Anti-Predator Coloration and Behaviour: A Longstanding Topic with Many Outstanding Questions

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1 Introduction
The study of anti-predator coloration and behaviour has a long and rich history in biology. It has from the very outset of Darwin’s theory of natural selection provided numerous areas to test mechanisms and function in evolution. While Darwin perhaps concentrated most of his attention regarding animal coloration on his theory of sexual selection (Darwin, 1871), his contemporaries placed much greater emphasis and time to explain the variety of ways that coloration and behaviour protected animals from attack from predators. Wallace in particular devoted considerable effort in discussing anti-predator coloration in nature, playing a leading role in developing key concepts regarding camouflage and warning signals (aposematism) (Wallace, 1867, 1877, 1889). Alongside him, and subsequently, other pioneers such as Bates and Poulton (Bates, 1862; Poulton, 1885, 1890) conducted experiments and put forward other key concepts relating to mimicry and various areas of protective coloration. The basis of our current ideas regarding anti-predator coloration and behaviour still stems in no small part from these and other pioneers.

Defensive coloration continued to provide some of the most compelling evidence for evolution and adaptation, most notably the famous work of Kettlewell (1955, 1956) and others (e.g. Cook et al., 1986; Cook et al., 2012) on industrial melanism and the peppered moth *Biston betularia*. In the modern era, further examples incorporating modern advances such as genetics and molecular biology have continued this tradition (Nachman et al., 2003; Nosil and Crespi, 2006; Rosenblum, 2006). However, despite over 150 years of research, many questions remain in the study of anti-predator coloration, and behaviour and the subject is as active and vibrant a research area as it ever has been.

2 Camouflage
Probably the most widespread type of anti-predator coloration is camouflage. While in many regards an intuitively simple concept, this strategy is actually far more rich and complex than is often appreciated. To begin with, successful camouflage is not just about looking like the background (though clearly that is an essential basic component). Instead, there are multiple ways that camouflage can be achieved, including matching the general colour and patterns of the visual environment (background matching; e.g. Endler, 1984; Merilaita, 2003; Rosenblum et al., 2004; Bond and Kamil, 2006; Merilaita and Stevens, 2011), breaking up the body outline and key features by using disruptive patterns (e.g. Thayer, 1909; Cuthill et al., 2005; Merilaita and Lind, 2005; Schaefer and Stobbe, 2006; Stevens and Cuthill, 2006; Stevens et al., 2006; Stevens and Merilaita, 2009; Espinosa and Cuthill, 2014; Kang et al., 2015), using countershading to hide self-generated shadows and 3-D shape (e.g. Poulton, 1890; Thayer, 1909; Rowland et al., 2007; Rowland et al., 2008; Tankus and Yeshurun, 2009), through to resembling uninteresting or irrelevant objects in the environment, such as dead leaves or bird droppings (masquerade; e.g. Skelhorn et al., 2010; Skelhorn and Ruxton, 2010). These and other general principles of camouflage have been discussed since the seminal works of Thayer (1909) and Cott (1940), yet really only in the last 15 years or so have they begun to be quantitatively tested. As a result, despite much progress, we still have much to learn regarding how these types of camouflage work, are optimised, evolve, and the survival value that they provide. Disruptive coloration has perhaps piqued the interest of researchers studying camouflage more than any other possible route to concealment, and consequently has attracted considerable empirical work, not just from biologists but from computer scientists and vision psychologists too (Troscianko et al., 2009).

However, many questions regarding camouflage remain. For example, while much work shows that dis-
ruction is often successful by breaking up information corresponding to body edges, and likely preventing detection (e.g. Merilaita and Lind, 2005; Schaefer and Stobbe, 2006; Stevens and Cuthill, 2006; Stevens et al., 2006; Fraser et al., 2007; Stevens and Merilaita, 2009), there is also the possibility that it might also prevent predators from recognising a prey animal too (Webster et al., 2013; Espinosa and Cuthill, 2014). In this issue, Webster (2015) discusses the possibility and evidence for disruption working in this way. In addition, we also require a much better understanding of how the different types of camouflage relate to one another, and how features of the prey markings and background might contribute to successful concealment. Todd et al. (2015) in this issue present the findings of work investigating how the spatial arrangement, contrast, and size of markings on virtual prey presented to human ‘predators’ affects the likelihood of detection. Much work has also focussed on the initial detection/recognition of prey items by naïve observers, yet there is evidence that features of different camouflage types may be learnt at different rates (Troscianko et al., 2013), and this is also an important area of future work.

