Butterfly mimicry

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Synonyms: Protective resemblance

Definition: Protective resemblance between a butterfly and two or more species, or between a butterfly and an inanimate object.

Introduction

Butterfly mimicry is a form of protective coloration where a given species, commonly referred to as the *mimic*, increases its chance of survival by visually resembling a harmful species, the *model*, such that the receiver of the signal, the predator (e.g. birds, reptiles or predatory insects who attacks and consumes butterflies), gets confused between the two and avoids the mimic (Ruxton et al. 2004). The model can either be a different species of butterfly, or an entirely different species of animal. In its broadest sense, butterfly mimicry may also involve a third category, a camouflage strategy known as *Masquerade*, in which butterflies mimic inanimate objects such as leaves, bits of lichen or patches of tree bark (Ruxton et al. 2004). Traditionally, however, there are two main types of mimicry, and these are typically distinguished from each other by whether the mimic's signal involves deception of the predator or not (Turner 1984). In *Müllerian mimicry*, named after the German naturalist Johannes Friedrich "Fritz" Müller, who first proposed an evolutionary explanation for the phenomenon, both the mimic and the model species are harmful to the predator, which is why the signal is considered to be honest in both species and does not involve deception of the predator. Dishonest signaling through the mimicry of a harmful species by a harmless species, on the other hand, involves deception of the predator and is known as *Batesian mimicry*, named after the English naturalist Henry Walter Bates (Bates 1862).

Müllerian mimicry

In Müllerian mimicry, both the mimic and the model species have in addition to warning signaling coloration, also effective secondary defenses. These defenses can either morphological such as spines, or chemical such as toxins. Both species benefit, because a potential predator has more opportunities to learn the meaning of the signal, which is why the relationship between Müllerian mimic and model species is said to be *mutualistic* (beneficial to both organisms). The signal receiver (predator) also benefits from this system, as it avoids potentially harmful encounters. In 1879, Müller, who at the time studied Neotropical butterflies in Brazil, published a simple explanation for this phenomenon stating that "defended species may evolve a similar appearance so as to share the costs of predator education" (Müller 1879, Ruxton et al. 2004). Müller was also the first to mathematically describe a survival benefit of being a Müllerian mimic depending on the abundance of similar and dissimilar species in its environment. The mathematical model has recently been extended to include unequal levels of unprofitability of the species to predict the relative benefit (Mallet et al. 2001). Two types of experimental evidence for Müller's suggested predatory mechanism underlying Müllerian mimicry has been put forward. The first is that rare unpalatable forms tend to have lower survival rates when they are distinct in appearance compared to when they are more similar to a common unpalatable species (Benson 1972). The second is that naïve predators tend to typically take a few of each unpalatable form before they start to avoid them (Kaipan 2001).

Several examples of Müllerian mimicry are found among the distasteful Neotropical butterflies of the subfamily *Heliconiinae* (“longwings”) in South America (Ruxton et al 2004; Mallet & Gilbert 1995). Many longwings form assemblages of similarly looking mimic and model butterflies known as *mimicry rings*, or mimicry complexes. At least four distinct assemblages including butterflies from the *Heliconiinae* and other species are traditionally recognized, the *tiger*, *red*, *blue*, and *orange* ring (or complex) (Mallet & Gilbert 1995). The *tiger* ring consists of about 200 Neotropical species which all share a similar pattern of orange and yellow stripes on a black ground color. The *orange* ring is comprised of a group of bright orange species (including e.g. *Marpesia petreus*, *Dryas iulia* and *Eueides aliphera*). Additionally, there are several species pairs, the most well-known of which is the *red postman* butterfly (*Heliconius erato*) and the *common postman* (*Heliconius melpomene*). Another classic example of Müllerian mimicry is the monarch butterfly (*Danaus plexippus*), which forms a Müllerian complex together with the viceroy butterfly, (*Limenitis archippus*). This example was long believed to be a case of *Batesian mimicry*, with the viceroy mimicking the monarch, but research has shown that both species are harmful to predators as they both contain toxins (arguably even more so in the viceroy than the monarch) hence they are Müllerian mimics (Ritland & Bauer 1991). In addition to sharing similar coloration patterns, members of each mimicry complex also tend to display similar behaviors. For example, many butterflies of the same mimicry ring form communal roosts at night, a behavior that has been shown to deter predation by birds as it increases the strength of their warning signal (Finkbeiner et al. 2012). Butterflies of each ring also tend to fly together at day, occur in similar habitats and at similar heights above the ground, and also get together at the same time of year (Mallet & Gilbert 1995).

