

Keeping the band together: evidence for false boundary disruptive coloration in a butterfly

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Keywords:

Anartia fatima;
camouflage;
coloration;
crypsis;
false edges;
pattern;
plasticine models;
predation.

Abstract

There is a recent surge of evidence supporting disruptive coloration, in which patterns break up the animal's outline through false edges or boundaries, increasing survival in animals by reducing predator detection and/or preventing recognition. Although research has demonstrated that false edges are successful for reducing predation of prey, research into the role of internal false boundaries (i.e. stripes and bands) in reducing predation remains warranted. Many animals have stripes and bands that may function disruptively. Here, we test the possible disruptive function of wing band patterning in a butterfly, *Anartia fatima*, using artificial paper and plasticine models in Panama. We manipulated the band so that one model type had the band shifted to the wing margin (nondisruptive treatment) and another model had a discontinuous band located on the wing margin (discontinuous edge treatment). We kept the natural wing pattern to represent the false boundary treatment. Across all treatment groups, we standardized the area of colour and used avian visual models to confirm a match between manipulated and natural wing colours. False boundary models had higher survival than either the discontinuous edge model or the nondisruptive model. There was no survival difference between the discontinuous edge model and the nondisruptive model. Our results demonstrate the importance of wing bands in reducing predation on butterflies and show that markings set in from the wing margin can reduce predation more effectively than marginal bands and discontinuous marginal patterns. This study demonstrates an adaptive benefit of having stripes and bands.

Introduction

Predators can exert strong selective pressure on prey to go undetected and not become a meal. These pressures have led to many adaptations for concealment, including motion dazzle, masquerading and crypsis (Stevens & Merilaita, 2009a). Cryptic coloration prevents the detection of an object and can be achieved in many ways, ranging from distractive markings to background matching and disruptive coloration (Cott, 1940; Stevens & Merilaita, 2011). Although background matching involves colour patterns that match the spectral and spatial properties of the background, disruptive col-

oration utilizes contrasting markings that create false edges and/or boundaries, therefore hindering the detection and recognition of an object's true shape (Thayer, 1909; Cott, 1940; Stevens & Merilaita, 2009b). Although biologists since the early 1900s have stated the importance of disruptive coloration in fostering camouflage and survival, many components of the mechanisms of disruptive coloration are not well understood (Ruxton *et al.*, 2004; Stevens & Merilaita, 2009b).

Until recently, biologists accepted Thayer's (1909) and Cott's (1940) definitions of disruptive coloration despite empirical data. Fortunately, the last decade has seen several theoretical reviews clarifying the definition of disruptive coloration, along with a surge in empirical work testing its function and mechanisms (Cuthill *et al.*, 2005; Endler, 2006; Stevens *et al.*, 2006; Stevens, 2007;

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Stobbe & Schaefer, 2008; Dimitrova *et al.*, 2009; Stevens & Merilaita, 2009a,b). We now have a better understanding of how contrasting markings on potential prey affect predation. Marginally located contrasting markings that engender false edges may be optimal for decreasing predator detection as shown in studies utilizing artificial prey items or with human observers viewing artificial prey items on computer screens (Cuthill *et al.*, 2005; Stevens *et al.*, 2006; Webster *et al.*, 2013). In fact, because several studies using nonanimal models (e.g. triangular paper models with mealworm baits) demonstrated how important conspicuous marginal patterns were, some revised definitions of disruptive coloration state that contrasting patterns must be marginally located (Stevens *et al.*, 2006). However, several reviews have stated the importance of understanding how contrasting patterns that lie within the surface (i.e. centrally as opposed to the periphery) of the animal, such as stripes and bands, may function to reduce recognition and detection of an object (Hanlon *et al.*, 2009; Stevens & Merilaita, 2009a,b).

