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Some Possible Cases of Escape Mimicry in Neotropical Butterflies

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Abstract

The possibility that escape or evasive mimicry evolved in butterflies and other prey insects in a similar fashion to classical Batesian and Müllerian mimicry has long been advanced in the literature. However, there is a general disagreement among lepidopterists and evolutionary biologists on whether or not escape mimicry exists, as well as in which mimicry rings this form of mimicry has evolved. Here, we review some purported cases of escape mimicry in Neotropical butterflies and suggest new mimicry rings involving several species of *Archaeoprepona*, *Prepona*, and *Doxocopa* (the "bright blue bands" ring) and species of *Colobura* and *Hypna* (the "creamy bands" ring) where the palatability of butterflies, their ability to escape predator attacks, geographic distribution, relative abundance, and co-occurrence in the same habitats strongly suggest that escape mimicry is involved. In addition, we also indicate other butterfly taxa whose similarities of coloration patterns could be due to escape mimicry and would constitute important case studies for future investigation.

Introduction

Bates' (1862) theory of mimicry postulates that predators learn to avoid model species containing a "nauseous smell or taste" and palatable species, referred to as the "mimics," which obtain protection by resembling the model. The theory also carries an assumption that models are more abundant than mimics, so that predators would encounter them more frequently (but see Pinheiro 2007). Müller (1879) proposed that two or more unpalatable species could also benefit from sharing a similar color pattern by decreasing the costs involved in educating predators to avoid this pattern. 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 to all species involved, including the predators that could learn more quickly to avoid unpalatable species. In the neotropics, Müllerian and Batesian mimics usually form assemblages of similar looking butterflies, a phenomenon referred to as mimicry rings, which usually involves a number of species in a given locality (examples in DeVries 1987, Brown 1988, Chai 1990, Beccaloni 1997, Pinheiro 2003, Pinheiro *et al* 2008).

In contrast to chemically defended butterflies, which are usually aposematic (i.e., unpalatable and warning colored; Poulton 1890), fly slowly and regularly (Chai & Srygley 1990, Srygley & Chai 1990, Srygley & Dudley 1993) and have tough wings, apparently to resist bird handling while smelling or tasting captured individuals (Carpenter 1941, DeVries 2003), butterflies lacking defensive chemicals are usually cryptic at rest, fast and erratically fliers, which help them to evade bird attacks, and with more brittle wings, which allow them to escape by losing a piece of the wing when caught by a bird (Poulton 1890, Pinheiro *et al* 2014). Moreover, many palatable and fast flying butterflies seem to exhibit an apparent aposematic coloration on the upper wings that probably render them easily detected and identified by visually hunting predators. The idea that species may use conspicuous coloration to advertise difficulty of capture to predators has been suggested by many authors (reviewed by Huxton *et al* 2004). Yet, it has been also suggested that hard to catch species may form mimetic associations in a similar fashion to classical Batesian and Müllerian mimicry (van Someren & Jackson 1959), including the possibility of the best escapers being used as "models" by species with similar (Müllerian) or less (Batesian) effective escaping tactics.

Whether or not escape mimicry exists, however, has been the subject of intense debate. This form of mimicry requires that predators learn to avoid insects that are proficient at escaping, as well as they learn to avoid chemically defended prey. Such a possibility was tested by Gibson (1974, 1980) and Hancox & Allen (1991) whose results indicated that insectivorous birds do learn to avoid prey with an efficient escape mechanism. This, however, was contested by Brower (1995) who argued that conditioned aversion to escaping prey lasts only a few days in predators, whereas aversion to chemically defended prey may be retained in predators' memory for several months or years. Brower's comparison, however, did not take into consideration that memory of difficulty of capture in predators is likely to be constantly reinforced by seeing rapidly flying individuals. Moreover, being reminded that prey were hard to catch may happen much more easily than for unpalatable prey—in the former, only a slight, unsuccessful attempt at capture may be sufficient to jog a predator's memory, whereas in the latter, it is necessary to actually capture, smell or taste, or even consume an individual to remember (see also Srygley 1999). Huxton *et al* (2004) used mathematical models involving the relative abundance of models and mimics and the relative abundance of Müllerian mimics to test the conditions under which escape Batesian mimicry and escape Müllerian mimicry would have evolved and reached the conclusion that both forms of mimicry are possible but relatively unlikely. In addition, few attempts have been made to investigate the ability of Neotropical butterflies to escape attacks by insectivorous birds. Chai (1990) tested the escaping ability of butterflies to caged Rufous-tailed Jacamars (*Galbula ruficauda* Cuvier), and Pinheiro (1996) tested the escaping ability of butterflies (mostly males) to wild tropical kingbirds (*Tyrannus melancholicus* Vieillot). In spite of these problems, several possible cases of escape mimicry among butterflies have been proposed, usually without reaching a consensus among lepidopterists.