Much of what we currently know about camouflage comes from studies based on artificial systems (e.g. laboratory studies, artificial or virtual prey). Such work has proven valuable to understand camouflage function and the mechanisms involved. However, there is now a real need to study in more detail the camouflage of real animals, and how results and predictions from artificial systems bear out in nature. Work investigating camouflage in real animals has largely focussed on a few specific areas, including the ability of some animals to rapidly (seconds and minutes) change colour for concealment (Kelman et al., 2007; Hanlon et al., 2009; Chiao et al., 2011; Zylinski and Johnsen, 2011). This has yielded substantial insights, including into which aspects of the visual environment trigger camouflage expression. However, we need to investigate how camouflage strategies like disruptive coloration, masquerade, and countershading more widely evolve and operate in a range of real species in complex natural systems, including those with more fixed appearances, and the survival advantages they provide.

While rapid colour change is a valuable tool for testing how animals tune their camouflage to different visual environments, relatively slower colour change (over hours, days, weeks, and months) is likely to be more widespread in nature. Such slower processes also apparently enable animals to impressively tune their appearances to the local environment for concealment (phenotype-environment associations and matching), which has been most widely investigated in crustaceans (e.g. Todd et al., 2006; Stevens et al., 2014a; Stevens et al., 2015). Such systems present a valuable opportunity to study processes of development and the use of visual information because, unlike cases of genetic adaptation to environments (Nachman et al., 2003; Rosenblum et al., 2004), matching is likely driven by both physiological and morphological colour change and developmental plasticity (Umbers et al., 2014; Nettle and Bateson, 2015, underpinned by visual feedback from the eyes. In addition, many animals that have slow colour change for camouflage appear to be highly polymorphic (or have very high continuous variation), within a habitat or visual environment and among habitats (e.g. Todd et al., 2006; Stevens et al., 2014b; Stevens et al., 2014a), presenting an opportunity to understand the mechanisms and selection pressures that lead to high within species diversity. In this issue, Jensen & Egnotovich (2015) and Hultgren & Mittelstaedt (2015) investigate some of these issues in the camouflage of crabs and isopods. Finally, there is a growing appreciation of the role of behaviour in optimising camouflage, and this is an area that deserves much more attention (Lovell et al. 2013, Bian et al. 2015, Kang et al. 2015).

3 Eyespots and Warning Signals

In contrast to trying to evade detection and recognition by predators, many animals instead use bright and conspicuous displays to avoid being attacked and eaten. Such defences can manifest themselves as colourful signals showing that the prey item is toxic, dangerous, or unprofitable, so that predators avoid them (aposematism; Poulton, 1890; Mappes et al., 2005; Stevens and Ruxton, 2012). Many conspicuous displays are also bluffs, with the prey item being perfectly edible but relying on mimicry or startle displays to prevent predator attacks.

One example of conspicuous signals used by normally edible species is eyespots: paired circular markings on the body of a range of butterflies and moths, many fish, and certain other animals (Stevens, 2005; Kodandaramaiah, 2011). Eyespots are generally thought to defend prey animals in one of two main ways. First, they may deflect the attacks of predators to non-vital parts of the body (such as the wing edges), allowing the victim to escape, and second they may intimidate or startle predators, preventing an attack from occurring or concluding. There is considerable evidence that eyes-
pots are effective in preventing attack (e.g. Blest, 1957; Vallin et al., 2005, 2007; Stevens et al., 2007, 2008; Skelhorn et al., 2014), and although less clear-cut, recent work has also provided evidence for a deflective function (e.g. Olofsson et al., 2010; Olofsson et al., 2013).

