Mimicry: butterflies of a feather flock together

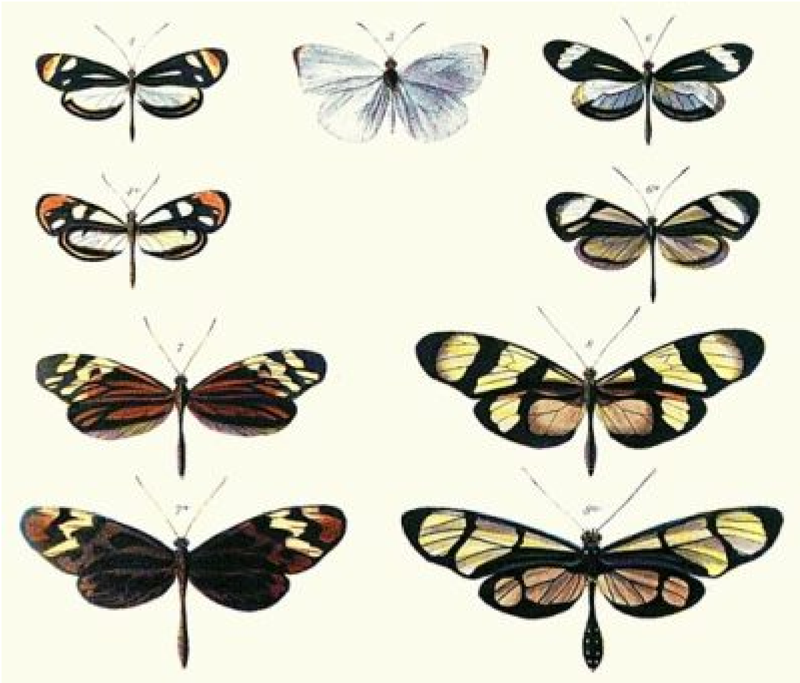


Figure 1. Plate illustrating Batesian mimicry between edible butterflies of the Pieridae family (subfamily Dismorphiinae, first and third rows) and alkaloid-defended butterflies of the Nymphalidae family (tribe Ithomiini, second and fourth rows) (Source: Bates 1962). These two families diverged over 90 million years ago. The species in the middle of the first row, the non-mimetic Pseudopieris nehemia (Dismorphiinae), is probably close to the ancestral form from which the mimetic Dismorphiinae of the Ithomiini evolved. [Source: Illustration Henry Walter Bates, Public domain, via Wikimedia Commons]

When British naturalists Henry Walter Bates and Alfred Russell Wallace arrived in the Amazon in 1848 in search of examples illustrating the process of natural selection, they were struck by the astonishing similarity in the colour patterns of butterfly species belonging to very different lineages (Figure 1). Noting that some of these species are inedible, while others that resemble them are, Bates hypothesized that edible butterflies are confused by predators with poisonous ones, and thus benefit from protection against predation. Mimicry as Bates calls it, and today known as Batesian mimicry, it refers to the resemblance between individuals belonging to an edible species and individuals belonging to another species with chemical defenses, giving them an unpleasant taste, or even toxicity. Batesian mimicry is a remarkable case of evolution by natural selection, for which we know precisely which variants are advantageous: in the edible species, any variation that increases resemblance to individuals of the toxic species will be advantageous, as it is more likely to be avoided by predators.

Since Bates' observation, numerous cases of edible species mimicking toxic species have been reported in butterflies, as in other animals. In butterflies of the genus Papilio, in particular, mimetic patterns are observed in females, while males harbour non-mimetic patterns. One hypothesis to explain this sexual dimorphism is the greater predatory pressure exerted on females, which have a slower flight and more predictable behavior, due to their propensity to fly around their host plant.