Purported cases of escape mimicry

One of the most debated cases of escape mimicry concerns the similarities of dorsal color patterns among several *Adelpha* Hübner (Limenitidinae) and *Doxocopa* Hübner (Apaturinae) species. An investigation conducted by Aiello (1984) on the larval host plants of *Adelpha* butterflies led her to propose that butterflies whose larvae feed on Rubiaceae, which contain alkaloids, would serve as models to non-Rubiaceae feeding species, which would constitute a classical case of Batesian mimicry between the two groups. However, experiments conducted by Chai (1990) and Pinheiro (1996) showed no evidence for unpalatability in these and similar looking *Doxocopa* species but showed a relatively high ability to escape bird attacks, leading Srygley (1999) to propose that similarities of color patterns among these butterflies would constitute a case of escape mimicry (see also Willmott 2003). Srygley (1999) also called the attention to the fact that both *Adelpha* and *Doxocopa* species exhibit the characteristic wide thorax and short body lengths of palatable and fast flying butterflies.

Another possible case of escape mimicry involves species in the "orange" ring such as *Dryas iulia* (Fabricius) (Heliconiinae) and *Marpesia petreus* Cramer (Biblidinae) proposed by Srygley (1994, 1999). *Dryas iulia* was 100% palatable when fed to jacamars (Chai 1986, 1990) and tropical kingbirds (Pinheiro 1996), but it was sometimes taste-rejected by caged silverbeak tanagers (Brower *et al* 1963). Like other Cyrestini, *M. petreus* is also palatable to jacamars (Chai 1990). Both butterflies are widespread in the neotropics and occur in a variety of habitats. Males of both species can also be found side by side on puddles. In many habitats, however, including those relatively disturbed, these butterflies are found together with the more unpalatable *Dione juno* (Cramer), *Dione moneta* Hübner, *Eueides lybia* Fabricius, *Eueides aliphera* (Godart), and *Dryadula phaetusa* (Linnaeus), a less similar species widespread in the neotropics. In addition to escape mimicry, it is possible therefore that these butterflies form a classical case of Batesian mimicry, with *D. iulia* being a model for *M. petreus* (Batesian mimic), or with both species using *Dione* spp., *Eueides* spp., and/or *D. phaetusa* as models in a classical case of Batesian mimicry.

One of the most intriguing cases concerns the "green and black" *Philaethria* spp. and *Siproeta stelenes* (Linnaeus). The genus *Philaethria* Billberg contains several large butterflies which are predominantly green with black stripes and which are widely distributed in the Neotropical region (Emsley 1965, Brown 1981). *Philaethria dido* (Linnaeus) is probably the most widespread species, found in the whole Amazon basin. *Philaethria ostara* (Höber), *Philaethria diatonica* (Fruhstorfer), *Philaethria constantinoi* Salazar, and *Philaethria andrei* Brévignon have distributions restricted to northern South America, whereas *Philaethria pygmalion* (Fruhstorfer) occurs in central South America and parts of western Amazon, and *Philaethria wernickei* (Röber) in the south, southeast, and northeast regions of Brazil (Suomalainen & Brown 1984, Penz 1999, Constantino & Salazar 2010). In virtually all these regions, *Philaethria* species are joined by *S. stelenes*, a nymphalini butterfly that shows an amazing similarity to them and uses the same habitats—usually sunny places in clearings and edges of rain forests where they perch and remain with wings opened for longer periods—and fly at similar heights. Apparently, these butterflies form a classical case of Batesian mimicry with *Philaethria*—a member of the Heliconiinini known to use cyanogenic glycosides as defensive chemicals against predators, serving as a model to palatable *S. stelenes* (=Batesian mimic), as first suggested by Brower *et al* (1963). Such a possibility, however, was not accepted by DeVries (1987), who reported that *P. dido* and *S. stelenes* in Costa Rica use different habitats and regards *S. stelenes* as a Batesian mimic of *Heliconius charitonia* (Linnaeus) (Heliconiinae), and by Srygley (1999) who suggested that these butterflies form an escape mimicry ring. The palatability of *S. stelenes* to many bird species has been demonstrated in several feeding experiments (Brower *et al* 1963, Brower & Brower 1964, Brower 1984, Chai 1990, Pinheiro 1996). However, the few palatability experiments conducted with *Philaethria*, especially *P. dido*, have indicated that this butterfly is also palatable to birds (Chai 1990, Pinheiro 1996). In addition, both butterflies exhibited a relatively high ability to escape attacks by Rufous-tailed jacamars (6 of 18 attacks or 33% for *P. dido* and 27 of 45 attacks or 60% for *S. stelenes*) and by tropical kingbirds (3 of 7 attacks or 43% for both *P. dido* and *S. stelenes*). Srygley (1994, 1999) pointed out that these butterflies converged on several morphological traits that affect their flight performance (a phenomenon described as “locomotor” mimicry) and suggested that they constitute a case of escape Müllerian mimicry.