Stripes and bands (markings parallel and perpendicular, respectively, to the length of the body part on which they are located) can decrease predation in many ways, such as aposematism, motion dazzle, background matching and disruptive coloration (Ruxton *et al.*, 2004; Stobbe & Schaefer, 2008; Hanlon *et al.*, 2009; Stevens & Merilaita, 2009b). Many nonaposematic, sexually monomorphic animals across diverse taxa exhibit conspicuous stripes and bands that cannot be explained functionally as motion dazzle or background matching. Although motion dazzle coloration requires conspicuous stripes, bands or markings, it also requires movement, which together with the markings makes perception of speed and direction of movement difficult for a viewer to follow, and is especially effective when the animal is moving through vegetation (Stevens *et al.*, 2011). There are many cases of animals that exhibit stripes and bands that do not appear to match the background, possibly making them vulnerable to predation when not in motion (Fig. 1; see Cott,

1940 and Stevens & Merilaita, 2011). Therefore, it is likely that stripes and bands that are located centrally on flat surfaces (e.g. wing) with minimal marginal contact function disruptively by creating false boundaries that render the object unrecognizable to predators as hypothesized by Cott (1940) and later more fully developed by Stevens & Merilaita (2009b).

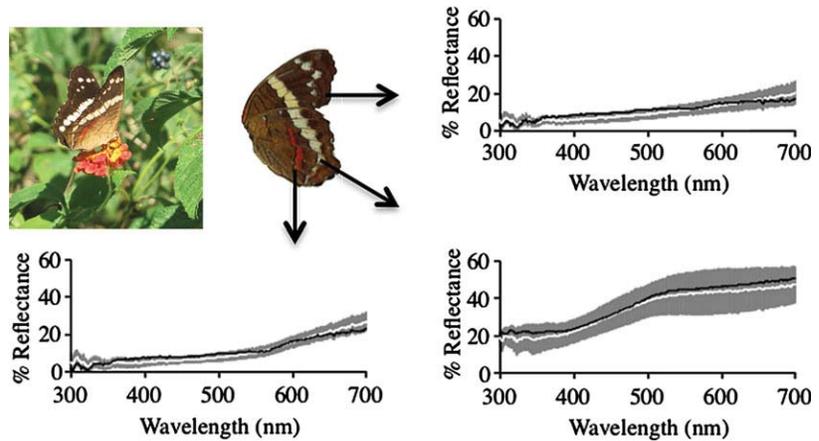
Current research indicates that both marginally located contrasting markings and internally located contrasting ones can serve a protective function because predators perceive them as independent objects that divide the whole object into visually unconnected portions (Osorio & Srinivasan, 1991; Merilaita, 1998; Cuthill *et al.*, 2005; Merilaita & Lind, 2005; Schaefer & Stobbe, 2006; Fraser *et al.*, 2007; Stobbe & Schaefer, 2008; Stevens *et al.*, 2009; Webster *et al.*, 2013). Stevens *et al.* (2009) demonstrated maximum survival benefits for artificial prey that have high internal (centre of wing) contrast and low marginal contrast compared to artificial prey that have homogenous contrast, and artificial prey with low internal contrast and high marginal contrast. However, there are very few tests of the functional differences between marginally and internally located markings using naturally coloured animals (Stevens & Merilaita, 2009b). Here, we test whether false boundaries produced by a butterfly wing band increase or reduce survival more than if the individual had a broken marginal band creating a false edge, or a continuous band located marginally. A continuous band on the margin of the animal removes the false boundary effect and instead should emphasize the outline of the animal and render it more detectable (Endler, 1984; Ruxton *et al.*, 2004).

We used *Anartia fatima* (Fabricius) (Nymphalidae), the banded peacock butterfly, to test the hypothesis that false boundaries produced by centrally located contrasting bands increase an individual's chance of survival. *Anartia fatima* has a conspicuous yellowish to cream-coloured band set against a dark brown background on both the dorsal and ventral surfaces of the hind and forewings (Fig. 2). This colour pattern serves



Fig. 1 Examples of putative false boundary disruptive coloration across taxa (Cott, 1940). From top left clockwise: Giant Anteater (*Myrmecophaga tridactyla*), Common Snipe (*Gallinago gallinago*), Common Field Grasshopper (*Chorthippus brunneus*), White Admiral (*Limenitis arthemis arthemis*), two-striped Grass Frog (*Hylarana taipehensis*). Images courtesy of Wikimedia.

