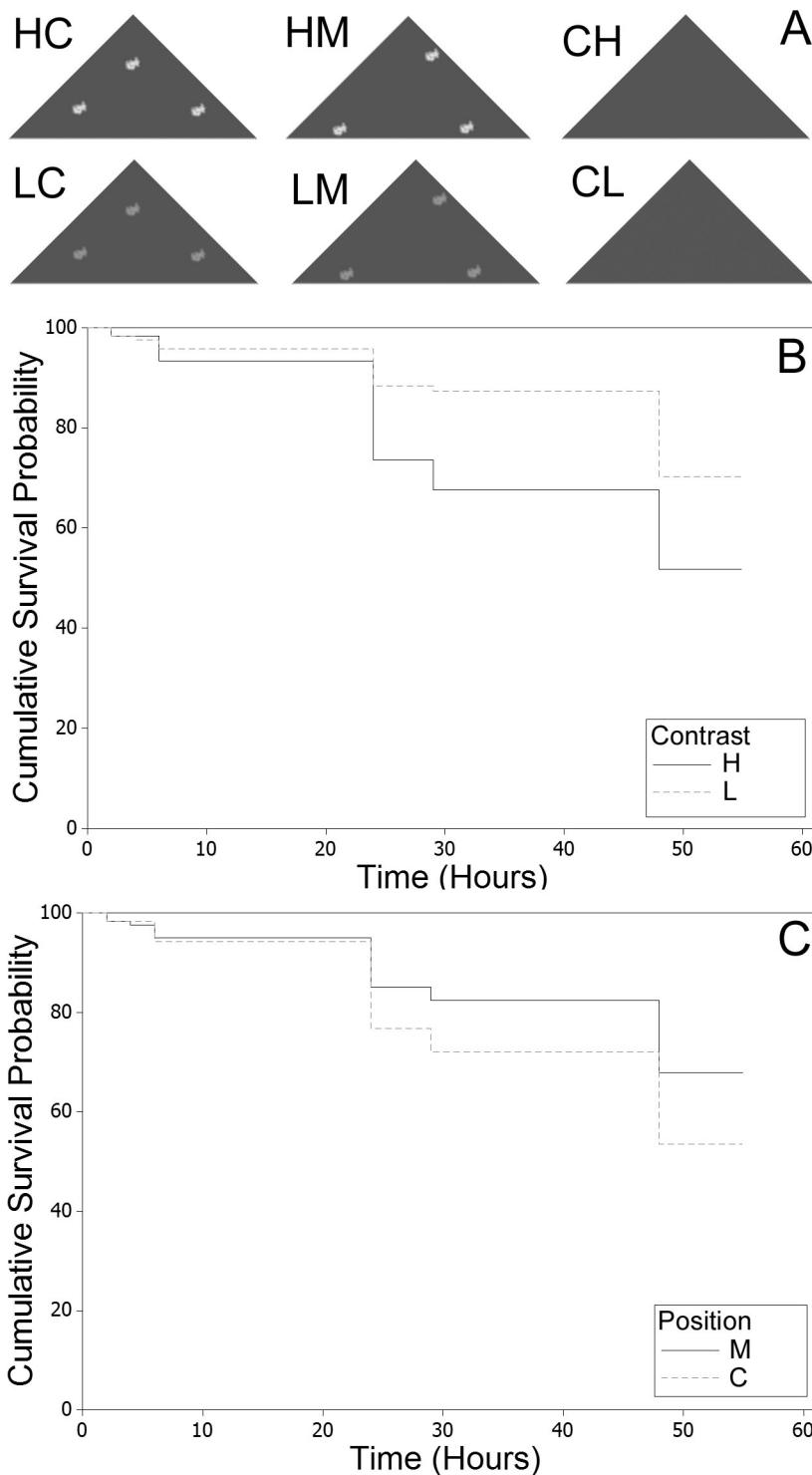
Figure 2
A. An example set of the 6 target types used in experiment 2. High-contrast control (CH), low-contrast control (CL), and targets with high-contrast distractive markings placed toward the target centre (HC) or toward the margins of the target (HM), and equivalent targets of low contrast (LC and LM). **B.** Nonparametric survival plot with curves being the probability of surviving bird predation over time for targets with high- or low-contrast distractive markings. **C.** Nonparametric survival plot for targets with distractive markings placed toward or away from the margins of the target. See Supplementary Material for color version.