Evolution of Müllerian mimicry

The more than century-old question of how Müllerian mimicry evolves is not yet fully understood. Broadly speaking, mimicry can evolve either via *advergent* or *convergent* evolution. In advergent evolution, the model species would remain the same, while selection acts on the mimetic species, bringing about a resemblance to the model species. In convergent evolution, a common selective pressure would act on all species involved, bringing about an overall resemblance between them. Advergent evolution via the so called *two-step hypothesis* is the most widely accepted model for the evolution of both Müllerian and Batesian mimicry (Ruxton et al. 2004). The *two-step hypothesis* entails that mimicry evolves in two stages, the first stage is a mutational leap of the mimic towards the model which establishes an approximate similarity. This stage is then followed by gradual evolutionary change which fine-tunes the mimic's similarity to the model (Turner 1984). One of the most frequently asked questions related to the evolution of Müllerian mimicry is: how do we know which one is the model and which one is the mimic? If Müllerian mimicry evolves through advergent rather than convergent evolution, scientists have argued that the *models* are expected to be: (1) more unpalatable, (2) more common, (3) earlier (in seasonal species), (4) larger, (5) more conspicuous, (6) more gregarious, and should have (7) a wider geographic distribution, (8) less "fuzzy" color patterns, (9) more ancient color patterns, (10) less polymorphism, and (11) less overall divergence from an ancestral color pattern than their *mimics* (Mallet 2001).

Batesian mimicry

In Batesian mimicry, the mimic itself lacks an effective secondary defense and so it is harmless to the predator, but the mimic still gains protection from predators by resembling a harmful model. As opposed to the mutualistic relationship between Müllerian mimics, Batesian mimicry is considered to be *parasitic* (beneficial to the mimic while harmful to the model). Predators that attacks the harmless mimics would soon learn that such organisms are profitable to attack and consequently, an increased number of Batesian mimics would lead to a decrease of the efficiency of the model's warning signal and so the survival of both model and mimic is reduced. Thus, the efficiency of Batesian mimicry is highly dependent on the abundances of the models and mimics and is normally considered to be effective when the unpalatable species are more abundant than the palatable species. However, the efficiency of Batesian mimicry is also dependent on the level of harm caused by models and the abundance of alternative prey (Ruxton et al. 2004). The most fundamental empirical evidence to support Batesian mimicry is that predators that have prior experience with unpalatable model species subsequently also avoid harmless species that resemble them.

Some examples of Batesian mimicry in butterflies can be found between species of the Neotropical, palatable *mimic sulphurs* (subfamily *Dismorphiinae*) and unpalatable *Ithomiini* butterflies which belongs to the *milkweed butterflies* (subfamily *Danainae*). The palatable spicebush swallowtail (*Papilio troilus*) is considered a Batesian mimic of the unpalatable pipe-vine swallowtail (*Battus philenor*). Some hawkmoth caterpillars (family *Sphignidae*), and pupa (e.g. *Dynastor darius*) have been suggested to be Batesian mimics of snakes (Ruxton et al. 2004), although this resemblance has not been tested with non-human predators. In cases where caterpillars and pupa resembles snakes, the resemblance between mimics and models can't be explained by shared ancestry, however, in some cases of resemblances between adult butterflies, it is likely that the resemblance between species can be explained by shared ancestry.

Conclusions

Many mimetic systems involve a complex interplay of species which vary in their defensive attributes and predators which vary in their abilities to deal with them. Even in Müllerian mimicry, prey may be unequally unpalatable and edibility may not be an absolute condition (Speed 1999). Different predator species may have different degrees of tolerance and an individual predator's motivation to attack prey might vary with its nutritional state, meaning that predators may still feed on weakly unpalatable prey when it is hungry or when there is a lack of alternative prey. In such cases the mimetic relations between unequally defended species could be parasitic, and this phenomenon has been referred to as quasi-Batesian mimicry. As there exists a whole range in between the two Müllerian and Batesian mimicry, it may not always be appropriate nor simple to divide mimetic species between these two categories.

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