Fig. 2 *Anartia fatima* ventral surfaces with spectral reflectance comparison of model colour to the natural ventral wing surface of *Anartia fatima*. Arrows from model depict colour patches for spectra. White lines are averages of natural wing spectra, black lines are averages for model spectra, and grey shading represents one standard deviation for natural wing spectra. Photograph credit Beryl Jones.



well as a model to test the prediction of producing false boundaries, because *A. fatima* is very common in tropical disturbed areas and edge habitats that provide heterogeneous backgrounds of dark- and light-coloured vegetation (Silberglied *et al.*, 1979). Furthermore, *A. fatima* has not been shown to be a Batesian mimic of unpalatable butterflies and it is a common prey item for a gamut of visually guided insectivorous predators including passerine birds (Passeriformes) and whiptail lizards (*Ameiva spp.*) (Boyden, 1976; Silberglied *et al.*, 1979, 1980; Bowers *et al.*, 1987). We predict that individuals of *A. fatima* with a naturally located band will be predated less often than individuals in which the band is moved to the wing periphery. Furthermore, we predict that *A. fatima* individuals in which the band is broken and moved to the periphery will have predation rates comparable to those of naturally banded individuals. This study tests the importance of band patterning on predation rates of an animal in a natural setting.

Materials and methods

Model construction

We collected male *A. fatima* butterflies near Gamboa, Panama, in March–April 2013 using aerial nets. These animals were used in November–December 2013 to develop artificial models following the methods of Finkbeiner *et al.* (2012). Bowers *et al.* (1987) demonstrated that *A. fatima* has the greatest predation rates when perched with the wings closed. Therefore, the models were constructed using scanned images (Brother MFC-J4510DW Scanner, Brother Industries) of ventral wing surfaces of *A. fatima* individuals with the wings closed (Fig. 2). This wing position also accurately represents a butterfly at rest, which is when the ventral band is visible to predators.

To test the possible disruptive function of the yellowish wing band, three model types were used, and within each model type the pattern was the same.

Pattern geometry was altered for two of the three model types to produce a discontinuous edge model and a nondisruptive model (Fig. 3); the natural wing model was unaltered to represent our hypothesized example of false boundary disruptive coloration. The nondisruptive alteration reduced the effect of disruption by relocating the band to the wing margin, enhancing the animal's outline (see Endler, 1984 and Ruxton *et al.*, 2004). The discontinuous edge alteration had a segmented band on the wing margin, which mimics marginal disruptive coloration due to high-contrast marginal markings (see Endler, 1984; Ruxton *et al.*, 2004; Cuthill *et al.*, 2005). All alterations were executed in Photoshop CS5, and total yellow area was the same for each treatment as measured using ImageJ. High-resolution models were printed onto Whatman filter paper with a Brother MFC-J4510DW (Brother Industries) printer and then cut and inserted into the 'body', a 2.5-cm-long piece of black, nontoxic plasticine clay, which remains malleable in the field and thereby allows assessment of beak marks from avian predators (Finkbeiner *et al.*, 2012; Merrill *et al.*, 2012).

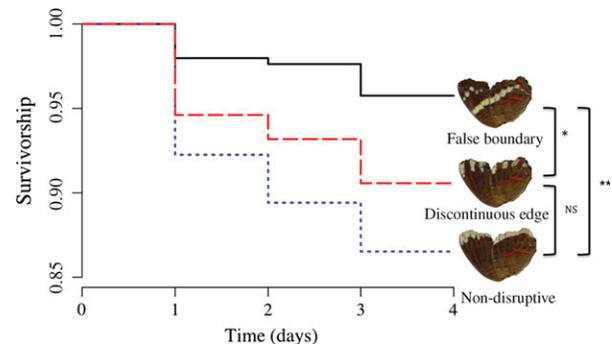


Fig. 3 Survival curves of the three model types. The only difference among the three model types is band continuity and placement. False boundary was significantly different from the other two model types. Discontinuous edge and nondisruptive did not differ significantly from one another. * $P = 0.05$, ** $P < 0.001$.