The marked targets had a background color and luminance that fell within the range of ash tree bark in terms of bird photon catch values. Markings were irregular shapes extracted from the sample images of ash bark using the threshold selection ("Lasso") tool in Photoshop Elements v. 5.0 (Adobe Systems Inc.). We quantified the contrast of the markings with a log form of the Vorobyev and Osorio (1998) receptor noise model, using blue tit sensitivity values for the 4 single cones for color and the double cones for luminance contrast against ash bark. We used a Weber fraction value of 0.05 for the most abundant cone type and relative proportions of cone types in the retina for a blue tit (long wave = 1.00, medium wave = 0.99, short wave = 0.71, and ultraviolet = 0.37; Hart et al. 2000). A just noticeable difference (JND) of more than 1.0–3.0 means that 2 stimuli are discriminable (depending on the light conditions). The high-contrast markings were simply white (JND color and luminance contrast values against the target background color: 14.1, 23.5), whereas the color and luminance of the low-contrast markings fell within the range of ash bark photon catch values (JND color and luminance

contrast values: 3.2, 3.3). The low-contrast stimuli have discriminable markings but are not technically distractive (in terms of color and luminance at least) because they have values found in the background. The CH and CL matched the average values of the corresponding marked stimuli.

Marking proximity to the edge of the target was standardized using the measuring grid in Photoshop Elements to ensure consistency across replicate sets. Marginal markings were close to but not touching target edges, whereas more central markings were away from the edge but not clumped in the centre of the target, as this could increase the likelihood of detection. The experiment comprised 6 blocks with 10 replicates per treatment (60 replicates per treatment, 360 stimuli in total).

Statistical analysis

We used survival analysis for the field experiments, which can incorporate censored data and nonuniform changes in predation risk over time (as Cuthill et al. 2005 and subsequent experiments). We used nonparametric survival analysis, with Kaplan–Meier estimates for survival functions and a log-rank test statistic to compare survival curves (Stevens et al. 2009a). We used planned pairwise comparisons (Ruxton and Beauchamp 2008) to test between treatments (or sets of treatments), with no more tests than "spare" degrees of freedom, meaning that P-value correction was not required (see Stevens et al. 2009a). Such comparisons most effectively test our specific predictions. Effect sizes are odds ratios (OR) where a value of 1.00 indicates that 2 treatments have equal survival probabilities.

In experiment 1, we predicted that distractive markings of any color would be either costly (as Stevens et al. 2008a), or beneficial (as Dimitrova et al. 2009) versus the controls with no markings. Therefore, we compared each distractive treatment in turn against the control. In experiment 2, we compared sets of treatments that best reflected our aims: 1) all targets with low-contrast markings versus CL; 2) all targets with high-contrast markings versus CH; 3) all targets with high-contrast markings versus all targets with low-contrast markings; and 4) all targets with markings near the centre of the target versus all targets with markings located near the body margins. Therefore, comparisons 1 and 2 test whether high- or low-contrast distractive markings influence survival, and comparisons 3 and 4 test whether markings are more costly/beneficial when of either high or low contrast or placed away from or near to the body edge, respectively.

Laboratory experiments

Experiment 3: does the location of distractive markings influence detection times and learning?