The question of why eyespots work is more controversial. Historically, intimidating eyespots have been thought to work by mimicking the eyes of the predator’s own enemies (Blest, 1957), although objective evidence for this has been scarce (Stevens and Ruxton, 2014). In contrast, eyespots may work simply by presenting a highly salient conspicuous signal that promotes avoidance behaviour in predators or overloads the sensory system, causing the predator to pause or abort its attack (Stevens, 2005; Stevens and Ruxton, 2014). In recent years, studies have found evidence in support of both the eye mimicry (Blut et al., 2012; Skelhorn et al., 2014; De Bona et al., 2015) and conspicuous signal hypotheses (Stevens et al., 2007, 2008, 2009; Brilot et al., 2009; Yorzinki et al., 2015), and so the mechanism underlying eyespot function may vary depending on the context and species involved. More work investigating when eyespots mimic eyes is now needed, and how close the resemblance needs to be. In addition, no study has yet compared the appearance of eyespots to real eyes, while accounting for predator vision, and so similarity of eyespots to purported models lacks investigation. There remain other areas where work is needed to understand eyespot function and how they work, including testing the role of predator experience and the relation between potentially deflective and intimidating eyespots, as is investigated in this issue by Olofsson et al. (2015). In addition, the behavioural adaptations that many prey animals have to enhance eyespot displays requires further study. In this issue, López-Palafox et al. (2015) investigated the behavioural displays used by some butterflies with false head markings and morphology.

Much work has also studied the evolution and effectiveness of warning signals in nature. While early worked focussed substantially on the initial evolution of warning coloration, there are many plausible explanations for how warning signals may have initially evolved (Marple et al., 2005). More recent work has tended to focus on what makes an effective warning signal, whether warning signals are quantitatively honest indicators of prey toxicity, and the interaction of warning signals with other functions and life history traits (Stevens and Ruxton, 2012). Here, there remain many areas for future work. For example, despite much theoretical work and some empirical studies, it remains unclear if and when the strength of warning signals should be honest indicators of prey defences both within and among species (e.g. Leimar et al., 1986; Summers and Clough, 2001; Darst et al., 2006; Blount et al., 2009; Cortesi and Cheney, 2010; Speed et al., 2010; Blount et al., 2012; Arenas et al., 2015; Summers et al., 2015). In addition, many warning signals do not, to human eyes at least, appear to be highly conspicuous, which raises the question of whether the animal colour patterns are trading-off warning signal form with other functions (for which there is increasing evidence; e.g. Maan and Cummings, 2008; Lindstedt et al., 2009). We also need to identify more about how the ecology of a species affects the selection that operates on warning signal form, including the habitat where a prey animal lives, and the effects of predator communities and seasonal factors (Endler and Mappes, 2004; Mappes et al., 2014; Nokelainen et al., 2014). Finally, a remaining issue that requires greater investigation is why so many aposematic animals are polymorphic (or have high continuous variation; Wang and Shaffer, 2008; Nokelainen et al., 2014). This would seem to go against conventional predictions that warning signals should converge on a similar form in order to reduce the amount of predator learning required to promote avoidance behaviour. While there are various potential explanations (Stevens and Ruxton, 2012), this remains somewhat of an unresolved issue. In addition, greater work into the behaviour of colour morphs may shed light on this conundrum. In this issue, Rojas et al. (2015) investigate the role of flight activity in morphs of an aposematic moth.

4 Other Areas of Anti-Predator Coloration and Behaviour

Finally, links between anti-predator behaviour and coloration need more research in other areas too, outside of defensive coloration. For example, bright conspicuous coloration, such as widely used of mate selection, is often thought to carry a potential cost in increasing detection by predators. Instead of evolving duller colour patterns, animals may instead evolve changes in behaviour to cope with this heightened risk. In this issue, Hensley et al. (2015) investigate the question of whether more conspicuous and colourful birds flee sooner when at risk of predation than those with duller plumage. Studies of anti-predator behaviour are also important in other sensory modalities too, with many animals responding to threats based on olfactory or auditory cues, for example. In this issue Frynta et al. (2015)
test how mice respond to odour cues of potential threats, including introduced predators and competitors. Above all, the study of anti-predator behaviour and defensive coloration has much to reveal regarding the workings of ecology and evolution, species interactions, and the optimisation of traits in general. Despite a long history of study, we have much left to discover.

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