Model colour measurements

To confirm that the model coloration was visually indistinguishable from *A. fatima* coloration, we ran avian visual models. We measured the ventral reflectance of three colours (yellow band, brown wing and red band) of five natural male *A. fatima* and of three of each printed model type using an Ocean Optics USB2000 spectroradiometer and an Ocean Optics Xenon pulse as a standardized light source. Wing colour reflectance was measured as the proportion of a white reference standard (WS-1-SL, Ocean Optics Dunedin, FL, USA) using a coaxial fibre cable (QR400-7, Ocean Optics). We evaluated avian visual models using the PAVO program within R (Maia *et al.*, 2013) to confirm that the artificial models accurately represented the coloration of *A. fatima* wings, as seen through the eyes of both ultraviolet- and violet-sensitive birds (Vorobyev *et al.*, 1998; Osorio & Vorobyev, 2005). There are two different visual systems for birds in which the shortest wavelength sensitivity differs. Most songbirds, parrots and some shorebirds have UV-sensitive vision, whereas most other birds have violet vision (Hart, 2001). We modelled both visual types due to the likelihood that birds of both types were likely to attack the models (DeVries, 1987). We applied von Kries transformation to account for receptor adaptation and used the default parameters for Weber's fraction (0.05), illumination (D65 irradiance spectrum for standard daylight), background and cone ratios of $N1 = 1$, $N2 = 2$, $N3 = 2$, $N4 = 4$ (Hart, 2001; Maia *et al.*, 2013). We calculated both achromatic and chromatic Just Noticeable Differences (JNDs) for each of the three comparisons: yellow model vs. yellow natural, brown model vs. brown natural and red model vs. red natural. JNDs are a value that represents the ability of a visual system to perceive two colours differently with a JND value of less than one being indistinguishable in ideal conditions and a JND value of less than three being indistinguishable under natural conditions (Siddiqi *et al.*, 2004). All comparisons had JNDs of less than 2 for achromatic comparisons and less than 3 for chromatic comparisons. Therefore, we assumed that the model coloration would be perceived as similar coloration of live *A. fatima*. Furthermore, the spectral reflectance for each model fit within the natural colour variation of *A. fatima*, see Fig. 2.

Survival experiments

We tested the survival of our model types in disturbed forest near Gamboa, Panama (09°07.778'N, 079°41.854'W). Models were tied with black thread to vegetation 0.2 m to 2 m above the ground, matching natural perch sites of *A. fatima*. The vegetation upon which the models rested were leaves and branches of rainforest plants. Although we did not specifically control for background, there is no evidence that *A. fatima*

chooses a particular type of vegetation to rest. Models were set out in blocks of three that included one of each type. Within each block, models were randomly arranged 1 to 3 m apart and the blocks were placed 100 m apart to reduce the risk of the same bird attacking models in more than one block (Hurlbert, 1984; Finkbeiner *et al.*, 2012). On each of three different days in January 2014, we placed 297 models, 99 of each type, for a total of 891 models. These experiments took place during the dry season for two reasons: because predation rates on insects increase then, perhaps due to decreased abundance of insect prey in general, and to avoid rain damage to the models (Kricher, 1999). Each model was checked daily for 3 days for beak, teeth and mandible marks (see Finkbeiner *et al.*, 2012). Attacked models were removed from the experiment and not replaced, to avoid inflating mortality rates among treatments (Cuthill *et al.*, 2005; Finkbeiner *et al.*, 2012; Merrill *et al.*, 2012). We counted only beak marks (i.e. triangular indentations) as predation and censored models that went missing (Hurlbert, 1984) as well as presumed attacks by mammals (i.e. teeth marks and gashes) and insects (i.e. small holes), as these most likely were not visually guided and therefore not an accurate test of pattern type (Finkbeiner *et al.*, 2012). Differences in survival probabilities after 72 h were analysed using Cox proportional-hazards regression ('survival' package) in R (R Development Core Team 2011). Missing models were incorporated into the Cox proportional-hazards regression as censored. We also calculated effect sizes with odds ratios (OR), where a value of 1.00 indicates that two treatments have identical survival probabilities.

Results

After three days in the field, 8.5% (76 of 891) of the models had been attacked by birds, 8.4% (75 of 891) were missing (one area with 27 models was clear-cut), and 1.6% (14/891) were attacked by nonavian predators (e.g. rodents, ants). Attack rate on the nondisruptive models was 12.4%, whereas it was 9.7% for the discontinuous edge models and 3.3% for the false boundary models. Missing and non-avian-attacked models comprised 11.4% of all false boundary models, 11.1% of the discontinuous edge models and 7.4% of the nondisruptive models (Table 1).