In experiment 3, we presented 20 human participants (naïve to the experimental aims) with a series of frames on a touch-screen monitor (Elo 1515L 15 in.; Tyco Electronics, Shanghai) and asked them to locate the 3 motionless camouflaged targets, each presented against a series of natural background images. We presented all 3 treatment types together in each frame to replicate a natural foraging situation that directly pits the immediate "detectability" and the "learnability" of the different treatments over successive trials as perceived by a predator. Targets were triangles 150 pixels wide × 85 pixels high (40.2 × 22.6 mm, displayed at a 1:1 resolution, matching the monitor), from a distance of *ca.* 60 cm. Targets were constructed from random samples of the natural background that they were presented against (images of ash tree bark) and were modified to create the after treatments:

1) targets with a single marking placed somewhere in the central portion of the triangle comprising 50 white pixels in an irregular shape (centre); 2) targets with the same white marking placed toward the edge of the target, although not touching the edge (marginal), and 3) a control prey with no markings (Figure 3; see Supplementary Figure 5). One replicate of each treatment was presented in each frame. All targets were made using Inkscape release 0.48.2 and saved as portable network graphic (lossless compression) images with an alpha (transparency) channel and were scaled to match the resolution of the background image and monitor. Twenty unique background images were created from photographs of mature ash bark taken with a Fuji Finepix S7000 digital camera under natural lighting conditions in Madingley Wood, Cambridgeshire, UK. The resolution of the background images was reduced in Photoshop Elements to match the touch-screen monitor used to display them at 1280 × 1024 pixels, creating a 1:1 ratio with the monitor when displayed full-screen, and saved as uncompressed TIFF images. One set of targets was created for each of the 20 background images used (i.e., 20 different replicate sets of targets). For a given replicate set of targets, the background sample was identical, and only the presence and location of a distractive marking differed between them. The location of the distractive markings differed across replicates.

The experiment was created in Multimedia Fusion (version 2.0, Build R239; Clickdream 2006). Targets were positioned randomly in each frame, subject to the constraints that the centre of each did not fall within 100 pixels of the edge of the screen, or within 200 pixels of the centre of another prey item, ensuring there could not be overlap between targets. Participants were asked to touch the targets as soon as they located them; these were classed as successful "captures," resulting in that prey's immediate disappearance. The experiment progressed to the next frame 2 s after all 3 prey were successfully captured (i.e., the participant touched the target), or after a timeout of 30 s from the start of the trial if all prey were not found. Misses were recorded but did not affect the progression to the next frame. Frames were presented in a pseudorandom order so that each of the 20 participants received one of the 20 different background types as their first frame. The remaining 19 frames were presented in a crossed and balanced sequence ensuring that all frames had a uniform temporal distribution across the entire experiment. The timing (to the nearest hundredth of a second) of the participants' screen taps was recorded by the software.

Experiment 4: does the size and number of distractive markings influence detection times and learning?

