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Quick guide

Aposematism

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What is aposematism? The word comes from the Greek απο (away) and σεμα (sign) and describes a strategy whereby animals warn predators about their unprofitability. It consists of two elements: a primary defence, such as distinctive colours, odours or sounds, that operates before the predator attacks; and a secondary defence, be it chemical, morphological or behavioural that make prey unprofitable for predators. For example, the bright colours of many animals, such as poison frogs and wood tiger moths, warn predators about their toxic or distasteful chemical defences. When predators encounter and attack them in the wild, the prey will provoke a bad experience that the predator will learn to associate with the prey's colouration. As a result, predators will start to avoid defended prey. After several generations of coevolution, aposematic animals are often conspicuous and distinctive (Figure 1), but not all conspicuous animals are aposematic. Likewise, not all aposematic species are overtly conspicuous (Figure 1) and, thus, aposematism should be considered as a continuum of conspicuousness and secondary defence rather than as an unconditional anti-predator strategy.

How does aposematism evolve? Although it has been studied since the times of Wallace and Darwin, the origin and evolution of aposematism is not yet fully understood. Despite being clear evidence of natural selection, aposematism is somehow a paradoxical adaptation. It is unclear how the first conspicuous individuals were able to survive and reproduce such that predators would encounter them often enough to be able to learn about their unprofitability. Conspicuousness, as well as chemical defence, may have increased gradually. Alternatively, both defences could have been selected for other reasons (e.g. sexual selection). Moreover the initial cost of being conspicuous might be lower in environments where alternative prey is abundant, given that most predators prefer familiar over unfamiliar food objects. Aposematism has presumably evolved several independent times, as suggested by its occurrence in many groups of animals.

What are the theoretical assumptions about aposematism, and why is variation in warning signals puzzling? In order to work for the aposematic animal, signals have to be clear and easy to learn and remember for predators. Warning signals thus should evolve to be conspicuous and distinct. The more individuals bearing the warning signal, the more effective, easier to learn and memorable the signal will be for predators. Essentially, successful aposematism relies on strength in numbers. In fact, aposematism could have been initially favoured in aggregations of defended prey. Predators presumably also learn more easily to avoid one signal rather than several, and that their learning depends on the rate of unpleasant encounters with defended

Figure 1. Aposematic animals.
Top left: dyeing poison frog (*Dendrobates tinctorius*); top center: female of the wood tiger moth (*Parasemia plantaginis)*; top right: coral snake (*Micrurus surinamensis)*; Bottom left: Brazil's lancehead (*Bothrops brazili)* is not overtly conspicuous to us, but both the patterns and head shape of some vipers can function as warning signals to predators; bottom center: firebug (*Pyrrhocoris apterus)*; bottom right: common wasp (*Vespula vulgaris)*. (Photos: Bibiana Rojas; wasp: Tom Houslay).

prey. Thus, selection is expected to favour uniform warning signals and suppress variation. Nevertheless, warning signal variation is evident across the natural world. The mechanisms maintaining this puzzling variation are still poorly understood, but it is thought that this may arise for various reasons. Some warning signals may serve other purposes, such as intra-specific signalling, or be a response to different selective pressures which would trade-off with the pressure exerted by predators. For example, in the colour polymorphic wood tiger moth (*Parasemia plantaginis*), yellow males are generally better defended from predators. In contrast, under some circumstances, white males are more successful at mating and have higher flying activity, which might help them find emerging females quicker or compensate behaviourally for a less efficient anti-predator colouration. In cold environments, increased black wing pattern elements bring thermoregulatory benefits to these moths, but at the cost of reduced warning coloration (white or yellow). Recently, local predator communities have also been shown to aid in the maintenance of warning signal variation. Hence, it is likely that different properties of warning colouration become costly or beneficial in changing environments. Finally, it cannot be discarded that the variation is not adaptive, but the product of hybridisation or drift.

Are warning signals honest? According to the 'handicap principle', signals that provide reliable information about an individual's quality should be selected for. Such signals must be costly for the signaller and, thus, unaffordable for low-quality individuals. Warning signals can be honest, if they are reliable indicators of prey unprofitability. Therefore, secondary defences may vary as well, and this variation may by no means be less relevant. For example, in the strawberry poison frog (*Oophaga pumilio*) great variation in toxicity among populations is positively correlated with conspicuousness. Likewise, in the seven-spot ladybird (*Coccinella septempunctata*), the amount of coloured pigments correlates positively with the level of chemical defences. At least for the ladybirds, this correlation seems to depend on resource availability. This means that there can be costs associated with the production of primary or secondary defences, or both, that may affect the effectiveness of aposematism.

Are there cheaters? Yes. When predators learn to avoid a warning signal that is shared among aposematic individuals, organisms of other species may mimic that signal and get protection benefits without investing in secondary defences or predator education. In Batesian mimicry, a palatable organism is protected by its resemblance to an unpalatable one. Thus, Batesian mimics should not be considered aposematic, because they lack a secondary defence. The increase of Batesian mimics in a population decreases the efficacy of the signal, because predators start to ignore it as it becomes less reliable. Maybe the most well known Batesian mimics are hoverflies, which resemble wasps and bees. In Müllerian mimicry, on the other hand, two or more aposematic animals have evolved a similar appearance that is avoided by predators. Textbook examples include the famous *Heliconius* butterflies and dart poison frogs in the *Ranitomeya imitator* complex. In fact, mimicry is one of the first and strongest pieces of evidence for Darwinian natural selection.

Where can I find out more?

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Quick guide
Deaf white cats

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What are deaf white cats? The term 'deaf white cat' is used to describe domestic cats with completely white fur (short-hair or long-hair) that have no functional hearing; they typically have blue eyes (Figure 1A). It is estimated that in the overall cat population, 5% are white, and a subpopulation of these are blue eyed. As early as 1868, Charles Darwin noted in his book *The Variation of Animals and Plants under Domestication* that "white cats, if they have blue eyes, are almost always deaf". This observation has been substantiated in many subsequent studies. Deafness identified in white cats can be bilateral (both ears), or, less frequently, unilateral (one ear) with residual hearing in the opposite ear.

What makes deaf white cats so interesting? Any mammal can fail to develop functional hearing. In many species, such as domestic cats and dogs, there is a higher incidence of deafness in animals with a white coat. The association between white coat and deafness is greatest in white cats with blue eyes. Animals bred for this trait are a natural model for human congenital deafness. Consequently, deaf white cats are ideal for studying the effects of hearing loss on development and function of the auditory system. Furthermore, studies examining this animal model have demonstrated the beneficial effects of hearing restoration with cochlear prosthetics (implants). These experiments were essential for evidence-based recommendations on the treatment of congenital deafness in children. Today, approximately 400,000 hearing impaired individuals world-wide benefit from cochlear implants in their daily life. Given the present rate of implantation, the number of people using cochlear implants is projected to reach one million in 2020. Overall, the cochlear implant is the most successful neuroprosthetic device.