Table 1 Number of models attacked by birds, and combined missing and nonavian attacks for each model type.

Model	N	Avian attack	Missing and nonavian attacks
False Boundaries	297	10 (3.4%)	34 (11.4%)
Discontinuous Edge	297	29 (9.8%)	33 (11.1%)
Nondisruptive	297	37 (12.5%)	22 (7.4%)
Total	891	76 (8.5%)	89 (10.0%)

Survivorship curves differed significantly with model type (Cox regression, $F = 2.173$, $P = 0.029$) but not with date of placement (Cox regression, $F = 0.895$, $P = 0.371$). Pairwise comparisons revealed that the false boundary models survived significantly longer than either the discontinuous edge or nondisruptive models (Wald = 5.98, d.f. = 2, $P = 0.050$, OR = 0.321 and Wald = 14.57, d.f. = 2, $P < 0.001$, OR = 0.245 respectively). Nondisruptive and discontinuous edge models did not differ in survival (Wald = 4.29, d.f. = 2, $P = 0.111$, OR = 0.762). The proportion of missing models did not differ across the three model types (Cox regression, $F = 0.186$, $P = 0.852$).

Discussion

The higher survival of false boundary models than both discontinuous edge and nondisruptive models confirms that the centrally located band of *A. fatima* functions to reduce predation. These findings are in line with another study that tested the disruptive function of bands in the Eurasian White Admiral (*Limenitis camilla*; Stobbe & Schaefer, 2008). However, we did not find support for a difference in survival between the discontinuous edge models and the nondisruptive models. These findings are contrary to previous research demonstrating that false edges increase survival more than false boundaries (Cuthill *et al.*, 2005; Stevens *et al.*, 2006), but follow the findings of Stevens *et al.* (2009), in which individuals with high internal contrast had high survival. Unlike the study by Stevens *et al.* (2009), which was an excellent test of the psychophysics of disruptive coloration in novel, unnatural prey items, our aim was to test, in the natural habitat, whether internally banded animals survived better than animals with a marginal band or marginal markings (Cuthill *et al.*, 2005; Stevens *et al.*, 2006, 2009). It is possible that the regularly repeating stripes of the discontinuous edge treatment might have increased detection and prevented any marginal disruptive effect. Follow-up research is needed to blend the methods of Cuthill *et al.* (2005) and Stevens *et al.* (2009) with this studies' methods to determine how randomly patterned blotches on natural animals in their habitats affect survival. Lastly, it is also possible that birds were attacking the non-natural wing patterns because they were novel. Previous research has shown that avian predators which have learned to avoid aposematic prey will attack butterflies with novel wing patterns (Langham, 2004). It is unlikely that the attack rates in this study were due to birds attacking novel patterns because research has shown that birds exhibit neophobia when known palatable prey are available (Marples *et al.*, 1998; Marples & Kelly, 1999), and therefore, it is more plausible that birds would be less likely to attack the novel models (i.e. discontinuous edge and nondisruptive) than the natural pattern models. Of course,

further studies using all novel wing patterns will clarify the role of novelty in avian predation of disruptively patterned animals.

Most research on disruptive coloration has focused on peripheral markings instead of central markings; however, Silberglied *et al.* (1980) and Stobbe & Schaefer (2008) both tested the potential role of bands in butterfly disruptive coloration. Utilizing the same species as this study, *A. fatima*, Silberglied *et al.* (1980) found that individuals with the band survived as well as cryptic *A. fatima* individuals that had the band blacked out, most likely rendering the individual more cryptic (Endler, 1984). However, their study involved blacking out the dorsal band, not the ventral one, so they were testing butterflies in flight, not at rest. Stobbe & Schaefer (2008) tested the survival of artificial butterflies (*Limenitis camilla* (Linnaeus), the Eurasian white admiral) dependent upon the chromatic contrast of the ventral band. They found that artificial butterflies with a naturally coloured band survived as well as butterflies without a band (a cryptic control), but butterflies that had their bands altered to have higher internal chromatic contrast were attacked more, demonstrating that disruptive coloration utilizing false boundaries is dependent upon the coloration of the band and background (Stobbe & Schaefer, 2008). However, their study did not test location or geometry of bands. Therefore, our study builds on previous research and demonstrates the importance of band location.

