Reliability in aposematic signaling
Thoughts on evolution and aposematic life

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In light of recent work, we will expand on the role and variability of aposematic signals. The focus of this review will be the concepts of reliability and honesty in aposematic signaling. We claim that reliable signaling can solve the problem of aposematic evolution, and that variability in reliability can shed light on the complexity of aposematic systems.

Reliability and Honesty

What constitutes honesty and reliability? A signal can not be reliable without also being honest. Regardless of this connection, these concepts are quite different in their function and nature. Honesty is from the perspective of the prey, while reliability pertains to the predator. An honest signal is honest at all times, so long as the signal is supported by an actual defense. Sadly, honesty does not go a long way in aposematic signaling. From the predators point of view, there is now way of knowing whether a purely symbolic (non reliable) signal is honest or not. As we shall see, this fact opens the door for the parasitizing of symbolic honest signals (batesian mimicry) and also gives rise to the long standing problem of explaining the evolution of warning coloration.

All aposematic signals which are supported by low profitability or a cost to the predator, for instance low nutrient content, long handling time, toxicity, ability to bite back, are good, honest aposematic signals. They are also reliable, but the important point is that they are not reliable all the time. An aposematic signal becomes reliable the moment the unprofitability/cost is inferred on the predator. The unpalatable prey’s signal becomes reliable when the predator perceives its foul taste, the toxic prey’s signal becomes reliable when the toxins start to adversely affect the predator (post-ingestion), the spiny animal’s signal is reliable the second it pricks the predator, the signal of the prey with the long handling time becomes reliable when the predators waste time on it and the released volatile toxin is a reliable signal when it causes discomfort. It is this reliability, i.e., the defense, that is the basis on which aposematism stands.

To our knowledge, apart from our recent publication, where we propose that odor signals can be reliable, and a short note by Harvey and Paxton, which also mentions olfactory cues, unpalatability is the only signal that has been described as reliable.

Evolutionary Aspects

It is a matter of logic that a toxic insect can cause greater harm if it is ingested. From the prey individual’s point of view this is not the best approach. It does not benefit the prey to harm the predator if the prey dies in the process. For prey where other signaling individuals are related, such post-ingestion toxicity can be explained by kin selection arguments. However, when aposematism first evolved, the initial small sibling group of signaling individuals would have been quickly eaten and the lesson taught by the post-ingestion toxicity would not stand to benefit any siblings as there would be none left. The same logic applies to unpalatable animals, so long as they are killed when tasted. Any visual warning signals of such prey would likely have been remembered and avoided by the predators who sampled the toxic/unpalatable prey, but by that time the aposomes, and with them the signal, would have gone extinct. Signals which are reliable at an earlier point in the predator-prey interaction can solve this problem of sampling by uninformed predators. If prey can provide the predators with reliable information regarding their (low) profitability without themselves being harmed or killed, the “classic problem” of aposematic evolution falls. If we focus on chemically defended prey, there are two signal forms which can provide reliable information at an early enough point in time, namely taste and odor.

As we have already established, for the successful evolution of aposematic traits, the first signaling individuals must avoid being eaten. By this standard, taste is not the best signal form. However, some predators have the ability to taste their prey without actually harming them. Common Mynah (Acridotheres tristis) have been observed catching butterflies in mid flight, only to reject them unharmed after a second of tasting/smelling. This is a good strategy, as seen from the point of view of the predator. If the prey has a detectable amount of unpalatable compound on its surface, it pays not to crush the exoskeleton of the insect, releasing still more noxious substance/toxins. If we assume that unpalatability evolved before visual warning signals, such cautious predation probably also evolved before visual warning signals. It may have provided a last line of defense against predators. Such prudent precision would probably have required quite some time to evolve, so the time period between the evolution of defense and...
visual cues would have had to be substantial, which is a drawback for this hypothesis. Regardless, taste could have provided the necessary protection during the initial phase of the evolution of visual warning signals. There is a more substantial problem with this evolutionary path however, as not all predators of defended insects are cautious.

Odor has the upper hand on taste, based on the fact that odor signals are reliable over long distances and therefore do not require direct contact between the predator and prey. Although insects can survive being tasted by certain predators, to completely remove the physical interaction is a far superior strategy. Tasting and rejecting prey is time consuming for both parties, and the level of stress inflicted on the prey could only stand to affect it adversely. Odor, in our opinion, has rarely received its deserved recognition as an aposematic signal. Although odor has been discussed in the context of multimodality, where several signals act together to increase the effectiveness of information transfer and/or facilitate learning in the predator, odor on its own has been largely overlooked as an evolutionary force in aposematic lore. Both Coté \(^7\) and Rothschild \(^8\) expanded on how odors could act as both signals and deterrents, but no one has to our knowledge proposed that this duality could explain how aposematism first evolved.