Experiment 4 followed the general methods described for experiment 3. However, the 20 (new) participants were presented with 4 prey items in each frame, and the frame time-out was increased to 40 s (owing to 4 rather than 3 stimuli). The 4 targets presented were new samples of the same ash-bark background images used in experiment 3, modified to create the following treatments: 1) targets with a single irregularly shaped white marking 49 pixels in area (single), 2) targets with three markings 49 pixels each, distributed over the triangle (three), 3) targets with a single marking of the same area as three markings (147 pixels) (large), and 4) an unmarked control (Figure 3; see Supplementary Figure 5). In all instances, markings were placed randomly within the bounds of the prey item, without touching the edge. As with experiment 3, each background had a new replicate set of targets, and the design was balanced across subjects to control for order effects.
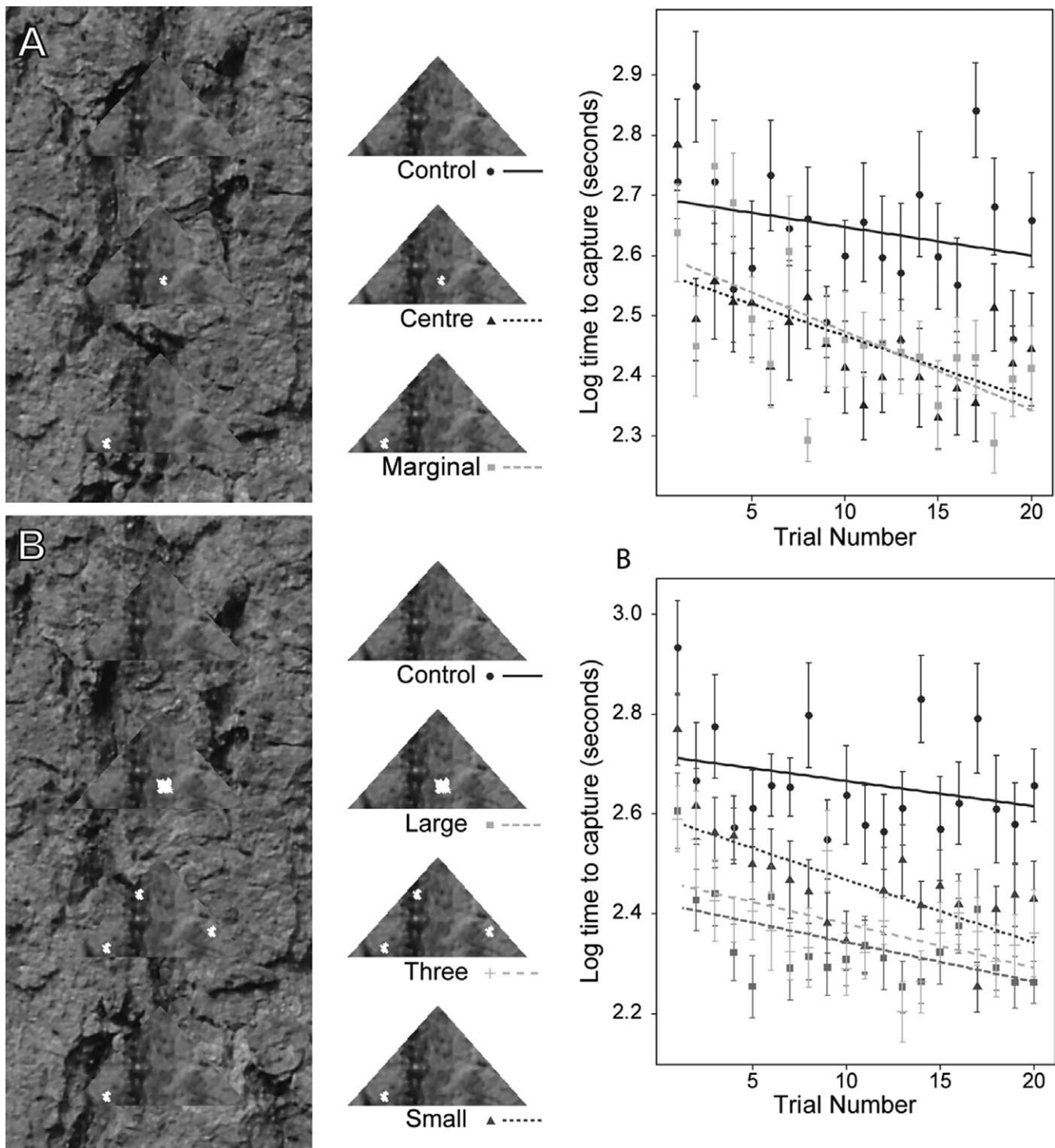
Figure 3

Example targets of the treatments used in Experiments 3 and 4 (panels A and B, respectively); targets are shown against a small subsection of natural ash bark background (left) or on their own (centre). Plots (right) show the time to detect each treatment type with regression lines highlighting the decline in detection times more than 20 trials; error bars show mean ± 1 standard error of the mean. See Supplementary Material for color version of figure.

Statistical analysis

Statistical analyses were performed in R version 2.12.2 (R Development Core Team 2011). We analyzed data using generalized linear mixed modeling (GLMM) due to the repeated measures within random nested factors (participants) utilizing

the lme4 package (version 0.999375–42) with a Gaussian error structure and a REML approximation. Note that GLM and GAM analyses assume that data are independent, an assumption that is violated in an experiment where repeated measures and nesting of random factors are required (Zuur et al. 2009). In mixed models using residual maximum likelihood

