WHAT IS MIMICRY?

BY

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Batesian and Müllerian mimicry

On 28th May 1848 two young British naturalists reached Belém (Pará State, Brazil) on the lower Amazon with plans of exploring the region and obtaining some material from the extraordinary local fauna that could be sold to private and public museums in Europe. One of them, Alfred Russel Wallace, stayed in the region for almost five years. A large part of his collections were lost when a ship caught fire and sank in the Rio Negro.

The other, Henry Walter Bates, stayed longer: eleven years. After a long time enjoying good health, he got Malaria and decided to go back to England (Stearn, 1981). Bates developed a deep interest in the region, the fauna, the people and their costumes, which he described beautifully in “The Naturalist on the river Amazons” (1876). His studies on butterflies led him to propose the theory of mimicry, read at a meeting of the Linnean Society of London in 1861 and published in the following year under the title “Contributions to an insect fauna of the Amazon Valley” in the Transactions of the Linnean Society.

The high diversity of bright, conspicuous color patterns of neotropical butterflies, usually shared by several species in a same locality (currently called mimetic rings), had always attracted the attention of naturalists traveling in the region. Darwin himself was

very impressed by the phenomenon, but attributed butterfly color patterns mainly to sexual selection (Darwin, 1871). Bates was the first to relate butterfly color patterns to unpalatability. His theory of mimicry postulates that predators avoid species containing “nauseous smell or taste”, and a profitable species, usually referred as the “mimic”, could obtain protection by resembling an unpalatable one, or “model”. The theory also brings the assumption that models are more abundant than mimics, so that predators can meet and learn to avoid them first.

As evidence to support his theory, Bates mentioned first, that presumably unpalatable Ithomiinae, Danainae and Heliconiinae, which he called danaoid and acraeoid Heliconiidae, and presumably palatable Dismorphiinae (Pieridae), often converged in color patterns in a same region, despite a large geographical variation throughout the Amazon valley, and second, that he had never seen a single attack by any of the numerous insectivorous birds of the region on these butterflies, which were usually very frequent, conspicuous and with a slow flight that could make them easy prey.

Some years later, a German naturalist called Fritz Müller working in South-eastern Brazil, proposed that two unpalatable species could also benefit of sharing a similar color pattern (Müller, 1879). Differing from Batesian mimicry, in which the mimic gains its advantage at the expense of the model, and of the predator which it deceives, Müllerian mimicry sought to explain how advantage could be conferred on all species involved, including the predators that could learn more quickly to avoid the unpalatable species (Fisher, 1930).

Mimicry theory played a very important part in the early understanding of natural selection theory that, at the turn of the century, was still regarded as a very controversial issue (Fisher, 1930; Owen, 1971). However, several basic aspects of classical Batesian and Müllerian mimicry have been questioned.

One major source of problems concerning mimicry theory involves what kind of phenomena should be included under the term. The discovery of several different types of mimicry and other forms of protective coloration in many animals and plants (Cott, 1940; Wickler, 1968; Robinson, 1969; Rettenmeyer, 1970; Edmunds, 1974a; Wiens, 1978, Paster, 1982; Starret, 1993) has led to several controversies over the classification of these events. Some authors (e.g. Cott, 1940; Edmunds, 1974a) regard similarities of organisms with the substrate or background, for instance the resemblance of a leaf-like butterfly to a leaf, as a special case of mimicry. Although these kinds of similarity may also lead to deception of predators, they are now recognised as very distinct phenomena, more commonly referred to as crypsis or camouflage (Vane-Wright, 1980; Edmunds, 1981; Endler, 1981, 1991).

Other authors (e.g. Wickler, 1968; Wiens, 1978) have also excluded similarities of organisms with the background, and restrict the term mimicry to cases which necessarily involve deception of predators (or other selective agents involved in different kinds of mimicry). One problem with this view, however, is that classical Müllerian convergence is also excluded from mimicry.

