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Update

Aposematic coloration

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A discussion of the evolution of conspicuous coloration in distasteful prey

Introduction

'And as they walked Piglet said nothing, because he couldn't think of anything, and Pooh said nothing, because he was thinking of a poem. And when he had thought of it he began:

What shall we do about poor little Tigger?
If he never eats nothing he'll never get bigger.
He doesn't like honey and haycorns and thistles
Because of the taste and because of the bristles.
And all the good things which an animal likes
Have the wrong sort of swallow or too many spikes.'

(A. A. Milne, *The House at Pooh Corner*, 1928)

Being eaten is terminal. In response, prey have evolved numerous methods for defending themselves (Edmunds, 1974; Endler, 1991). Some species blend in with their background, a ruse adopted by Pooh when we last met him, ballooning into the sky in a vain attempt to raid the bees' honey (Allen and Cooper, 1985). Others display conspicuous coloration, which predators learn to associate with distastefulness ('because of the taste and because of the bristles'), so that they are less likely to attack on subsequent encounters with the same sort of prey. Most of us are aware of the effectiveness of such 'aposematic' or 'warning' coloration, as demonstrated by our antics when disturbed by a wasp with its vivid yellow and black markings, loud buzz and casual 'advertising' flight. In the wild, experienced vertebrate predators avoid wasps and other aposematic species with similar wariness.

Abstract
Aposematic prey are distasteful and conspicuously coloured. Aposematism is adaptive because visually hunting predators learn to associate the coloration with the distastefulness, and thereby avoid prey of the same appearance. Its evolution raises at least three major problems for biologists, which can be used to stimulate classroom discussion on the process of evolution.
Key words **Aposematic coloration, Evolution, Predation.**

Aposematism is a thought-provoking topic for discussion of the mechanisms of evolution. The evolution of cryptic coloration (for example, in the peppered moth, *Biston betularia*) is not too difficult to understand because cryptic varieties are less detectable than conspicuous varieties, and so will be correspondingly fitter. But imagine a population of an ancestral palatable cryptic species (figure 1(a)) which, for some reason, evolves distastefulness (figure 1(b))—perhaps because it is a herbivorous insect whose larvae have adapted to a new food plant. A conspicuous mutation now appears (figure 1(c)). All seems set for the evolution of aposematism (figure 1(d)) but, in fact, this outcome is by no means guaranteed, for at least three important reasons (Endler, 1991; Guilford, 1990a).

The problems

The first obstacle is one of simple logic: how can the genes of a rare conspicuous form survive and spread (figure 1(c), (d)) when predators have to eat it to learn that it is distasteful? This is a telling question to ask a biology class; if they fail to see the paradox, then they have yet to master the concept of natural selection! One solution they may discover is that learning takes place after the prey has been attacked but *before* it has been consumed. If this were true, then aposematism should be more likely to evolve in prey that are capable of surviving at least as long as it takes their unpleasant properties to register with the predator (Wiklund and Järvi, 1982). Aposematic species do tend to be very resilient in their morphology and physiology, but this has usually been assumed to be a consequence of

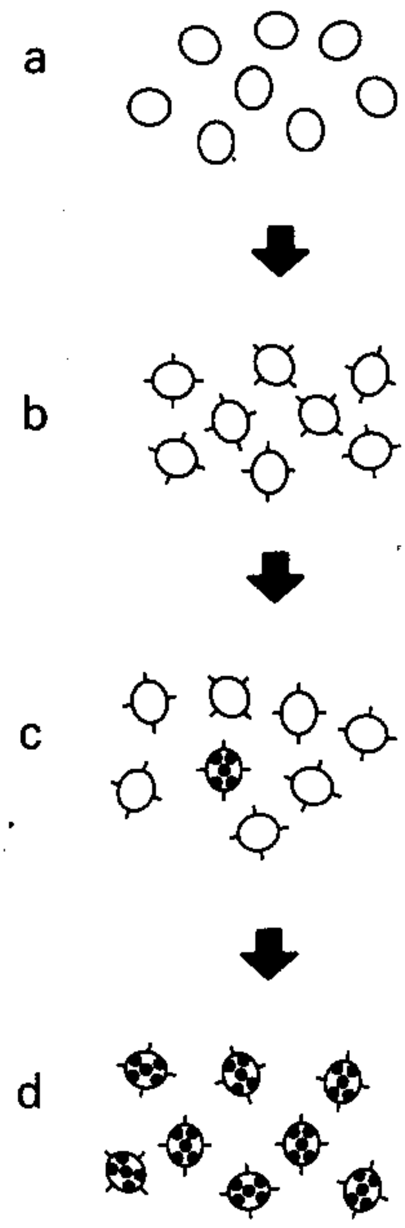

Figure 1 The evolution of aposematism: (a) an ancestral population of cryptically coloured individuals; (b) distastefulness (represented by prickles) evolves; (c) a conspicuous (spotted) mutant appears; (d) the conspicuous mutant spreads, but how? See text.

aposematism rather than a cause. Another possible solution to the paradox is that the attacked mutant does indeed die, but thereby decreases the chances of like-coloured individuals suffering the same fate. Like-coloured individuals will benefit from such altruism whether they are related ('kin selection') or not ('green beard effect' or 'synergistic evolution'); for a more detailed discussion, see Dawkins, 1976; Guilford, 1985; Maynard Smith, 1989.