estimates, one cannot assume that the F statistics follow an F distribution; therefore, these values are not provided. Instead, confidence intervals and *P*-values could be generated from lme4 REML-generated models by using a Markov chain Monte Carlo (MCMC) method implemented using the language R package version 1.2, using the pvals function with 10 000 model iterations (Baayen et al. 2008). Detection time (the response variable, based on the time taken to "capture" a target after the start of the trial) was found to have a normal (Gaussian) error distribution following a log transformation in both experiments. The timeout feature of the software created a theoretically bounded response variable; however, participants rarely failed to find all targets in the time allowed ($n = 15$ and $n = 17$ failed detections out of 400 trials in experiment 3 and 4, respectively). Full interaction terms with explanatory variables treated as random and fixed effects (if applicable) were run initially, with nonsignificant interaction terms dropped if the model Akaike information criterion (AIC), a measure of relative goodness of fit, was lower following their removal (Zuur et al. 2009). Participants were modelled as random effects on the intercept in all models; trial number was initially included as a random effect on the slope of the error, and as a continuous fixed effect, background type was treated as a random effect on the intercept and as an additional fixed effect in full models (Crawley 2005).

RESULTS

Experiment 1: does the color of distractive markings influence survival?

There was no significant effect of treatment ($x = 1.253$, degrees of freedom [df] = 4, $P = 0.869$; see Supplementary Figure 2), but there was of block ($x = 216.107$, df = 7, $P < 0.001$) on survival. Planned pairwise comparisons showed no significant differences in survival between the following treatment pairs: unmarked control versus distractive white ($x = 0.168$, df = 1, $P = 0.682$, OR = 1.079), control versus red ($x = 0.257$, df = 1, $P = 0.612$, OR = 0.912), control versus green ($x = 0.024$, df = 1, $P = 0.877$, OR = 1.083), and control versus blue ($x = 0.171$, df = 1, $P = 0.679$, OR = 0.870). Overall, the distractive markings did not influence survival.

Experiment 2: do marking contrast and location influence survival?

There was a significant effect of treatment ($x = 19.566$, df = 5, $P = 0.002$) on survival (see Supplementary Figure 4), but not of block ($x = 2.504$, df = 5, $P = 0.776$). Planned pairwise comparisons showed no significant difference in survival between CL and low-contrast distractive targets ($x = 0.012$, df = 1, $P = 0.911$, OR = 0.967) or between CH and high-contrast marked targets ($x = 3.601$, df = 1, $P = 0.058$, OR = 0.626), although the latter showed a strong trend toward significance and the OR indicates a very strong difference in survival probability, with the CH targets being 1.6 times more likely to survive than targets with the high-contrast distractive markings. Targets with high-contrast markings survived significantly worse than targets with low-contrast markings ($x = 9.976$, df = 1, $P = 0.002$, OR = 1.900; Figure 2b; see Supplementary Figure 3b), and targets with markings away from the edge survived significantly worse than targets with markings closer to the edge ($x = 4.931$, df = 1, $P = 0.026$, OR = 0.642; Figure 2c; see Supplementary Figure 3c). Overall, distractive markings did not influence survival when of low contrast (and especially when near the target edge) but were costly to survival when of high contrast and near the target middle.

Experiment 3: does the location of distractive markings influence detection times and learning?

Both distractive treatments (marginal and central) had shorter detection times than the control (Figure 3; see Supplementary Figure 5). The interaction between trial and treatment shows that participants learnt to capture the central distractive target type significantly faster than the control (reduction in detection times over trials) (GLMM model: *logCaptureTime ~ Treatment* ($n = 3$) * *Trial* ($n = 20$) + (*1|Participant* [$n = 20$]) + (*1|Background* [$n = 20$]); $P = 0.045$), although there is only a nonsignificant trend for shorter detection times of the central distractive target type across all trials compared with the control ($P = 0.065$). The targets with marginal distractive markings were captured significantly faster (shorter detection times) across all trials than the control ($P = 0.013$). However, there was no difference in the rate of learning between the control treatment and targets with marginal markings ($P = 0.157$). Removal of the interaction term from the previous model improves the model fit (based on AIC) and reveals a highly significant difference in capture rates across all trials between control and marginal ($P < 0.001$), and control and central ($P < 0.001$). There is an overall significant reduction in capture time across all treatments as the experiment progressed (i.e., as trial number increases; $P < 0.001$).

