I am most grateful to E. Allen Hrere for his help in clarifying my arguments and for his emphasis on problems yet unsolved, to Jeremy Jackson for bringing the relevance of punctuated equilibria to my attention, to Robert Paine for mentioning the importance of life-history trade-offs, and to sundry reviewers, whose theoretical anonymity will be respected, for singularly helpful remarks.

Acknowledgements

References

Is Mimicry Theory Unpalatable?

Bates1 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 studied2, 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 review4, implicates selection for mimicry both more strongly and more generally than do experiments (e.g.Refs 5–7). As pointed out by Malcolm4, 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 pattern in an unpalatable species will. In addition, these experiments will apply only to the species, place and time of the experiment.

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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. A possible example is found among the morphines Tenebrio 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 the original pattern. Special cases, the enormous diversity of geographic races within unpalatable species, suggests other mechanisms of divergent evolution, such as kin selection and Sewall Wright’s “shifting balance.” Mallet’s new use of the term ‘individual selection’ 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 new morphs 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, so there is an immediate benefit of unpalatability to each individual. Mallet 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 “sign” (1972, 23). Poulton, who invented the term, clearly meant a “sign” (1972, 23). Admittedly there is another possible confusion between distastefulness, itself a possible form of aposematism, and unprofitability, which directly reduces the fitness of predators. Inocuous 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. 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