If the reliable odor component precedes the visual component, the classical problem of prey sampling is removed, and the evolution of warning coloration is unproblematic. If a reliable odor signal evolves, the next natural step is to increase the diversity and distance at which signaling is functional. In our recent publication, we discussed how a visual signal will also increase the assessment period of the odor signal and result in a divergence from the cryptic strategy, and hence the searching image of the predators. \(^7\) We conclude that the probability of predators making mistakes (with regards to the odor signal), in spontaneous attacks, is reduced once a visual warning signal/high conspicuousness evolves. In addition to the other positive effects coupled to the use of more than one aposematic signal, i.e., multimodality and signal diversification, olfactory aposematism paves the way for the evolution of warning coloration.

**Aposematic Life**

Not only is odor a potentially reliable signal, which provides a solution to the evolution of aposematism and warning coloration, but it works together with visual cues to diversify the act of signaling. It is unclear whether all odor signals are reliable, and if such reliability is strictly concentration dependent. If we assume that reliability of odors are concentration dependent, and that many aposomes do not secrete sufficient amounts to produce deterrence, an explanation is required. How could then odor signals solve the problem of aposematic evolution? The explanation is provided by the cost of constantly secreting large amounts of toxins. Considering the fact that the classic visual signals, i.e. red and yellow/black, are apparently etched in the genetic memory of, at leastsome, predators, \(^9\) and since the loss of a few individuals to unexperienced predators is no longer of great consequence, the use of costly reliable predators are no longer economically sound. As we have seen, odor signals have many advantages beyond reliability when coupled to visual cues, and although reducing the amounts secreted *may* result in a purely symbolic odor signal, this is probably still the best strategy given the level of education among the predators. This idea shows how one has to apply different perspectives when discussing the initial evolution of aposematism and aposematic life. At present, an olfactory component in signaling provides diversification, not only in which habitat and situation an animal can convey information, but also to what predators. Very few animals are confronted with only one species of predator, and many are confronted by several species of predators with completely different sensory abilities. Most mammals are colorblind, and highly dependent on smell, which makes warning coloration a poor strategy (contrasts may be of importance) for conveying information regarding defense. However, insect aposomes are on a large scale predated on by birds, which might seem paradoxical in a discussion of olfactory signaling should on maintain the position that birds lack the sense of smell, but the misconception that birds are not reliant on smell in their everyday lives is rapidly being identified as scientific dogma. Recent work shows that many of bird species have a good sense of smell. \(^11,12\)

The effectiveness of odor signals is subject to many factors, such as wind, turbulence, barometric pressure and temperature. \(^13\) In most cases, odor also work over shorter distances than do visual cues. In some situations however, the tables are turned. Visual cues are nearly worthless in some habitats. Shrews for instance, are most likely olfactory, as well as auditory, aposomes, since visual signals are not effective in their habitat of tall grass and dense vegetation. Odors can circumvent physical objects between sender and recipient. With this perspective, it only stands to reason that for many aposomes, implementation of several different signals is a highly profitable strategy. It is difficult, but none the less important to keep in mind that the optimal strategy for any given individual is more or less in constant motion. The perfect signaling tool can never exist, as the habitats in which a organism travels, and the predators with which it is confronted are (for most animals) never static for long periods of time.

As many aposomes are subjected to one or a few “immune predators”, there is another level of variability in signaling that comes into play. Some signals can stop operating by choice of the individual. When such signals are implemented, the prey has the ability to choose between a cryptic and an aposematic strategy. Odor secretions that are controlled by glands, and of course most auditory signals can be controlled. Most visual signals are not controllable, but an interesting exception exists in the fire-bellied toad (*Bombina bombina*), which has warning coloration markings on its belly, and can choose to unkenreflex (defense posture) and actively display its underside. \(^14\) The unkenreflex pose is also utilized by the rough-skinned newt (*Taricha granulosa*), who at the same time releases toxic secretions from its skin. \(^15\) It is interesting to note that the rough-skinned newt, which has “on-off signals” is on a large scale predated on by a predator which shows “geographically variable resistance” to the newt’s toxin tetrodotoxin, \(^16\) namely the common garter snake (*Thamnophis sirtalis*). It is clear that the strategy of choosing when to signal or not has its advantages. However, in many situations constant signaling is
The literature on aposematism is filled with examples of Batesian mimicry, but as one would expect, these are limited to mimicry of purely symbolic signals, i.e., visual and auditory signals and behaviour. Odor signals are also widely mimicked, but in a Müllerian fashion, a type of mimicry where several defended species are mimicking each other's signals, which is a form of cooperation. Interestingly, Müllerian mimicry is also employed by highly unrelated species, which indicates convergence. To our knowledge, there is not a single example of Batesian mimicry of odor signals. This once again illustrates the importance of reliable signals and the protection they can provide, not only against predation, but also against signal parasitism.

Mimicking Different Signals

For defended organisms, there is a considerable cost involved with being mimicked by another undefended species, a phenomenon known as Batesian mimicry. If the mimicry is sufficiently convincing, the predators cannot know if the signaling individuals are defended or not. This will result in misguided predation attempts on the model population, which suffers a considerable cost due to the parasitic behavior of the Batesian mimic.

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