Experiment 4: does the size and number of distractive markings influence detection times and learning?

All 3 distractive treatments (small, large, and three) were captured faster than the plain control (Figure 3; see Supplementary Figure 5) (GLMM model: *logCaptureTime ~ Treatment* ($n = 4$) * *Trial* ($n = 20$) + (*1|Participant* ($n = 20$)) + (*1|Background* ($n = 20$)); *P*-values compared with the control: small $P = 0.006$, large $P < 0.001$, three $P < 0.001$). The small distractive targets took significantly longer to detect than the large and three treatments ($P < 0.001$ and $P = 0.004$, respectively), but there was no evidence for a difference between the large and three prey types ($P = 0.310$). The rate of learning for the small treatment was significantly greater than the control ($P = 0.042$), although there was no significant difference for the small distractive target type compared with the large and three treatments ($P = 0.202$ and $P = 0.294$, respectively). There was no support for a difference in learning rate between the control and large ($P = 0.4484$), or control and three treatments ($P = 0.324$). There is an overall significant reduction in capture time across all treatments as the experiment progressed (i.e., as trial number increases; $P = 0.003$).

DISCUSSION

Here, we present a body of experimental data from both the laboratory and field that shows no support for the efficacy of distractive markings in reducing prey capture. Distractive markings were either neutral or costly to survival in experiments measuring predation by wild birds against artificial targets. This finding was replicated in computer experiments with human subjects trying to detect hidden targets. Additionally, these experiments highlighted a further cost of distractive markings; that they facilitated faster learning compared with controls.

Increased marking contrast was found to reduce survival of artificial prey taken by wild birds. This is in accordance with a previous field study of distractive markings (Stevens et al. 2008a) and is consistent with studies investigating disruptive coloration, which show reduced survival of artificial prey with disruptive markings when they have contrasts that exceed

those found in the background (Stevens et al. 2006; Fraser et al. 2007; Stobbe and Schaefer 2008). Work investigating paired circular spots also shows that they are detrimental to camouflage (Stevens et al. 2008c). Therefore, evidence consistently indicates that contrasts exceeding those found in the background reduce camouflage. However, our results contradict the findings of Dimitrova et al. (2009), who found that higher contrasting patterns in both prey and background improved survival of artificial moths presented to captive blue tits. The discrepancy in these finding could be due to a number of shortcomings in the experimental design used by Dimitrova et al. (see INTRODUCTION). The use of multiple background patterns on our artificial prey and randomized distractive marking shapes eliminates the problems of pseudoreplication in Dimitrova et al. Furthermore, Dimitrova et al. pretrained their subjects to find the artificial prey, potentially encouraging them to disregard contrast information and simply search for background shapes that were semi-covered. Our wild avian predators had no prior experience of the prey and viewed them against a natural background where a background shape search strategy could not be used. We, therefore, believe that our findings offer a more ecologically plausible assessment of the efficacy of contrast in distractive markings.

Although we found no evidence for a difference in survival dependent on distractive marking color, the size of our markings may have been too small for the birds to resolve at typical foraging distances. This indicates, as would be expected logically, that small markings do not substantially affect survival even with novel colors or nonmatching contrasts.

Both computer-based experiments support previous (Stevens 2008a) and present field experiments in finding that distractive markings of various types reduced detection times. This could indicate why, despite some suggested candidate species, examples of potential distractive markings in real animals are rare. An alternative approach would be to investigate the coloration of real animals with potentially distractive markings (such as those species described above) to test whether the markings comprise colors or contrasts absent from the natural resting backgrounds. However, even if this were to be found, manipulative experiments would still be needed to demonstrate that the markings do function in distraction as opposed to working in other ways (e.g., signaling or during movement). Furthermore, in this paper, we have focused on distractive markings defined in terms of color and luminance. However, spatial and temporal characteristics of animal coloration are also important (see Rosenthal 2007), and there may be other types of marking that may be worth investigating as potentially distractive, such as markings that deviate from the spatial orientation of patterns in the background.

