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Camouflage

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Synonyms

Concealment, Disguise

Definition

A phenomenon whereby organisms avoid detection or recognition by resembling the general background or specific objects therein.

Introduction

Camouflage is a phenomenon, which hides or prevents something from being noticed. As an umbrella term, it covers all strategies involved in concealment including prevention of detection and recognition (Stevens and Merilaita 2009). Camouflage exists across many biological taxa and provides among the most remarkable examples of adaptation. For example, cuttlefish (*Sepia officinalis*) can adjust their appearance in terms of color and patterning to match their respective visual habitat, but also change their shape to increase resemblance to natural objects such as coral, stones, or seaweed (Hanlon et al. 2009). Likewise grouse, ground-dwelling birds, avoid being seen by potential predators by closely resembling the background on which they nest (Thayer 1896). Despite being an ubiquitous anti-predator strategy in nature, and important in many areas of human application (e.g., military, hunting, test cars), only recently has science moved from descriptive accounts to test what camouflage types exist, how they work, and what their adaptive value is (Nokelainen and Stevens 2016). There has been a revival in the study of camouflage among scientists spanning molecular, sensory and evolutionary biologists, visual psychologists, computer scientists, and art historians. Although camouflage can function via any sensory modality, here we outline the most extensively studied one: visual camouflage in animals.

A Short History of the Study of Camouflage

After Charles Darwin's hallmark book *On the Origin of Species by Means of Natural Selection*, much of the background in terms of what types of camouflage exist in nature was concluded prior to the 1950s. Three bodies of work were (and still are) particularly influential: *The Colours of Animals: Their Meaning and Use Especially*

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Considered in the Case of Insects by Edward B. Poulton (1890), *Concealing-Coloration in the Animal Kingdom: An Exposition of the Laws of Disguise Through Color and Pattern* by Gerald Thayer (1909), and *Adaptive Coloration in Animals* by Hugh Cott (1940). Since then the theory of camouflage has been refined particularly from the perspective of being an effective anti-predator strategy (Ruxton et al. 2004; Stevens and Merilaita 2011). These excellent accounts have made camouflage a textbook example of natural selection and a long-standing model system for understanding adaptation. Moreover, we know that being able to hide has been important from the very early days, as the earliest organisms bearing a coloration that suggestively served a camouflage function date back to marine animals in the Cretaceous period. However, it has proven challenging to quantify camouflage in natural settings (i.e., difficulty to quantify something that is hard to detect or recognize) and to understand how animals may appear to the appropriate receivers' perceptual systems (i.e., difficulty of seeing world through other animals' eyes).

How Different Types of Camouflage May Work

An organism that is hard to detect is cryptic. The best-known form of this is background matching, whereby both the color and pattern of the organism closely resemble visual properties of the background (Endler 1978). For example, the appearance of many nocturnal moths closely resembles the tree trunks on which they rest during daytime. Disruptive coloration, in contrast, is distinguished by high contrast elements that break up the body contour (Cuthill et al. 2005). The conspicuously striped patterns make an animal harder to detect or recognize in its respective visual environment. Detectability can also be reduced through countershading, whereby an object is darker on the surface facing higher light intensity (Rowland et al. 2007). The pale underside combined with a dark above side seen in many mammals reduces the obviousness of a shadow casted by the animal's own body (i.e., self-shadow concealment). This may also conceal the three-dimensional form of the body (i.e., obliterative shading). In aquatic environments, where there is no background to match, camouflage could be achieved through transparency, where light transmitted through the body renders the bearer virtually invisible. The silvering flanks of many species of fish may function as camouflage too (Ruxton et al. 2004). The scales construct a reflective surface that hinders detection or recognition because the vertically aligned scales operate like tiny mirrors, thus letting its bearer blend in with scattered light. Masquerading organisms (e.g., decorator crabs, stick insects) share a resemblance to inanimate objects that are typically of no interest to a predator (Skelhorn and Ruxton 2010) such as twigs, leaves, or stones (or even bird droppings). Although categorizing different types of camouflage is a useful exercise to understand how they may work, it is important to acknowledge that they are not mutually exclusive and should be considered as a continuum of a set of adaptive traits (Fig. 1).

Advantages of Camouflage in Nature

Predation is one of the strongest selective pressures in nature. Camouflage confers increased survival benefits to prey either during vulnerable life stages or during the whole life of an organism. Early work on camouflage, such as classical work on grove snails and peppered moths, underlined the importance of background resemblance. Grove snails (*Cepaea nemoralis*) carry pale shells on grasslands, whereas snails from shaded woodlands carry darker shells. These differences in shell shading are plausibly caused by divergent bird predation on different colored appearances for better background resemblance in a given light environment (Cain and Sheppard 1954). Similarly, peppered moths (*Biston betularia*) were among the earliest well-documented examples of how camouflage brings survival benefits to its carrier. Peppered moths have two color morphs: pale and dark. The appearance of the pale morph resembles more deciduous, light-colored tree trunks, whereas the dark morph