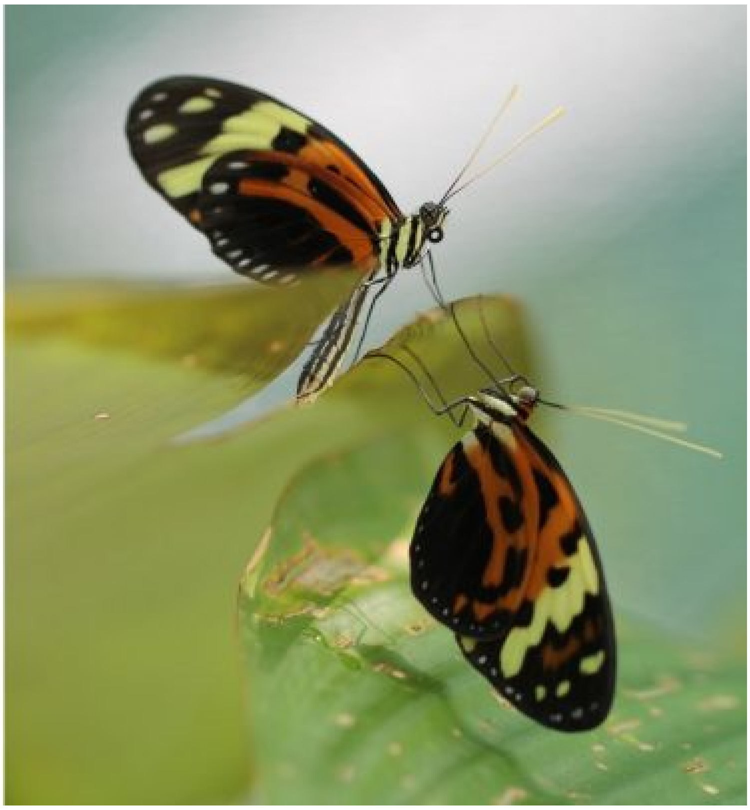
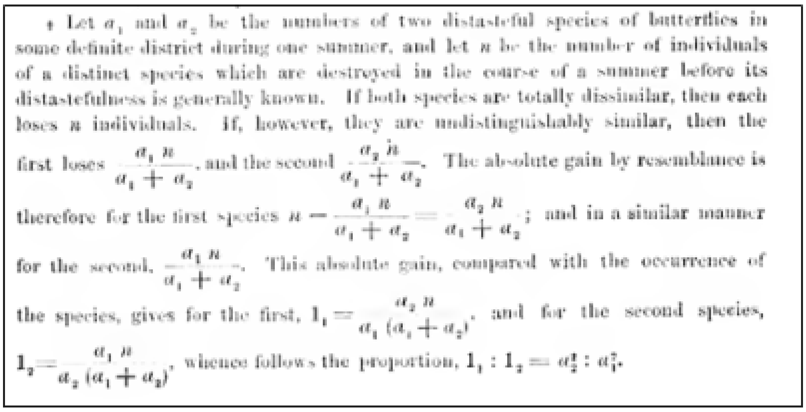


Figure 2. An example of Müllerian mimicry. Heliconius humata (top), defended by cyanogenic glucosides, and Melinaea mneme (bottom), defended by pyrrolizidine alkaloids, coexist in the Amazon rainforest and have converging aposematic patterns. They belong to lineages that diverged over 80 million years ago. [Photo © by Mathieu Chouteau, reproduced with permission of the author]

However, Bates struggled to explain the cases where similar looking species all have defenses, and are therefore all unpalatable (Figure 2): for an **aposematic butterfly** [1], signalling its toxicity and thus protected from predation, what advantage would there be in mimicking the patterns of another toxic species?

It wasn't until 1878 that a German biologist living in Brazil, Fritz Müller, put forward a convincing hypothesis in an article that was translated into English the following year. Müller noted that before predators could learn to associate an aposematic pattern with the bad taste of the butterflies bearing it, they had to taste, and therefore kill, a certain number n of these butterflies. So, if two species with distinct aposematic patterns coexist in the same environment, n butterflies of each species will die as a result of the predators' learning. But if the species are so similar that predators confuse them, a total of n butterflies will die, these sacrificed butterflies being divided between the two species in proportion to their respective abundances. Ultimately, mortality within each species is lower when the two species are similar than when they are different. There is therefore an advantage to similarity for butterflies of aposematic, unpalatable species, which are exposed to the same predators, as similarity dilutes the risk of predation. The resemblance between these species could thus evolve under the action of natural selection, leading to the evolutionary convergence of aposematic motifs. By equating the risk of predation for individuals of different species subjected to the same predators, Müller defined what is now known as Müllerian mimicry, to distinguish it from Batesian mimicry, and produced the first theoretical model of evolutionary biology (Figure 3).