In this study, we demonstrate that internal bands on male *Anartia fatima* butterfly wings reduce predation rates compared to external bands or discontinuous marginal patterns. These findings are consistent with the original hypotheses of Thayer (1909) and Cott (1940) and are not necessarily incongruent with recent work on pattern geometry effects on disruptive coloration. Cuthill *et al.* (2005) and Stevens *et al.* (2006) both found that triangular paper models with marginal patterns were attacked less often by avian predators than internal patterns were. However, in this current study, we tested the role of a band that does intersect the leading edge (costal margin) of the wing and therefore may have a stronger disruptive effect. Interestingly, the discontinuous edge model, in which the markings were located along the wing outer margin, was attacked more often than the false boundary model, a finding that does differ from most of the previous research, which demonstrates that optimal disruptive patterning is dependent upon context (e.g. species, habitat, predators; Cuthill *et al.*, 2005; Stevens *et al.*, 2006). However, Stevens *et al.* (2009) did test the role of contrast geometry on prey and found that high internal contrast with low marginal contrast had the highest survival. Our findings here follow nicely with the work of Stevens *et al.* (2009) in which high internal contrast due to a wing band increases survival of individuals relative to high marginal contrast.

As in *A. fatima*, wings of many tropical butterflies have a conspicuous central band, including species of *Doxocopa* (Hübner), *Adelpha* (Hübner), *Siproeta* (Hübner), *Pyrrhogyra* (Hübner) and *Papilio* (Linnaeus) (DeVries, 1987). None of them has been shown to be unpalatable or warningly coloured (Pinheiro, 1996), and it is likely that their wing patterning makes them difficult for predators to detect when they are at rest. Several species of aposematic butterflies occur sympatrically with *A. fatima*, including *Heliconius sapho* (Doubleday), *Heliconius cydno* (Bates), *Danaus plexippus* (Linnaeus) and *Danaus gilippus* (Bates) (Brower, 1957; DeVries, 1987; Pinheiro, 1996; Srygley & Ellington, 1999). Aposematic patterns are hypothesized to be conspicuous to increase predator detection, recognition and memory, and these unpalatable butterflies have their margins emphasized with a continuous band (DeVries, 1987; Brakefield *et al.*, 1992). Previous discussion has suggested that high-contrast disruptive coloration could be coupled with aposematism (Tullberg *et al.*, 2005; Stevens & Merilaita, 2009b; Stevens *et al.*, 2013), but these results indicate that the interaction between false boundary disruption and aposematic coloration is more complicated and most likely depends on band location and habitat background. These observations reveal that many questions remain about how the behaviour and ecology of animals affect band location and pattern geometry.

In summary, our experiment shows that an internal conspicuous band on a wing surface increases survival more than marginally located discontinuous patterns (false edges) or a marginally located band. These data demonstrate the importance of false boundary disruptive coloration in a butterfly and indicate that further research is needed to understand the effects of false boundary disruptive coloration, geometry and behaviour in other taxa.

Acknowledgments

Beryl Jones, Emily Brodie, Lindsey Siebert and W. Owen McMillan were crucial for the success of model preparation, data collection and analysis. We are thankful for suggestions on the manuscript from Beryl Jones, Rick Simpson, Ron Rutowski and Kevin McGraw and from the McGraw laboratory. The thoughtful criticisms from anonymous reviewers greatly strengthened our manuscript. Logistical support from the Smithsonian Tropical Research Institute and financial support provided by Arizona State University Graduate and Professional Student Association and the Smithsonian Tropical Research Institute were paramount for this research. We are grateful to the Autoridad Nacional del Ambiente of the Republic of Panama for collecting permit SE/A-8-14.

Data accessibility

All data collected for and used in this study are present in this manuscript. The reflectance spectra of the butterfly models and the attack rates are listed in tables and figures.

