A

Aposematism

Sandra Winters
New York University, New York, NY, USA

Synonyms

Warning coloration; Warning displays; Warning signals

Definition

A characteristic that signals to potential predators that an animal is unprofitable as prey

Introduction

Many animals are toxic, unpalatable, or otherwise unsuitable as prey items to potential predators. Such species often advertise their unprofitability to predators using warning signals, which is referred to as aposematism. This is generally advantageous to both predator and prey: the former avoids the costs of pursuing an unsuitable meal (ranging from wasted energy to illness or death) and the latter avoids a predation attempt. Aposematic signals contain two components: a secondary defense used upon attack by predators – such as chemical toxicity – that makes the prey unprofitable and a primary defense – such as a distinctive color or odor – that advertises this unprofitability and therefore functions to prevent attack. For instance, ladybird beetles are toxic to predators and advertise this with brightly colored (red, orange, or yellow) wings with black spots (Arenas et al. 2015). Aposematism is a well-studied topic within evolutionary biology, and aposematic signals have been found in many species across the animal kingdom. Extensive research has also been conducted documenting both learned and naïve predator responses to aposematic prey.

The concept of warning signals was originally proposed by Alfred Russel Wallace (1889) as an explanation for the bright colors often displayed by caterpillars, which at the time were seemingly at odds with the theory of natural selection. Wallace referred to the advertisement of noxious qualities as "warning coloration," and the vast majority of early studies focused on colorful aposematic signals in the visual modality; however, warning signals have now been demonstrated in many sensory modalities and aposematic signals can include visual, acoustic, olfactory, gustatory, and behavioral components. The term "aposematism," derived from the Greek απο (away) and σεμα (sign), was coined by Edward Poulton (1890) to describe Wallace's concept of warning coloration in his proposed nomenclature of antipredator defenses.

J. Vonk, T. K. Shackelford (eds.), *Encyclopedia of Animal Cognition and Behavior*,
https://doi.org/10.1007/978-3-319-47829-6_313-1

Evolving Aposematism

Aposematism has been characterized as a paradoxical adaptation. Whereas there are clear benefits to advertising unpalatability to predators and aposematic signals have been documented in many species, the processes by which aposematic traits have originated are less straightforward. The effectiveness of aposematic signals increases with their density, yet aposematic species are also generally more conspicuous than their cryptic counterparts. How would the first individuals with mutations that increase conspicuousness survive long enough to facilitate predator learning and therefore gain a selective advantage?

Multiple hypotheses have been proposed to address this "rare conspicuous mutant" problem (reviewed by Mappes et al. 2005; Ruxton et al. 2004; Skelhorn et al. 2016). Some focus on stochastic events such as the temporary absence of predators, chance survival of mutants, or random shifts in prey population dynamics. If aposematism evolves by chance in one region, it can then spill over into neighboring populations. Species traits may also be important. A tendency for similar individuals to aggregate (potentially but not necessarily because they are closely related) could give rise to aposematism because the concentration of similar prey items aids in predator learning and dilutes the costs per individual, thus allowing even a small number of early aposematic individuals to give rise to predator avoidance. Similarly, better secondary defenses in conspicuous individuals can lead to increased survival rates from predation attempts and quicker predator learning. Characteristics of predator psychology and perceptual mechanisms may also be important. Predator characteristics such as neophobia (avoidance of novel items) and dietary conservatism (a preference for familiar food items) may explain the perpetuation of early mutants. Conspicuous aposematic signals may also interact with predator perceptual systems in ways that facilitate rapid learning and retention. Predatory-prey dynamics may also play a role. For instance, the presence of more profitable prey species may ease selection for crypsis, and there is increasing evidence that strategic decision making by predators may be important. Multiple explanations can also be combined into more complex models of the evolution of aposematism, and modeling and simulation studies have demonstrated varying circumstances in which aposematism can arise and be maintained.

Another option is to circumvent the rare conspicuous mutant problem, postulating that aposematism can originate without an initial mutation event (reviewed by Ruxton et al. 2004). Aposematic signals could arise because they confer advantages in other contexts such as mating (i.e., via sexual selection), foraging, or thermoregulation, with evolution proceeding based on multiple selective pressures. Similarly, when prey are densely populated and the likelihood of detection by predators is high, relaxed selection on crypsis may allow for the evolution of aposematic signals. Aposematism could also develop following a rapid environmental change that causes a previously cryptic signal to become conspicuous. Finally, when defenses are visually apparent, such as sharp spines, increased conspicuousness may simply amplify the salience of an existing visual cue. It is important to note that these hypotheses are not mutually exclusive, and that aposematism, which has evolved multiple times across animal groups, may have done so via different routes in different species.

Phylogenetic analyses and reconstructions can be informative when studying trait evolution and can help to understand the context in which aposematism has arisen (reviewed by Härlin and Härlin 2003; Ruxton et al. 2004). For instance, in some animal groups aposematism is associated with prey aggregation, but aposematism appears to be the older trait, suggesting that prey aggregations were unlikely to have influenced its evolution. More research involving phylogenetic comparative analyses is likely to uncover other interesting trends.

Signal Form

Why do aposematic signals look the way they do? A good warning signal should facilitate predator learning and long-term avoidance. Although aposematic signals are diverse, they also share many common characteristics that are related to their function.

