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Aposematism

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Synonyms

Warning coloration; Warning display; Warning signal

Definition

Anti-predator strategy in which prey exhibit warning signals coupled with some form of secondary defense.

Introduction

Among the many strategies that animals have evolved to deter predators, aposematism is one of the most intriguing. Already in 1877, Sir Alfred Russell Wallace provided thoughts about how distasteful butterflies would benefit from displaying "showy" colors that made them stand out among other butterflies. This, Wallace suggested, helped them being easily seen and recognized, and, consequently, avoided by their enemies (Wallace 1877). The term aposematism, first used by Sir Edward Poulton in 1890, is composed of two words of Greek origin, *apo* (away) and *sema* (sign) and refers to an anti-predator strategy that consists of the display of warning signals by prey in order to inform predators about their unprofitability (Poulton 1890). The warning signal, often a conspicuous color or pattern, a characteristic odor, or a distinctive sound, functions as a primary defense. This means that it operates *before* the predator attacks the prey. Prey unprofitability is in turn conveyed by any physical, chemical, or morphological attribute that deters the predator *after* the attack. These attributes are considered a secondary defense. Once the predator attacks the prey, it goes through an unpleasant experience that will evoke an aversive reaction to that particular kind of prey in future encounters. Thus, the predator learns the association between the warning signal and the secondary defense, which leads to aversion (Ruxton et al. 2004). Although aposematic organisms are frequently conspicuous, not all conspicuous animals are aposematic and, indeed, not all aposematic species are obviously conspicuous (Endler and Mappes 2004).

What Makes Warning Signals Efficient?

Warning signals are often distinctive and conspicuous, because they must be easy to recognize,

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learn, and remember for predators (Ruxton et al. 2004). For example, it has been suggested that red, yellow, and black are efficient warning signals because they endow a high contrast against most vegetation, but also because their appearance is relatively constant regardless the light environment (Stevens and Ruxton 2012). Furthermore, red and yellow are simply colors that undefended prey do not often bear, as they clearly increase prey detectability. A few studies have shown there is an innate bias toward these colors, but there is still evidence that, in most cases, this aversion is learnt. Colors such as red, yellow, and black (Fig. 1) combined with odors such as pyrazine are thus common features among aposematic prey.

Theoretical Expectations and Cognitive Aspects

Previous studies have shown that there can be some extent of innate aversion to certain colors and color patterns. However, there is also a wide consensus supporting the idea that learning is an important process involved in the eventual avoidance of aposematic prey by their predators. In that respect, a basic assumption of aposematism theory is that predators find easier to learn one signal to be avoided rather than several (Mappes et al. 2005). Therefore, natural selection is expected to exert a powerful pressure against warning signal variation. Despite this expectation, there are several aposematic organisms displaying variable warning signals even within the same population

Aposematism, Fig. 1. Examples of aposematism in nature. (**a**) *Arctia plantaginis*, the wood tiger moth; (**b**) Amazonian caterpillar (**c**) *Dendrobates tinctorius*, the dyeing poison frog; (**d**) a butterfly of the genus *Heliconius*. Note the prevalence of yellow and red in combination with *black* (polymorphism), spanning from insects and arachnids to amphibians and reptiles (Rojas et al. 2015). One among several non-mutually exclusive explanations for the maintenance of this variation is related to another cognitive process, *generalization*, which occurs when a predator transfers its learned avoidance from an aposematic prey to another one bearing a similar appearance. Aposematism, however, is not an all-or-none strategy (Mappes et al. 2005). Some aposematic prey are not overtly noxious but only have an unpleasant taste that does not represent a major risk for the predator. This illustrates how secondary defense is about relative profitability, as high toxicity is not required. Accordingly, predators in search of food are capable to assess the toxin content of some prey and decide whether or not to eat it depending on their hunger level and their previous toxic load.

Secondary Defenses Can Vary Too

In the same way that primary defenses are expected not to vary in order to enhance predator learning, secondary defenses are predicted to exhibit little or no variation within a population of individuals bearing the same warning signal. This variation is, however, more common than previously assumed (Speed et al. 2012). In fact, its implications are far from trivial for the dynamics of aposematism because individuals with weaker than average defenses may delay or obstruct predator learning, with negative consequences for the prey population. In several cases the production or sequestration of secondary defenses can be costly, as can be the production of the primary defense, and thus their effectiveness might depend on the availability of resources in the animal's environment. The variation in secondary defenses can be linked to a corresponding variation in the primary defense, such that stronger warning signals are coupled to more efficient secondary defenses. In these cases the warning signal might be considered an *honest* indicator of the quality of the secondary defense (Summers et al. 2015).

Variation in Secondary Defenses Can Lead to Cheating

Once a predator has learned to avoid prey bearing a particular warning signal, other prey sharing their appearance can gain protection too (Ruxton et al. 2004). This has given rise to the imitation of the warning signal by individuals of a different species who lack the secondary defenses. Thus, the non-defended species gets protection from predators without having to incur the expenses that the secondary defenses entail. This phenomenon is known as *Batesian mimicry*, and it works only if the number of "cheaters" (i.e., the non-defended individuals) is kept under a threshold where predators have still enough encounters with defended prey to maintain the aversion. Textbook examples of Batesian mimicry include the coral snakes, which serve as models to species of brightly colored, non-defended, or mildly defended colubrid snakes, and the swallowtail butterflies in the genus *Papilio*, whose coloration mimics that of several different species of unpalatable butterflies. But Batesian mimicry can also occur between animals of completely different groups, such as the nestling of the Cinereous Mourner bird whose coloration and behavior resemble an aposematic caterpillar. It can also be the case that two or more defended species share a common warning signal, in a phenomenon known as *Müllerian mimicry*. This results in a benefit for all species involved because they share the costs of predator education, decreasing the per capita risk. Among Müllerian mimics, probably the best well-known cases are the *Heliconius* butterflies and the frogs in the *Ranitomeya imitator complex,* both of which occur in the Neotropics.