Whichever reason is correct, the mutant variety must be fitter than the common cryptic form, otherwise the genes will fail to spread. This brings us to the second problem: why should a conspicuous coloration give greater protection than an inconspicuous one? Endler (1991, after Guilford, 1990a) lists four possible answers. First, predators may more quickly learn to associate a colour pattern with distastefulness when it is conspicuous rather than inconspicuous. Second, certain patterns may be easier to associate with distastefulness, and these happen to be conspicuous (for a short discussion on this possibility, see Guilford, 1990b). Third, patterns which are new may be easier to remember. Fourth, conspicuousness may reduce recognition errors; perhaps because predators can detect brightly coloured prey from a long distance, and thereby have time to reconsider the decision to attack (Guilford, 1985, 1992). There is some experimental evidence in support of the first hypothesis (Endler, 1991), but not all the studies controlled for the three alternative explanations. This also raises the important point that the four solutions are not necessarily exclusive of one another; in theory, all of them could contribute to the evolution of conspicuousness.

We should also consider the possibility that avoidance of certain colour patterns may sometimes be innate rather than learned. An innate aversion is especially likely when the aposematic species is lethal, an idea that is supported by observations on the behaviour of hand-reared motmots (*Eumomota superciliosa*), predatory birds that live in the same neotropical environment as the highly poisonous and apparently aposematic coral snakes of the genus *Micrurus* (Smith, 1975). These birds instinctively avoid wooden models with the same coloration as the snakes. There is also evidence that domestic chicks have an innate tendency to avoid certain colour patterns such as yellow-and-black stripes, but it is curious that they actually seem to prefer to attack objects with red-and-black stripes, another pattern commonly adopted by aposematic prey (Roper and Cook, 1989; Guilford, 1990b).

We now come to the third problem. Predators will encounter the rare conspicuous variety so infrequently that they may fail to remember that it is distasteful. They will then eat the conspicuous form disproportionately more often than the cryptic form, and we are again faced with the question of how rare conspicuous mutants spread. Endler (1988, 1991) and Guilford (1992) discuss six possible answers to the problem, all of which are virtually untested. First, the frequency of the rare variety could increase by random processes, such as genetic drift. Second, aggregation of kin could locally increase the density of individuals carrying the rare gene. Third, predators may tend to overlook rare varieties of prey, irrespective of their palatability and conspicuousness (Allen, 1988; Allen and Cooper, 1988). Fourth, if the mutant differs but slightly from the ancestral form, experiences with the latter may help 'remind' the predator of the mutant's distastefulness when next encountered. Fifth, the ancestral cryptic population may be composed of individuals that differ in their degree of crypsis, so that the conspicuous form is already at a high density. Sixth, if an insect becomes noxious because it has shifted to a new host plant, its coloration is likely to be more conspicuous than it was when on the original species. The astute student may think of further reasons. For example, he or she may question the basic assumption that crypsis, because of its ubiquity, is ancestral. Is it not possible that early organisms retained many of their metabolic by-products and were thus distasteful?

Once the new variety is sufficiently common, predators should learn quickly that it is distasteful. Populations of aposematic species should consist of individuals that are identical in their colour-patterns, because predators will more readily associate distastefulness with one colour pattern, rather than two or more. The commonest form will tend to become increasingly common and will eventually become 'fixed' in the population. This is the variety that will be encountered the most frequently, and therefore will 'train' the predators the most effectively. It is something of a surprise, then, to find that the populations of some aposematic species are polymorphic. Well-known examples are the two-spot ladybird beetle (*Adalia bipunctata*) in Europe, several species of Acraeid and Danaid butterflies in Africa, and Heliconiid butterflies in central and south America (Edmunds, 1974; Endler, 1991). Once again, aposematism has thrown up a testing little problem to exercise the enquiring mind.

Several explanations have been proposed (see, for example, Brakefield, 1985). The variants may only occur where two geographical races meet, and this seems to apply to some of the Heliconiid butterflies (Brown and Benson, 1974; Mallet and Barton, 1989). In many species, including *A. bipunctata*, racial hybridization can be ruled out. Sometimes the polymorphism may be maintained by non-random mating (Majerus, O'Donald, and Weir, 1982) or by frequency-dependent selection by predators (and this is supported by evidence from experiments with wild birds and distasteful pastry prey (Greenwood, Wood, and Batchelor, 1981)). Brakefield (1985) has suggested that the polymorphism in *A. bipunctata* is maintained by the different morphs mimicking other beetle species. Recent computer simulations have shown that selection by predators can then result in a balanced polymorphism, in much the same way as when the prey are palatable (Batesian) mimics (Speed, 1993).

Conclusion

There are obviously no clear-cut answers to the questions raised here. Like all good controversies in science, those associated with the evolution of 'the wrong sort of swallow' will tax our minds for many years to come.

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