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Diversity in mimicry

Joron and Mallet's recent perspective in *TREE*[1] gives a good overview of current thinking on the evolution of mimicry, but in spite of an acknowledgement that mimicry has evolved in a wide range of organisms, the discussion was confined to butterflies. There is much recent work on other mimetic animals ranging from coral snakes[2] to spiders[3,4]. The article was unfortunately written before publication of a recent paper by McDougall and Dawkins[5] who show that when predator discrimination is introduced into behavioural models similar to those used by Speed[6], the results obtained are very different. These authors show that the criterion used in deciding whether a mimic is Müllerian or Batesian should not be palatability but the benefit that the mimic gains: if only one species benefits from the resemblance and the other loses, then the mimicry is Batesian, but where both species benefit, then the mimicry is Müllerian.

Butterflies are unusual among mimetic animals in that very often only the female is mimetic, and it is the female that is heterogametic. Furthermore, butterflies are unusual among Lepidoptera in being diurnal. Most Lepidoptera are nocturnal and relatively palatable to insectivorous predators, so it is mainly those taxa that are chemically protected and aposematic that have been able to escape the restrictions imposed by a nocturnal lifestyle (e.g. Zygaenidae and Ctenuchidae, as well as butterflies). This might help explain why butterflies that were originally thought to be Batesian mimics have now been shown to be unpalatable[7]. A comparable spectrum of palatability does not occur in many other mimetic taxa, such as the Araneae and Diptera. A great many syrphid Diptera are mimetic but none has been shown to be unpalatable, so these would seem to be Batesian mimics[8]. The models are all well protected Hymenoptera, some of which are Müllerian mimics.

Because of this clear-cut difference between Batesian mimics and models, there is less advantage to a wasp or a bumblebee in embarking on an evolutionary chase to evolve away from their mimics than there is to

butterflies. As with mimetic butterflies, most syrphids are monomorphic, but there are several polymorphic species mimicking bumblebees in the genera *Merodon*, *Eristalis*, *Volucella* and *Criorhina*[9]. If the genetic-architecture problems involved in the evolution of such polymorphisms are as great as implied by Joron and Mallet, then, because so many mimetic species are polymorphic, the advantages of polymorphism must be very substantial.

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Joron and Mallet's recent *TREE* perspective on diversity in mimicry[1] oversimplifies our views[2] on anomalous pattern polymorphisms in the African Queen butterfly, *Danaus chrysippus*. We did not explain these anomalies by an overload of Batesian mimics; rather, we discussed this possibility in the context of hybridization between previously allopatric colour pattern races of this species. We agree with Joron and Mallet's objections to the overload hypothesis (and would add a third), but we note that they apply more to the origin of a polymorphism than to its maintenance. In a hybridization context, theory suggests that Batesian overload can contribute to polymorphism dynamics.

Because the polymorphism of *D. chrysippus* is so interesting, it is often forgotten that this species is actually monomorphic over most of its range in Africa. Pattern polymorphism is restricted to east and central Africa, albeit in an area larger than Europe[3]. It is unlikely that special conditions (e.g. lower deterrence leading to Speedian mimicry[4,5]) prevail here but not in the rest of Africa. Given that it is in east and central Africa that the different colour pattern morphs of *D. chrysippus* overlap in their geographical distributions, Occam's razor suggests a hybrid origin for the

polymorphism. This interpretation is supported by independent evidence from segregation anomalies for sex and colour pattern[3], large scale migrations[6], assortative mating[7,8] and heterosis for body size[9]. Polymorphism dynamics are highly complex, and they are most definitely not determined by predation alone.

The take-home message from all this is that mimicry and aposematism are not the whole story. Predictions from the theory of mimicry and aposematism depend not only on accurate modelling of predator behaviour and prey characteristics, but also on several other things being equal. In particular, they assume that predation determines the frequencies of colour pattern genes without interference from other selection pressures, ecological circumstances or other loci. This *ceteris paribus* clause can be generalized as an extreme form of beanbag genetics, in which there is optimal, independent tracking by individual loci of contemporary selection pressures. In reality, genes for mimetic colour patterns are the products of complex and particular processes, in which various selection pressures (not just predation) and historical contingencies may be important. Colour pattern genes may also

have epistatic and pleiotropic effects, and they may be linked with other segregating loci with effects on fitness[10]. In this situation, the beanbag model does not apply, and the resolution of each example of a mimetic anomaly requires a special investigation into all the other things that are not equal in that particular case.