Another major source of problems in mimicry theory concerns real differences between Batesian and Müllerian mimicry. The concept of Batesian mimicry implies that unprotected species would be selected to resemble commoner unpalatable species, whereas Müllerian mimicry would involve the convergence of two or more unpalatable species to an intermediate color pattern. While the existence of unidirectional convergence of Batesian mimics on the color patterns of protected species has never been questioned in the vast literature of mimicry, there are several doubts whether Müllerian mimics converge to an intermediate color pattern or not. As pointed out by Mallet and Gilbert (1995), Bates was the first to suggest that rare unpalatable species, such as the "silvaniform" butterflies (*Heliconius numata*, Heliconiinae), should converge on the color patterns of commoner or more highly protected species as *Melinaea* spp. (Ithomiinae). Marshall (1908) suggested that, for arithmetical reasons, of two equally unpalatable species inhabiting the same region, the less numerous species will tend to resemble the more numerous species, and not *vice versa*. Turner (1977, 1984) suggested that commoner species could even lose protection by mimicking rarer species and Huheey (1976) developed a mathematical model for Müllerian mimicry in which the less unpalatable species acts as a Batesian mimic of the more unpalatable one. In spite of Benson's (1977) criticism that Batesian and Müllerian mimicry are qualitatively different phenomena, several authors now believe that Müllerian convergence evolves in a fashion similar to Batesian convergence (e.g. Turner, 1977, 1984; Gilbert, 1983; Mallet and Gilbert, 1995). Mallet and Gilbert also proposed a hypothesis to explain the high diversity and maintenance of mimetic color patterns in the neotropics, which involves massive unilateral convergence of "unpalatable mimics" on the color patterns of some "key" models.

In view of the above difficulties, Vane-Wright (1976, 1980, 1981) proposed a very comprehensive definition of mimicry, that not only excludes similarities of organisms with the background and the need of deception by predators, but also accounts for possible similarities between Batesian and Müllerian mimicry: “mimicry involves an organism (the mimic) which simulates signal properties of a second living organism (the model), which are perceived as signals of interest by a third living organism (the operator), such that the mimic gains in fitness as a result of the operator identifying it as an example of the model.” Although Rothschild (1981), Cloudsley-Thompson (1981), Edmunds (1981), Brown (1988) have presented examples that challenge this and virtually all other previous definitions of mimicry, Vane-Wright’s definition brings the problem of how to establish what is of interest to predators or not. Furthermore, it is always difficult to identify “models” and “mimics” between unpalatable organisms, especially when mimicry may involve a very large collection of species, as in the case of neotropical butterflies.

For these reasons, I have decided to apply the common usage of the term Batesian mimicry to cases in which a palatable butterfly resembles one or more unpalatable species, and Müllerian mimicry to any mimicry between unpalatable species, regardless of their abundance, differing degrees of unpalatability, or the evolutionary steps that led to convergence of the color patterns (Pinheiro, 1996; 2003). These definitions are basically Bates and Muller’s definitions of mimicry, and naturally exclude the similarities of organisms with their background (= crypsis or camouflage), as well as many other forms of protective coloration found in butterflies (such as the “eye

spots” of many Brassolinae, Morphinae and Satyridae that resemble vertebrate eyes, and the “false head” on the hindwings of many Lycaenidae). Yes, I’m happy.

Selected References

Bates, H. W. 1862. Contributions to an insect fauna of the Amazon valley. *Transactions of the Linnean Society of London*, **23**: 495-566.

Bates, H. W. 1876. *The naturalist on the river Amazons*. London: Murray.

Benson, W. W. 1977. On the supposed spectrum between Batesian and Müllerian mimicry. *Evolution*, **31**: 454-455.

Brower, L. P. 1984. Chemical defence in butterflies. In: *The Biology of Butterflies*. (Ed. VaneWright, R. I. and P. R. Ackery), pp. 109-134. London: Academic Press.

Brown, K. S. Jr. 1988. Mimicry, aposematism and crypsis in Neotropical Lepidoptera: the importance of dual signals. *Bulletin de la Société Zoologique de France*, **113**: 83-101.

Cloudsley-Thompson, J. L. 1981. Comments on the nature of deception. *Biological Journal of the Linnean Society*, **16**: 11-14.