In addition to the above cases, there are many other “rings” composed by palatable butterflies such as among *Catoblepia* Stichel (Brassolini) species or between species in the genera *Lasiophila* C. Felder & R. Felder and *Pedaliodes* Butler (Satyrini), *Physcopedaliodes* Foster and *Panyapedaliodes* Foster (Satyrini), *Chloreuptychia* Foster and *Cepheuptychia* Foster (Satyrini), *Chloreuptychia* (Satyrini) and *Euselasia* Hubner (Euselasini) that could also constitute cases of escape mimicry (Bristow 1981, Adams 1986, Mallet & Singer 1987). However, in most cases, the similarities of coloration patterns among butterflies could be simply due to common ancestry, and not to mimetic convergence. Below, we describe some mimicry rings whose palatability, escaping ability, geographic distribution, relative abundance, and co-occurrence in the same habitats suggest that escape mimicry has evolved. Moreover, these rings contain both related and unrelated species, which indicates that similarities of coloration patterns are not only due to common ancestry.

The “Bright blue bands” ring

The tribe Preponini occurs in tropical regions around the globe. Recent investigations on the taxonomy of Neotropical species based on male genitalia morphology (Bonfantti *et al* 2013) and DNA sequence data (Ortiz-Acevedo & Willmott 2013) indicate that *Archaeoprepona* Fruhstorfer and *Prepona* Boisduval constitute well-defined sister genera. In spite of marked variations in coloration patterns on the underwings, usually consisting of dull colors that render the butterflies cryptic at rest, most of these large and robust butterflies, such as *Archaeoprepona amphimachus* (Fabricius), *Archaeoprepona chalciope* (Hübner), *Archaeoprepona demophon* (Linnaeus), *Archaeoprepona demophoon* (Hübner), *Archaeoprepona licomedes* (Cramer), *Archaeoprepona meander* (Cramer), *Prepona dexamenus* Hopfer, *Prepona laertes* (Hübner), *Prepona pheridamas* (Cramer), and *Prepona pylene* Hewitson, exhibit a bright blue-greenish transverse band crossing the middle of the upperwings that make them very similar when flying or perched with opened wings (Fig 1a, b).

Most of these butterflies are widespread in the neotropics and coexist in a variety of forest habitats. Although living mostly in the canopy, they come to the ground to feed on dung and rotting fruits (Brown 1992). Males in both genera perch head-downward on tree trunks in clearings and forest edges, and at least some *Archaeoprepona* species are known to chase passing butterflies, sometimes producing long erratic circles before returning to the same perching place (DeVries 1987). Data obtained with traps containing fermented fruits as baits in forest sites as diverse as in central Brazil (Pinheiro & Ortiz 1992), western Amazon (Pinheiro 1996, Ribeiro & Freitas 2012), Ecuador (DeVries *et al* 1997), and Costa Rica (DeVries *et al* 2012) showed that *A. demophon* was the most abundant species in all sites. Combining high speed and very unpredictable maneuvers, this butterfly was able to escape in 73 of 83 (88%) attacks by Rufous-tailed Jacamars (Chai 1990) and 8 of 18 attacks (44%) by tropical kingbirds (Pinheiro 1996), which suggests a high ability to escape bird attacks. Although tests are lacking for other species, it is possible that all other *Archaeoprepona* share the same ability to evade predator attacks and, in this case, would constitute true escape Müllerian mimics. This, however, may not be the case for the *Prepona* species (one species identified as *Prepona laertes* tested by Pinheiro also showed a high ability to escape bird attacks, but there are doubts concerning the identification of this butterfly). These butterflies exhibit relatively large eyespots close to the margin of the underwings (Fig 1b) that might function to attract bird attacks to less vital parts of the body (Poulton 1890, Pinheiro *et al* 2014). Although not directly related to the potentially mimetic coloration on the upperwings, the presence of eyespots in *Prepona* (absent in *Archaeoprepona*, Fig 1a) could somehow indicate differences in the ability to escape predator attacks between the two genera. Interestingly, individuals in both genera produce a rustling sound like “sheets of newspapers in the wind” in ordinary undisturbed flights (DeVries 1987), and this sound might also act as a signal associated to color patterns to advertise high evasive ability to predators.