References

- Bowers, M., Crabtree, R.C., Harrison, S.P., Sobrevilla, C., Wells, M. & Wolfe, L.M. 1987. Predation on adults of *Anartia fatima*. *J. Lepid. Soc.* **41**: 75–76.
- Boyden, T.C. 1976. Butterfly palatability and mimicry; experiments with Ameiva lizards. *Evolution* **30**: 73–81.
- Brakefield, P.M., Shreeve, T.G. & Thomas, J.A. 1992. Avoidance, concealment, and defence. In: *The Ecology of Butterflies in Britain* (R.L.H. Dennis, ed.), 93–118. Oxford University Press, Oxford, UK.
- Brower, J.V.Z. 1957. Experimental studies of mimicry in some North American Butterflies. Part one: The Monarch, *Danaus plexippus*, and Viceroy, *Limenitis archippus archippus*. *Evolution* **12**: 32–47.
- Cott, H.B. 1940. *Adaptive Coloration in Animals*. Methuen & Co. Ltd, London, UK.
- Cuthill, I.C., Stevens, M., Sheppard, J., Maddocks, T., Parraga, A. & Troscianko, T.S. 2005. Disruptive coloration and background pattern matching. *Nature* **434**: 72–74.
- DeVries, P.J. 1987. *The Butterflies of Costa Rica and Their Natural History*. Princeton University Press, Princeton, New Jersey.
- Dimitrova, M., Stobbe, N., Schaefer, H.M. & Merilaita, S. 2009. Concealed by conspicuousness: distractive prey markings and backgrounds. *Proc. R. Soc. Lond.* **276**: 1905–1910.
- Endler, J. 1984. Progressive background matching in moths, and a quantitative measure of crypsis. *Biol. J. Linn. Soc.* **22**: 187–231.
- Endler, J. 2006. Disruptive and cryptic coloration. *Proc. R. Soc. Lond.* **273**: 2425–2426.
- Finkbeiner, S.D., Briscoe, A.D. & Reed, R.D. 2012. The benefit of being a social butterfly: communal roosting deters predation. *Proc. R. Soc. Lond.* **279**: 2769–2776.
- Fraser, S., Callahan, A., Klassen, D. & Sherratt, T.N. 2007. Empirical tests of the role of disruptive coloration in reducing detectability. *Proc. R. Soc. Lond.* **274**: 1325–1331.
- Hanlon, R.T., Chiao, C.C., Mäthger, L.M., Barbosa, A., Buresch, K.C. & Chubb, C. 2009. Cephalopod dynamic camouflage: bridging the continuum between background matching and disruptive coloration. *Proc. R. Soc. Lond.* **364**: 429–437.
- Hart, N. 2001. The visual ecology of avian photoreceptors. *Prog. Retin. Eye Res.* **20**: 675–703.
- Hurlbert, S.H. 1984. Pseudoreplication and the design of ecological field experiments. *Ecol. Monogr.* **54**: 187–211.
- Kricher, J.C. 1999. *A Neotropical Companion*. Princeton University Press, Princeton, New Jersey.
- Langham, G.M. 2004. Specialized avian predators repeatedly attack novel color morphs of *Heliconius* butterflies. *Evolution* **58**: 2783–2787.
- Maia, R., Eliason, C.M., Bitton, P., Doucet, S.M. & Shawkey, M.D. 2013. PAVO: an R package for the analysis, visualization and organization of spectral data. *Methods Ecol. Evol.* **4**: 906–913.