Cott, H. B. 1940. *Adaptive coloration in animals*. London: Methuen.

Darwin, C. 1871. *The descent of man and selection in relation to sex*. London: Murray.

Edmunds, M. 1974. *Defence in animals: a survey of anti-predator defences*. Essex: Harlow.

Edmunds, M. 1981. On defining mimicry. *Biological Journal of the Linnean Society*, **16**: 9-10.

Endler, J. 1981. An overview of the relationship between mimicry and crypsis. *Biological Journal of the Linnean Society*, **16**: 25-31.

Endler, J. 1991. Interactions between predators and prey. In: *Behavioural ecology: an evolutionary approach* (Ed. Krebs, J. R. and N. B. Davies), pp. 169-196. Oxford: Blackwell Scientific Publications.

Fisher, R. A. 1930. *The genetical theory of natural selection*. New York: Dover.

Gilbert, L. E. 1983. Coevolution and mimicry. In: *Coevolution* (Ed. Futuyma, D. J. and M. Slatkin) pp. 263-281. Sunderland, Massachusetts: Sinauer Associates.

Huheey, J. E. 1976. Studies in warning coloration and mimicry. VII. Evolutionary consequences of Batesian-Müllerian spectrum: a model for Müllerian mimicry. *Evolution*, **30**: 86-93.

Mallet, J. and Gilbert, L. E. 1995. Why are there so many mimicry rings? Correlations between habitat, behaviour and mimicry in *Heliconius* butterflies. *Biological Journal of the Linnean Society*, **55**: 159-180.

Müller, F. 1879. *Ituna* e *Thyridia*: a remarkable case of mimicry in butterflies. *Proceedings of the Royal Entomological Society, London*, XX-XXIX.

Owen, D. F. 1971. *Tropical butterflies*. Oxford, Clarendon Press.

Paster, G. 1982. A classificatory review of mimicry systems. *Annual Review of Ecology and Systematics*, **13**: 169-199.

Pinheiro, C. E. G. 1996. Palatability and escaping ability in Neotropical butterflies: tests with wild Kingbirds (*Tyrannus melancholicus*, Tyrannidae). *Biological Journal of the Linnean Society*, **59**: 351-365.

Pinheiro, C. E. G. 2003. Does Mullerian mimicry work in nature? Experiments with butterflies and birds (Tyrannidae). Biotropica. (In Press).

Rettenmeyer, C. W. 1970. Insect mimicry. *Annual Review of Entomology*, **15**: 43-74.

Robinson, M. H. 1969. Defenses against visually hunting predators. *Evolutionary Biology*, **3**: 225-259.

Rothschild, M. 1981. The mimicrats must move with the times. *Biological Journal of the Linnean Society*, **16**: 21-23.

Starrett, A. 1993. Adaptive resemblance: a unifying concept for mimicry and crypsis. *Biological Journal of the Linnean Society*, **48**: 299-317.

Stearn, W. T. 1981. Henry Walter Bates (1825-1892), discoverer of Batesian mimicry. *Biological Journal of the Linnean Society*, **6**: 5-7.

Turner, J. R. G. 1984. The palatability spectrum and its consequences. In: *The Biology of Butterflies*. (Ed. VaneWright, R. I. and P. R. Ackery), pp. 141-161. London: Academic Press.

Turner, J. R. G. 1987. The evolutionary dynamics of batesian and muellerian mimicry: similarities and differences. *Ecological Entomology*, **12**: 81-95.

Vane-Wright, R. I. 1976. A unified classification of mimetic resemblances. *Biological Journal of the Linnean Society*, **8**: 25-56.

Vane-Wright, R. I. 1980. On the definition of mimicry. *Biological Journal of the Linnean Society*, **16**: 33-40.

Vane-Wright, R. I. 1981. Only connect. *Biological Journal of the Linnean Society*, **16**: 33-40.

Wickler, W. 1968. *Mimicry in animals and plants*. London: Weidenfeld and Nicholson.

Wiens, D. 1978. Mimicry in plants. *Evolutionary Biology*, **11**: 365-403.