The location of distractive markings in relation to the preys' body edge was found to have a significant effect on the survival of artificial moths in the wild, being more costly when located further from the margins. In addition, humans learnt to find prey faster when distractive markings were located further from the body edge in comparison to controls or targets with markings nearer the body edges; that is, subjects' search times decreased most quickly for targets with more centrally placed distractive markings. These results go firmly against the idea that distractive markings could work by attracting the predator's "attention" away from the body edges, as Thayer (1909) proposed. It is possible that shifting the 3 markings away from the artificial prey margins in experiment 2 increased the concentration or regularity of markings near the middle of the body, decreasing background matching further. However, this is unlikely to be the sole reason for the poorer survival of this treatment because the displacement

was relatively small and cannot explain the learning rate difference of participants in experiment 3, where targets had a single distractive marking. The poorer survival of targets with centrally placed markings may occur because these give a more reliable cue as to the location of a target, being consistently nearer the body centre. This would also explain the faster learning rate of such prey types. In addition, more peripherally located markings could produce a disruptive effect. Our targets in experiment 2 were different from previous stimuli investigating disruptive coloration (e.g., Cuthill et al. 2005; Stevens et al. 2006), in that our current prey had markings that were low in number (just 3 spots) and were not touching the body margins. However, although our markings did not touch the edge, when viewed from a distance, they may have been close enough to produce some aspect of disruptive camouflage. It would be valuable to investigate this using a model of spatial vision, given that exploitation of mechanisms in visual processing for spatial information may underlie the effectiveness of different camouflage types and their relationship to each other (Rosenthal 2007; Stevens 2007). However, we note that there was no survival advantage of these targets over the controls.

In both computer-based experiments, at least one of the treatment types with distractive markings incurred a decline in detection times that was faster than for the controls. We suggest that subjects formed a search image for these distractive treatments, and that, as has often been proposed, the formation of a search image for one prey type diminished the ability of subjects to form a search image for another pattern type (e.g., Guilford and Dawkins 1987). Such an effect has previously been discussed for prey of the same type (background matching) but with different specific patterns. We propose that some camouflage types may facilitate search image formation and suggest that this is a major avenue for future research. For example, prey with high-contrast markings, such as disruptive camouflage, may provide predators with more reliable cues for learning and facilitate search image formation more readily than other camouflage types. Such costs may offset the benefit of some camouflage types in preventing initial detection. For example, disruptive coloration provides a survival advantage over and above background matching (Cuthill et al. 2005; Stevens et al. 2006; Fraser et al. 2007), but may be learnt more readily than background-matching patterns. Conversely, disruptive coloration could be beneficial in preventing both initial detection and predator learning if it defeats both object segmentation and reduces salient cues for learning. Potentially distractive markings on the other hand, based on this study, seem to promote both detection and learning. This suggests a double cost to having isolated high-contrast markings in camouflage. Overall, the specific camouflage types observed in nature may reflect outcomes of both these factors, warranting further attention and differentiation in future studies.

Much discussion in the past has suggested that high-contrast distractive and disruptive camouflage could afford a dual benefit with communication strategies such as aposematism and sexual signaling (e.g., Stevens and Merilaita 2009a). This could include distance-dependent camouflage and signaling, as possibly exists in some fishes, for example (Marshall 2000), and this merits greater work with regards to different types of camouflage. Generally, however, it seems, as with other types of markings such as banding and striped patterns used in motion dazzle (Stevens et al. 2011), that there exists a classical trade-off between possessing nonmatching signaling colors and patterns conferring effective camouflage. It may be that in those species where high-contrast markings are found

that the benefits of these markings in other functions (e.g., warning or sexual signals) outweigh the costs of increased detection. However, this cannot explain our current results because this would predict a greater survival of high-contrast stimuli with distractive markings not found in the background environment. In general, to understand how camouflage and signaling may relate or conflict with one another, we need to determine not just how different types of camouflage work but also how signals have evolved to optimize conspicuousness in complex natural environments (Rosenthal 2007). However, at present, there remains little evidence that, for a given viewing distance and visual system, animals can achieve a dual function of conspicuous signals and camouflage with the same coloration.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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