Camouflage, Fig. 1 Illustrative examples of different camouflage types in nature. *Top left* is a rock ptarmigan, a grouse bird, which resembles its background, but also has disruptive markings. *Top right* lion cubs show the general resemblance to the background. *Middle left* is a common shrimp illustrating transparency, and *middle right* is a ghost crab, which matches its background. *Bottom left* is a *green shore* crab, which resembles its background, but also has strong contrasting markings to break up the body shape. *Bottom right* a dolphin, which has countershading to mitigate its own body shadows (All photos by Ossi Nokelainen)

matches the background best when resting on tree trunks darkened through pollution. Foraging bird predators can find mismatched moths on the tree trunks more easily, which facilitates increased matching to specific background types (Kettlewell 1955). It is important to remember that camouflage may also grant benefits to predators, particularly to those who ambush their prey, to which camouflage allows increased foraging success by getting close to their prey. For example, felid coloration often resembles that of the respective habitat's vegetation. By closely resembling the surrounds, these large carnivores are ought to be better able to approach the prey unnoticed before engaging the final pursuit to catch the prey (Caro 2005). Recent studies have quantified camouflage and its adaptive value more directly than classical accounts. It has become possible to quantify how likely an individual is to be attacked with respect to how closely the animal resembles its background as seen through the eyes of ecologically relevant receivers (Kelber et al. 2003). When detailed information of the receivers' vision, light conditions and color properties of the organism, and the background are obtained, the match to the background may be quantified. For example, a recent study of ground-nesting plovers demonstrated that nest survival in the wild is dependent on the degree of camouflage of the eggs (Troscianko et al. 2016). In plovers, parents flee the nest early when a predator approaches, leaving the nest and the eggs vulnerably exposed on the ground. In contrast, in birds like nightjars that sit tight on the nest even when a predator is close, nest survival is dependent on the level of match of the adult plumage.

How Plasticity and Behavior May Facilitative Camouflage

Coloration is not a static property and some animals may change their appearance over time (Stuart-Fox and Moussalli 2009). In fact, some animals achieve background resemblance through color change. Many taxa are capable of this ranging from insects and crustaceans to reptiles and amphibians. Perhaps most impressively, cephalopods can change body coloration within seconds by using specialized pigments in their skin under neural control (Hanlon et al. 2009). However, color change is slower than this in most animals. For instance, marine crustaceans shed their carapace as they grow, and it has been shown they may adjust appearance between molts for better crypsis (Stevens et al. 2013). Also behavioral plasticity can be used to enhance the camouflage. Many animals can choose backgrounds that match their own coloration better. Quail hen chooses substrates for nesting that provide better match their own egg colors (Lovell et al. 2013). Moths adjust their body orientation and position after landing on a tree to decrease visual detection (Kang et al. 2012). Blue-footed boobies (*Sula nebouxii*) change their egg colors by rolling them in dirt, which increases the background resemblance and decreases nest predation (Mayani-Parás et al. 2015). Decorator crabs adorn themselves by attaching pieces of objects such as seaweeds on their skin that increases the resemblance to the environment (Nokelainen and Stevens 2016). The Pacific tree frog (*Pseudacris regilla*) exhibits color pattern-mediated microhabitat selection so that, in the presence of predator cues, individuals prefer a substrate that matches their own color (Wente and Phillips 2005).

How the Efficacy of Camouflage Links to Evolutionary Psychology

Beyond sensory capabilities, cognitive processes inevitably influence what makes an effective camouflage (Skelhorn and Rowe 2016). When contrasting color patterns are combined with movement that exceeds the temporal resolution of the viewer's perceptual range, the colors appear to blend together (Stevens 2007). This physiological effect is known as flicker fusion. Movement may also create an illusion, which results in false interpretation of the direction and speed of the target, known as motion dazzle. Thus, variable stimuli have the potential to mislead animal's behavioral output. Similarly, predators have been demonstrated to be worse at finding camouflaged prey when prey populations are polymorphic (Bond 2007). This is because predators tend to focus on prey types that they have most recent experience with. The phenomenon is known as search image formation, which results in overlooking the rare morphs by predators. The followed evolutionary mechanism is known as negative frequency-dependent selection, which can maintain polymorphic prey by fluctuating morph frequencies (Gray and McKinnon 2007). Learning and cognitive processes may thus have a major effect on the value of different camouflage strategies. It is possible that predators learn some types of camouflage more quickly than others, especially the ones with high contrast markings. The value of a given type of protective coloration therefore depends not just on initial detection but also on experience and cognition.

Concluding Remarks

Despite being intuitively easy to understand, camouflage has proven difficult to study in natural settings. We still have a relatively limited understanding on the survival advantage that different types of camouflage provide to wild animals. Although categorizations are useful in order to understand how different forms of camouflage work, they may not be mutually exclusive. Recent technological advantages allow for tests of more detailed hypotheses regarding camouflage in more natural settings, taking into account animal cognitive processes and sensory stimulation across different modalities. Excitingly, we are about to understand how animals may see the world and how this may shape the preservation of the favored forms in the struggle of existence. This will expand our understanding on camouflage and the diversity that has succeeded over the course of time on inherited characteristics under natural selection.

Cross-References

- ▶ Background Matching
- ▶ Countershading
- ▶ Crypsis
- ▶ Disruptive Coloration
- ▶ Flicker-Fusion
- ▶ Masquerade
- ▶ Motion Dazzle
- ▶ Protective Coloration
- ▶ Self-Shadow Concealment

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