How Does Aposematism Originate and Evolve?

One central question in evolutionary biology is how the first aposematic individuals appeared and, most importantly, managed to multiply and spread (Mappes et al. 2005). This is puzzling because presumably the first individuals showing, for instance, conspicuous coloration would have been easy to detect for predators (Alatalo and Mappes 1996). Thus, those prey would have been injured or killed without being able to reproduce and reach the numbers required in order to elicit avoidance learning in predators. Likewise, the first defended prey that did not display a memorable signal, such as conspicuous coloration, would have been eaten without offering learning possibilities to the predator, who would have found more difficult to associate dull-colored prey with their unprofitability. This paradox has been under active debate and is still partly unresolved. However, some explanations have been proposed. For example, it has been suggested that both the primary and secondary defenses may have increased gradually or that both defenses may have first been associated with a selective pressure other than predation. In addition to these, there is some empirical evidence that predators such as birds are often reluctant to attack unfamiliar prey items for either short (neophobia) or prolonged periods of time (dietary conservatism). In this context, especially if familiar prey are available and abundant, these biases may favor the rise and spread of novel color morphs and would have thus allowed for the spread of the first aposematic individuals. Other studies suggest that aposematism might have first appeared, and been favored, in aggregations of defended prey (Alatalo and Mappes 1996). This is because processes of learning and memorization of a signal will work better the more common the signal is. In other words, a predator is more likely to learn about the unprofitability of certain prey, if it encounters it frequently (Endler and Mappes 2004). Thus, the success of aposematism relies on "strength in numbers."

Aposematism and Multimodality

Aposematic organisms can have warning displays that stimulate two or more sensory channels in the receiver, the predator, in this case. For instance, they can stimulate their visual system when detected and then their taste receptors when attacked. For this reason, warning displays are thought to be multimodal (Rowe and Guilford 1999). Multimodal warning displays are assumed to improve associative learning, the type of learning that predators go through, because they supply more information than displays consisting of just one sensory modality. Consequently, the interaction between two types of signals (say visual (color) and chemical (taste)) is predicted to be more effective than each signal separately. Relatively recently researchers have started to redirect their attention to the role of multimodality in the dynamics of aposematism.

Conclusion

Aposematism is a strategy by which prey deter predators combining an easy-to-recognize and memorable warning signal with some type of secondary defense. As a result of coevolution between predators and prey, aposematic species are often conspicuous. Yet, not all conspicuous organisms are aposematic, just like not all aposematic individuals are conspicuous. For this reason, aposematism should be deemed as a continuum of warning signal conspicuousness and secondary defense efficiency rather than as an all-or-none anti-predator strategy. There is still much that warrants in depth investigation about the underpinnings of aposematism. For instance, it is essential to investigate in depth the role(s) of variation in predator community composition, as well as of interindividual differences in cognitive abilities among predators, in the evolution of warning signals, and the rise and maintenance of warning signal variation. Likewise, more attention should be given to the existing variation in secondary defenses and its function(s) in the interactions between predators and prey. Also, more studies are needed to gain a better understanding of the costs of both primary and secondary defenses and whether the resources for their production or sequestration are antagonist or synergistic. Finally, it is necessary to increase current knowledge on the link(s) between warning signals and secondary defenses, and life-history, behavioral, and ecological traits.

Cross-References

- ▶ Batesian Mimicry
- ▶ Müllerian Mimicry
- ▶ Secondary Defence

References

Alatalo, R. V., & Mappes, J. (1996). Tracking the evolution of warning signals. *Nature, 382*, 708–710.

Endler, J. A., & Mappes, J. (2004). Predator mixes and the conspicuousness of aposematic signals. *The American Naturalist, 163*, 532–547.

Mappes, J., Marples, N., & Endler, J. A. (2005). The complex business of survival by aposematism. *Trends in Ecology & Evolution, 20*, 598–603.

Poulton, E. B. (1890). *The colours of animals: Their meaning and use*. London: Kegan Paul, Trench, Trubner.

Rojas, B., Valkonen, J. K., & Nokelainen, O. (2015). Aposematism. *Current Biology, 25*, R350–R351.

Rowe, C., & Guilford, T. (1999). The evolution of multimodal warning displays. *Evolutionary Ecology, 13*, 655–671.

Ruxton, G. D., Sherratt, T. N., & Speed, M. P. (2004). *Avoiding attack: The evolutionary ecology of crypsis, warning signals and mimicry*. Oxford: Oxford University Press.

Speed, M. P., Ruxton, G. D., Mappes, J., & Sherratt, T. N. (2012). Why are defensive toxins so variable? An evolutionary perspective. *Biological Reviews, 87*, 874–884.

Stevens, M., & Ruxton, G. D. (2012). Linking the evolution and form of warning coloration in nature. *Proceedings of the Royal Society of London B, 279*, 417–426.

Summers, K., Speed, M. P., Blount, J. D., & Stuckert, A. M. M. (2015). Are aposematic signals honest? A review. *Journal of Evolutionary Biology, 28*, 1583–1599.

Wallace, A. R. (1877). The colours of animals and plants. *The American Naturalist, 11*, 641–662.