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Letters to the Editor

Is Mimicry Theory Unpalatable?

Bates[1] used mimicry to explain similarities between butterfly species within regions, and his argument was convincing chiefly because geographic changes in colour patterns of one species were paralleled by changes in others. The highly ordered geographic patterns of mimicry and the non-homologous nature of mimetic similarities, especially in the neotropical butterflies that Bates studied[2,3], remain the best evidence for selection. This comparative evidence, which has satisfied the majority of evolutionists and yet was ignored by Malcolm in his recent review[4], implicates selection for mimicry both more strongly and more generally than do experiments (e.g. Refs 5–7). As pointed out by Malcolm[4], field demonstrations of mimicry are open to other interpretations. In addition, these experiments will apply only to the species, place and time of the experiment.

Malcolm fails to mention that selection for mimicry and warning colour will be strongly density and frequency dependent. A rare mutant pattern in an unpalatable species will be strongly disfavoured, even if it is equally or more effective as a warning signal: predators will attack and reduce the fitness of a much larger proportion of the rarer morph during learning[8–10]. Mimicry between unpalatable species demonstrates that the frequency dependence exists, because without selection against rare warning patterns, there is no advantage of müllerian mimicry. Writers who ignore frequency dependence in proposing that warning colours evolve by standard, individual selection (IS)[4,11] essentially overlook the major difficulty with their hypothesis.

Nonetheless, some IS scenarios are likely[8]: (1) Preadaptation: species that use conspicuous signals before unpalatability is acquired (e.g. many sexually selected, flash-coloured or batesian mimetic butterflies) can simply use their patterns in a new message of unpalatability[12]. (2) Mimicry: warning colours can evolve in a newly unpalatable species by means of müllerian mimicry of other brightly coloured species[3]. Müllerian mimicry is so common that this is a strong possibility; however, it is obvious that virtually all mimicry present today has arisen long after the initial evolution of warning colour. (3) 'Runaway' selection: characteristics used by predators to distinguish unpalatable prey can become enhanced by IS if mutants produce a 'supernormal sign stimulus' of the original pattern[8]. A possible example is found among the morphines *Taenaris* and *Hyantis*. These butterflies apparently became unpalatable as a result of a host-plant shift from monocotyledons to cycads, and feature a prominent eyespot in the centre of the hindwing. This key feature is likely to be an enhancement of smaller eyespots such as those found among other morphine, brassoline and satyrine butterflies today[8].

Although IS seems likely in these special cases, the enormous diversity of warning colour patterns, even of geographic races within unpalatable species, suggests other mechanisms of divergent evolution, such as kin selection and Sewall Wright's 'shifting balance'[8]. A miserable feature of current evolutionary debates is that terminology often obscures comprehension. In the evolution of warning colour, 'kin selection'[13], selection acting on a 'green beard trait' among kin[14], 'shifting balance'[8], and now Malcolm's new use of the term 'individual selection'[4] might all refer to the same mechanism under some circumstances. It becomes hard to keep the process itself in mind. However, these authors all refer to the way in which population structure can help a novel warning colour pattern to increase in a local area. Under selection against rarity, mutations in small numbers of kin-founded groups, or genetic drift, may allow the frequency of the new morph to increase locally above the unstable equilibrium. Some authors have thought that this kin effect is deterministic, but the necessity for small numbers of families in the kin-founding model means that genetic drift is essentially responsible.

On the other hand, unpalatability and noxiousness seem much more likely to evolve by IS: predators can taste non-destructively[15], so there is an immediate benefit of unpalatability to each individual. Malcolm makes his arguments hard to follow by confusing unpalatability with warning signals within the term 'aposematism', although Poulton, who invented the term, clearly meant a warning signal (from άπο, 'away', and σημα, 'sign')[12]. Admittedly there is another possible confusion between distastefulness, itself a possible form of aposematism, and unprofitability, which directly reduces the fitness of predators[16]. Innocuous species that taste bad may be chemically mimetic of compounds that are both distasteful *and* toxic. These difficulties make warning colour and mimicry harder to understand than most people realize. Nature is often complex, and it is worth acknowledging that fact.

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Reply from Stephen Malcolm

The response by Jim Mallet to my mimicry article is interesting and appreciated, especially for his perspective on the importance of frequency-dependent selection in the evolution of conspicuousness and mimicry. Although I deliberately chose not to consider the population genetics of mimicry in my article, through both space limitations and a desire to make a specific point regarding the process of mimicry, I would like to comment on the points he raises. Before doing so however, I would point out that conspicuousness and defensive mimicry seem to me to be divisible into four aspects that need to be understood in the following order before their functioning, maintenance and evolution can be appreciated fully.

First, the most important and least understood aspect of these defences is probably the nature and diversity of selection by natural enemy foraging. Second, the phenotypic operation of conspicuous and mimetic defences against various natural enemy foraging tactics needs to be demonstrated (evidence is either rare or anecdotal). The major intention of my article was to emphasize that these two ecological aspects of mimicry need to be understood before the evolution of aposematism and mimicry can be appreciated. Third, the population dynamics of predator–prey interactions need to be described (again, evidence is rare). And fourth, the population genetics of mimetic or aposematic prey need to be understood. It is this fourth aspect that Mallet dwells on in his letter and, as he rightly points out, it is an aspect that I have largely ignored. However, I did so because the arguments are widely accepted and implicit in much of the material to which I referred.

Intuitively, everyone agrees with what Mallet says – selection for mimicry and warning colour are probably strongly density and frequency dependent. As Mallet considers, the likelihood that 'a rare mutant pattern in an unpalatable species will be strongly disfavoured' seems perfectly reasonable. Nevertheless, when Mallet and Singer[1] reviewed the evidence they concluded that more experiments were needed to test this prediction, because efforts that measured predation directly either failed to detect selection against rare morphs, or the rare form was actually favoured. In addition, Endler[2] lists five untested possibilities by which rare morphs could reduce their supposed disadvantage.

To me this suggests that the obvious is not quite as obvious as we are led to believe by the generality of published agreement and by Mallet's letter. Instead, I would rather we attempted the extremely difficult task