Aposematic signals are generally conspicuous and include components such as bright colors or strong odors. There are a variety of (non-mutually-exclusive) reasons why conspicuous colors may be particularly suited to a warning signal (reviewed by Ruxton et al. 2004; Stevens and Ruxton 2012). Conspicuousness can facilitate detection by predators at a distance and may prevent cases of mistaken species identity. Conspicuous signals may also facilitate predator avoidance due to biases in predators' psychology. Conspicuous signals may enhance predator wariness, accelerate predator learning, decelerate forgetting, and increase prey recognition accuracy relative to other types of signals. They might also help to maintain an honest system (see next section) because the costs of conspicuousness without a backup secondary defense are too high for other species to pay. Whereas conspicuousness is often considered a defining trait of aposematism, the benefits of conspicuousness may saturate, however, leaving some aposematic species only moderately conspicuous. This may be caused by factors such as physiological costs to signal production, variability in predator behavior, trade-offs between various selective pressures, or viewing distance effects.

In addition to general conspicuousness, aposematic signals often include other similar elements (reviewed by Ruxton et al. 2004; Stevens and Ruxton 2012). Simple patterns with repeated elements are common. Simple patterns and redundant components may facilitate predator learning, and repeated elements may also increase contrast if they are rare in the environment. Aposematic signals also often involve similar colors, generally reds, yellows, and black. This could be because by using similar colors, aposematic species can reduce species-level learning costs when predators learn (either individually or across evolutionary time) to generally avoid these commonly aposematic colors. In Müllerian mimicry (this volume), multiple aposematic species converge on a very similar phenotype, which is beneficial to all species involved. However, the common use of reds, yellows, and black may also be related to characteristics of the environment. Compared to other colors, reds and yellows contrast strongly against a green foliage background, remain distinctive in different lighting conditions, are distinctive in terms of both color and brightness, are distinctive from many other species, and may blend at a distance to create distance-dependent camouflage (i.e., the prey is camouflaged to avoid detection at a distance, but once a predator gets close they are conspicuous and advertise unprofitability) (Stevens and Ruxton 2012). This highlights the importance of considering ecology and species characteristics (e.g., different predators see colors differently) when studying aposematic signals.

Despite these general characteristics, aposematic signals remain variable both within species and between closely related species (Stevens and Ruxton 2012). This is somewhat puzzling because selection would be expected to favor close similarity between signals to facilitate predator learning. This diversity could be maintained by variation in the environment or predator community (e.g., across seasons or space), which could cause different morphs to be more successful in different times or areas. Additional selective pressures may also be involved, with phenotypes representing a trade-off between aposematism and other factors such as sexual selection.

Signal Honesty

Do aposematic signals consistently reflect underlying qualities linked to prey unprofitability? Work on honest signaling has often focused on the handicap hypothesis (this issue), which posits that high costs associated with producing signals can prevent cheaters because low quality individuals cannot afford to pay. But aposematic signals are not necessarily handicaps and the mechanisms of signal production and secondary defenses are not always linked (Guilford and Dawkins 1993; Ruxton et al. 2004). Conspicuous aposematic signals are often honest indicators of prey unprofitability in a qualitative sense because prey without secondary defenses such as toxicity are not able to pay the survival costs of being more noticeable to predators (reviewed by Summers et al. 2015). Without the secondary defense to back them up, the conspicuous signals associated with aposematism would lead to increased predation rates and lower fitness. The major exception is Batesian mimicry (this volume), in which an unprotected species mimics an aposematic species to gain the fitness advantages enjoyed by the latter without incurring the costs of defense. Batesian mimicry is well documented, but the local population density of mimics tends to be lower than that of the aposematic species they mimic because as the ratio of honest signalers to cheaters increases the degree of protection offered by the signal decreases.

Some aposematic species also exhibit quantitatively honest signals, where there is a positive correlation between the strength of aposematic signal and degree of unprofitability to predators (reviewed by Summers et al. 2015). This appears to be less common than qualitative honesty, although more research is needed. Quantitatively honest aposematic signals may be particularly likely when the signal is morphologically or physiologically linked to the method of defense.

Conclusion

Aposematism has been a major research focus of biologists since the early days of evolutionary thinking. While the benefits of advertising unprofitability to predators seem straightforward at face value, some aspects of aposematism are perplexing, including aspects of its origin, the presence of intragroup variability, and less conspicuous aposematic signals. Aposematism remains a common interest in biology, and continued work in this area will likely contribute to our knowledge of the process of evolution and the mechanisms that generate the incredible diversity of life on earth.

Cross-References

▶ Alfred Russel Wallace
▶ Avoidance
▶ Batesian Mimicry
▶ Communication
▶ Foraging
▶ Honest Signaling
▶ Interspecific Discrimination
▶ Mullerian Mimicry
▶ Neophobia
▶ Predator Defense
▶ Primary Defenses
▶ Risk-Sensitive Foraging
▶ Secondary Defenses
▶ Visual Recognition of Prey and Predators

References

Arenas, L. M., Walter, D., & Stevens, M. (2015). Signal honesty and predation risk among a closely related group of aposematic species. *Scientific Reports, 5*, 11021.

Guilford, T., & Dawkins, M. S. (1993). Are warning colors handicaps? *Evolution, 47*, 400–416.

Härlin, C., & Härlin, M. (2003). Towards a historization of aposematism. *Evolutionary Ecology, 17*, 197–212.

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

Poulton, E. B. (1890). *The colours of animals: Their meaning and use, especially considered in the case of insects*. New York: D. Appleton and Company.

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

Skelhorn, J., Halpin, C. G., & Rowe, C. (2016). Learning about aposematic prey. *Behavioral Ecology, 27*, 955–964.

Stevens, M., & Ruxton, G. D. (2012). Linking the evolution and form of warning coloration in nature. *Proceedings of the Royal Society B: Biological Sciences, 79*, 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. (1889). *Darwinism: An exposition of the theory of natural selection with some of its applications*. London: Macmillan and Co.