We therefore doubt Joron and Mallet's conclusion that anomalous diversity in mimicry provides a general model for the evolution of biological diversity. Instead, we believe that the overall lesson for evolutionary biologists is both more particular and more immediate: the genome is not a beanbag. It may be through this lesson that the paradox of anomalous mimetic diversity is best seen as its mirror image, a paradigm for understanding the complexities of adaptation.

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Reply from M. Joron and J.L.B. Mallet

There are many good general reviews of the evolution of mimicry[1,2], including Edmunds's own excellent book[3]. Our perspective dealt only with the paradox that mimicry rampantly diversifies in morphs, subspecies and species, even though simple theory explains only convergence in a reduction of diversity. (Also, we did refer to MacDougall and Dawkins, see Ref. 31 in our original article; however, their idea is now criticized[4].) We concentrated on butterflies because most studies relating theory, field data and genetics are done in this group.

We very much doubt the implication that butterflies are special; mimicry ought to work the same in less well known organisms. Edmunds and Golding suggest that female sex-chromosome heterogamety and female-limited mimicry in butterflies are related. However, mimetic sexual dimorphism in butterflies is due, in part, to sexual selection acting on males[5–7], and similar dimorphisms are also common in male-heterogametic organisms, such as mammals. In only one case – *Papilio glaucus* in N. America[8] – is a mimetic-switch gene linked to the female-specific W chromosome; most mimetic polymorphisms are inherited autosomally, with sex chromosomes merely serving to switch between mimetic and nonmimetic patterns through their effect on sex. Although no cases of female-limited mimicry are known in organisms other than butterflies, we don't see a good reason for this: where ecologically feasible, there are cases of male-limited mimicry in Lepidoptera[9], for instance in diurnal male moths that search for females that rest by day.

The assertion that butterflies have become diurnal because of unpalatability is clearly wrong. Basal groups like Hesperiidae are chiefly palatable, and the palatability of most Dismorphiinae, Coliadinae, Lycaenidae and Libytheinae argues for unpalatability evolving within the Pieridae and Nymphalidae, rather than before their radiation. Mimicry is associated with diurnality in Lepidoptera; but this is hardly surprising given that nocturnal predators rarely use details of colour and pattern when hunting prey. Rapid and unpredictable flight (Castniidae, Hesperiidae and Charaxinae), low profitability (Satyrinae and Lycaenidae), and camouflaged undersides (many Nymphalidae) are among other common attributes of Lepidoptera that allow diurnality. Unpalatability, warning colour and mimicry are clearly among adaptations that permit diurnality, but they are neither required nor unique to butterflies. Anyone who has been stung by a *Paraponera* and swarmed over by *Crematogaster* will be able to inform about great differences in the unpleasantness of ants, and it seems probable that similar palatability spectra exist in spiders and Diptera. Mimetic butterflies are better studied, rather than having special kinds of palatability or mimicry.

Gordon and Smith resent our correct citation of their group's earlier ideas on Batesian overload in *Danaus*. However, we also reported (p. 463 in our original article) their current hypothesis: 'recent contact… of previously isolated geographical races has been suggested as a nonadaptive cause of polymorphism in these species'. Although we did not say so in the perspective, secondary contact is not a good *deus ex machina* for explaining mimetic polymorphism. It has recently been found that in both *Acraea encedon*[10] and *Danaus chrysippus* (F. Jiggins, pers. commun.) sex ratio distortion is a result of infection by male-killing bacteria rather than hybrid breakdown. We have no doubt that similar nonhistorical ideas will explain other puzzling features of the genetics of *Danaus* and *Acraea*. In any case, geographic isolation in a refuge cannot by itself cause an initially unfavourable colour pattern to spread; drift and/or fluctuating selection are required initially, and these could also take place during parapatric contact, as in *Heliconius*[11], making allopatry unparsimonious. The *Danaus* anomaly also stubbornly refuses to disappear via an accusation of beanbag genetics. We must still explain an area larger than Europe with unexpected mimetic polymorphism. We suggest that this and other Müllerian polymorphisms might be maintained by spatiotemporal heterogeneity, as described in our article. Mimetic selection in *Danaus* may be fairly weak in the area of polymorphism, and balanced by fairly strong gene flow (large-scale migrations), leading to a wide band of polymorphism between areas of stable relative purity. Similar patterns of current selection are a likely source of widespread polymorphism in Müllerian mimetic ladybirds[12].

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