- Marples, N.M. & Kelly, D.J. 1999. Neophobia and dietary conservatism: two distinct processes? *Evol. Ecol.* **13**: 641–653.
- Marples, N.M., Roper, T.J. & Harper, D.G. (1998) Responses of wild birds to novel prey: evidence of dietary conservatism. *Oikos* **83**: 161–165.
- Merilaita, S. 1998. Crypsis through disruptive coloration in an isopod. *Proc. R. Soc. Lond.* **265**: 1059–1064.
- Merilaita, S. & Lind, J. 2005. Background-matching and disruptive coloration, and the evolution of cryptic coloration. *Proc. R. Soc. Lond.* **272**: 665–670.
- Merrill, R., Wallbank, R., Bull, V., Salazar, P., Mallet, J., Stevens, M. *et al.* 2012. Disruptive ecological selection on a mating cue. *Proc. R. Soc. Lond.* **279**: 4907–4913.
- Osorio, D. & Srinivasan, M.V. 1991. Camouflage by edge enhancement in animal coloration patterns and its implications for visual mechanisms. *Proc. R. Soc. Lond.* **244**: 81–85.
- Osorio, D. & Vorobyev, M. 2005. Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and color vision. *Proc. R. Soc. Lond.* **272**: 1745–1752.
- Pinheiro, C.E.G. 1996. Palatability and escaping ability in Neotropical butterflies: tests with wild Kingbirds (*Tyrannus melancholicus*, Tyrannidae). *Biol. J. Linn. Soc.* **59**: 351–365.
- R Development Core Team. 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>.
- Ruxton, G., Sherratt, T. & Speed, M. 2004. *Avoiding Attack: The Evolutionary Ecology of Crypsis, Warning Signals and Mimicry*. Oxford University Press, Oxford, UK.
- Schaefer, H.M. & Stobbe, N. 2006. Disruptive coloration provides camouflage independent of background matching. *Proc. R. Soc. Lond.* **273**: 2427–2432.
- Siddiqi, A., Cronin, T.W., Loew, E.R., Vorobyev, M. & Summers, K. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *J. Exp. Biol.* **207**: 2471–2485.
- Silberglied, R.E., Aiello, A. & Lamas, G. 1979. Neotropical butterflies of the genus *Anartia*: systematics, life histories, and general biology. *Psyche* **86**: 219–260.
- Silberglied, R.E., Aiello, A. & Windsor, D.M. 1980. Disruptive coloration in butterflies: lack of support in *Anartia fatima*. *Science* **4456**: 617–619.
- Srygley, R.B. & Ellington, C.P. 1999. Discrimination of flying mimetic passion-vine butterflies, *Heliconius*. *Proc. R. Soc. Lond.* **266**: 2137–2140.
- Stevens, M. 2007. Predator perception and the interrelation between different forms of protective coloration. *Proc. R. Soc. Lond.* **274**: 1457–1464.
- Stevens, M. & Merilaita, S. 2009a. Animal camouflage: current issues and new perspectives. *Philos. Trans. R. Soc. B* **364**: 423–427.
- Stevens, M. & Merilaita, S. 2009b. Defining disruptive coloration and distinguishing its functions. *Philos. Trans. R. Soc. B* **364**: 481–488.
- Stevens, M. & Merilaita, S. 2011. *Animal Camouflage: Mechanisms and Function*. Cambridge University Press, Cambridge, UK.
- Stevens, M., Cuthill, I.C., Windsor, A.M.M. & Walker, H.J. 2006. Disruptive contrast in animal camouflage. *Proc. R. Soc. Lond.* **273**: 2433–2438.
- Stevens, M., Winney, I.S., Cantor, A. & Graham, J. 2009. Outline and surface disruption in animal camouflage. *Proc. R. Soc. Lond.* **276**: 781–786.
- Stevens, M., Searle, W.T.L., Seymour, J.E., Marshall, K.L.A. & Ruxton, G.D. 2011. Motion dazzle and camouflage as distinct antipredator defenses. *BMC Mol. Biol.* **9**: 81.
- Stevens, M., Marshall, K., Troscianko, J., Finlay, S., Burnand, D. & Chadwick, S. 2013. Revealed by conspicuousness: disruptive markings reduce camouflage. *Behav. Ecol.* **24**: 213–222.
- Stobbe, N. & Schaefer, M. 2008. Enhancement of chromatic contrast increases predation risk for striped butterflies. *Proc. R. Soc. Lond.* **275**: 1535–1541.
- Thayer, G.H. 1909. *Concealing-Coloration in the Animal Kingdom; an Exposition of the Laws of Disguise Through Color and Pattern*. MacMillan, New York, NY.
- Tullberg, B.S., Merilaita, S. & Wiklund, C. 2005. Aposematism and crypsis combined as a result of distance dependence: functional versatility of the colour pattern in the swallowtail butterfly larva. *Proc. R. Soc. Lond.* **272**: 1315–1321.
- Vorobyev, M., Osorio, D., Bennett, A.T.D., Marshall, N.J. & Cuthill, I.C. 1998. Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Phys.* **183**: 621–633.
- Webster, R.J., Hassall, C., Herdman, C.M., Godin, J.J. & Sherratt, T.N. 2013. Disruptive camouflage impairs object recognition. *Biol. Lett.* **9**: 6.

Data deposited at Dryad: doi: 10.5061/dryad.k528j

Received 1 April 2015; revised 12 June 2015; accepted 15 June 2015