* Let a_1 and a_2 be the numbers of two distasteful species of butterflies in some definite district during one summer, and let n be the number of individuals of a distinct species which are destroyed in the course of a summer before its distastefulness is generally known. If both species are totally dissimilar, then each loses n individuals. If, however, they are undistinguishably similar, then the first loses $\frac{a_1 n}{a_1 + a_2}$, and the second $\frac{a_2 n}{a_1 + a_2}$. The absolute gain by resemblance is therefore for the first species $n - \frac{a_1 n}{a_1 + a_2} = \frac{a_2 n}{a_1 + a_2}$; and in a similar manner for the second, $\frac{a_1 n}{a_1 + a_2}$. This absolute gain, compared with the occurrence of the species, gives for the first, $l_1 = \frac{a_2 n}{a_1 (a_1 + a_2)}$, and for the second species, $l_2 = \frac{a_1 n}{a_2 (a_1 + a_2)}$, whence follows the proportion, $l_1 : l_2 = a_2^2 : a_1^2$.

Figure 3. Footnote to Fritz Müller's original 1979 article in the Transactions of the Entomological Society of London, in which he presents his model for the evolution of mimicry.

In practice, in the same locality, several species - sometimes more than ten - can be found sharing the same colour pattern. Some of these species have chemical defenses, and are therefore Müllerian mimes of each other, and others are edible, and are Batesian mimes of the former. The set of species sharing the same pattern is called a mimetic circle (Figure 4).

Batesian and Müllerian mimicry were first described in butterflies, and have been extensively documented in this group. However, there are numerous examples in other organisms, notably the many species of bees, bumblebees and wasps, all of which are defended by the ability to inflict a venomous sting (Müllerian mimicry), which are also mimicked by harmless butterflies of the Sesiidae family and flies of the Syrphidae family (Batesian mimicry). Mimicry is also present in other arthropods (beetles, spiders, etc.) and vertebrates (frogs, fish, snakes, etc.).

Figure 4. A mimetic circle in Peru. Left column, top to bottom: Hypothyris mansuetus (Nymphalidae: Ithomiini), Hyposcada anchiala (Nymphalidae: Ithomiini), Chetone sp. (Erebidae: Arctiinae). Right column, top to bottom: Mechanitis messenoides (Nymphalidae: Ithomiini), Heliconius numata (Nymphalidae: Heliconiini), Melinaea mothone (Nymphalidae: Ithomiini). [Photo © Mathieu Joron, reproduced with permission of the author].

Batesian and Müllerian mimicry are eloquent illustrations of the action of natural selection, thanks to the very fine resemblance between species that are sometimes extremely distant. In fact, these examples contributed greatly to the acceptance of the theory of evolution by natural selection, set out in Darwin's famous book The Origin of Species. Whereas Batesian mimicry has a negative impact on the populations of aposematic, inedible species (predators take longer to associate the aposematic motif with the bad taste of prey, as they sometimes eat Batesian, edible mimes), Müllerian mimicry has a positive impact on the populations of all species in the system, as the mortality linked to predator learning is diluted between these different species.

Learn more

- Bates, H.W. (1862). Contributions to an Insect Fauna of the Amazon Valley. Lepidoptera: Heliconidae. *Transactions of the Linnean Society. 23 (3)*: 495–566.
- Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life* (1st ed.). London: John Murray. ISBN 978-1-4353-9386-8.
- Müller, F. (1879). *Ituna* and *Thyridia*; a remarkable case of mimicry in butterflies. (R. Meldola translation). *Transactions of the Entomological Society of London. 1879*: 20–29.

L'Encyclopédie de l'environnement est publiée par l'Université Grenoble Alpes.
