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Chapter 28 *Most Spectacular Batesian Mimicry*

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The swallowtail butterfly, Papilio dardanus, occurs throughout most of Africa. While the males maintain a typical swallowtail appearance, the females occur in over thirty different mimetic forms that clearly resemble various species of two danaid genera.

Batesian mimicry involves a palatable, unprotected species (the mimic) that closely resembles an unpalatable or protected species (the model) (Devries 1987). This theory was first presented in 1861 by H. W. Bates in his attempt to explain the similar appearance and behavior of otherwise unrelated Central American butterfly species (Devries 1987). The larvae of these model butterflies eat plants that contain noxious substances which pass, either altered or unaltered, to the adult stage (Sheppard 1962). Such chemicals make the model undesirable to predators. The mimics lack these substances in their bodies making them quite edible. True Batesian mimicry is parasitic in nature with the model deriving no benefit and possible harm (Devries 1987). The mimics don't share the models nasty taste or painful sting, just its appearance and behavior. Thus, the models may be harmed by being mistaken for palatable mimics and should evolve to rid themselves of these relationships (Devries 1987).

Since its conception, Batesian mimicry has been the subject of great debate and countless papers. Charles Darwin, although accepting Batesian mimicry, viewed it as accidental with the mimic looking similar enough to the unrelated model to allow it slight protection (Clarke and

Sheppard 1960a). The theory is often misrepresented and confused with its counterpart, Mullerian mimicry. In this case, the model is not defined and several unpalatable species share warning colors or patterns to evade predation. Batesian relationships are found in many insect orders. This paper identifies the most spectacular example.

Methods

Primary literature on the subject was obtained from sources listed in the secondary literature. The secondary literature was gathered from several texts on the subject, as well as from books on insect ecology, specific insect orders, and geographical regions. Additional primary literature on the subject was located by a computer search of Agricola.

Results

Many relationships involving what were once thought to be Batesian mimicry are being reevaluated. The most common example, the Viceroy butterfly (*Limenitis archippus*), once thought to mimic the Monarch (*Danaus plexippus*), has through further investigation proven to be as distasteful to birds as the Monarch (Ritland and Brower 1991). Thus, the Monarch and Viceroy are Mullerian mimics. That such a disparity could go unnoticed for so long shows to what extent mimicry needs to be studied. However, after side-stepping this non-Batesian example in every text and article reviewed, several pure Batesian examples stand out.

In Borneo the grasshopper *Condylodera tricondyloides* resembles tiger beetles so closely

the tiger beetle's reputation for aggression. However, beetles and grasshoppers do develop differently. During its juvenile stage, this grasshopper lives in flowers with another tiger beetle, *Collyris sarawakensis*, which it closely resembles in size and color (Wickler 1968)

C. tricondyloides is a Batesian mimic with two partners, and several such Batesian relationships are known. However, a butterfly from Africa appears to be more spectacular. *Papilio dardanus* is a swallowtail with more than thirty mimetic morphs. The similarities between the mimetic morphs and their models are just as remarkable as that of the grasshopper and its beetles.

Discussion

Papilio dardanus has a highly specialized Batesian mimetic relationship with model species in the genera *Danaus* and *Amauris* (Lepidoptera: Danaidae). Caterpillars of the model butterflies feed on distasteful plants such as milkweed and pass the chemicals to the adult, making them distasteful to predators—namely, birds and monkeys (Sheppard 1962). The males and females of these model genera are similar; however, the species vary greatly in appearance. The mimic, *P. dardanus* contains some eight races (or subspecies) in Madagascar, the Comoro Islands and the southern two thirds of Africa (Sheppard 1962). The races are distributed so that only races *antinorii*, *meriones* and *humbloti* are completely isolated from other races. All other races hybridize at the edges of their respective ranges (Sheppard 1962). The races are distinguished by black markings on the males wings and male genital armature morphology (Clarke and Sheppard 1960b). The color pattern in males is always black and yellow, and differs only in detail from race to race (Clarke and Sheppard 1960a). The males have a typical swallowtail appearance and are readily eaten by birds.

The females are highly polymorphic, making this a spectacular mimicry. Only in the isolated races of *meriones* (on Madagascar), and *humbloti* (on the Comoro Islands) are the females

monomorphic and nonmimetic (Clarke and Sheppard 1963). Throughout the Ethiopian region can be found model species of the genera *Danaus* and *Amauris* each with its own mimic (morph), or in most cases, several morphs. *Amauris niavius* is an example of a model species. It is mimicked by ten different morphs throughout Africa. For example, the morph *hippocoön* mimics *A. niavius* in western Africa (Clarke and Sheppard 1960a). *A. echeria* has thirteen morphs mimicking it throughout Africa (Price 1984).

The success of a mimic's relationship to its model can be judged by color patterns, using a scale developed by Sheppard (1962). This scale plots a butterfly mimics relative fitness against its color pattern, with the color scale ranging from 0 to 5. A *P. dardanus* morph with a number 3 color pattern would have the greatest fitness. Primary factors influencing fitness of these color patterns would be abundance of the model and levels of predation (Clarke and Sheppard 1960a). Mimics falling into the color ranges above or below 3 will suffer decreased advantages because they appear less like the model (Sheppard 1962).

Each *dardanus* mimic has a specific host and cannot be found in any region without this host, but the morphs can be shared among races. For example, four races (*dardanus*, *cenea*, *tibullus*, and *meseres*) in eastern Africa share thirty-one morphs, however, no one morph is found in all nine races (Wickler 1968). How successful and common each morph is appears to be based on its model's abundance and its ability to closely match the model's color patterns and behavior. When a species develops many mimetic morphs in an area, such as *P. dardanus* has done throughout Africa, the ratio of each mimetic morph to the individuals of the model is reduced, improving the rate at which predators learn to avoid the color pattern.

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