Although slightly smaller than the above genera, males of several species of *Doxocopa* Hübner (Apaturinae) such as *D. cherubina* (C. & R. Felder), *D. clothilda* (C. & R. Felder), and *D. laurentia* (Godart) have a dorsal wing coloration pattern very similar to that of *Archaeoprepona* and *Prepona* (Fig 1c). Moreover, they use the same habitats utilized by

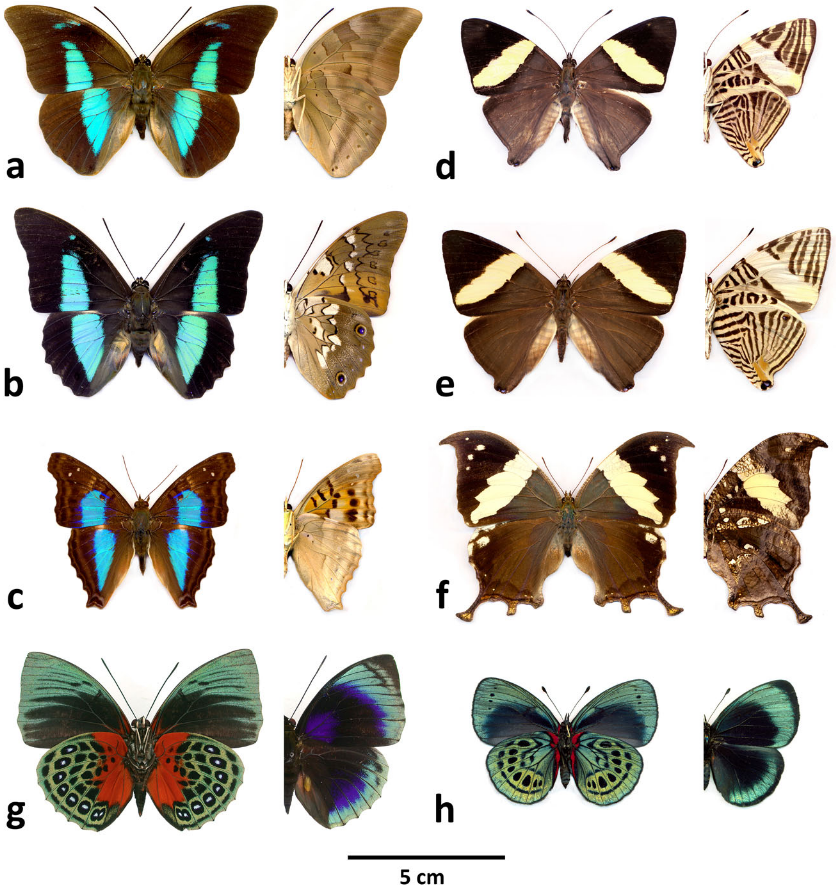

Fig 1 Selected species belonging to the mimicry rings discussed in the text. **a**–**c** “Bright blue bands” ring: **a** *Prepona demophon* (male), Mogi Guaçu, São Paulo, Brazil, **b** *Prepona pylene* (male), Querência, Mato Grosso, Brazil **c** *Doxocopa laurentia* (male), Campinas, São Paulo, Brazil; **d**–**f** “Creamy bands” ring: **d** *Colobura annulata* (male), Santo Antônio do Tauá, Pará, Brazil, **e** *Colobura dirce* (male), Linhares, Espírito Santo, Brazil **f** *Hypna clytemnestra* (female), Campinas, São Paulo, Brazil; **g**–**h** *Prepona*-*Asterope* ring: **g** *Prepona hewitsonius* (male), Napo, Ecuador, **h** *Asterope leprieuri* (female), Itaituba, Pará, Brazil **a**–**f** dorsal left, half ventral right **g**–**h** ventral left, half dorsal right.

these butterflies living in the canopy and on the ground where they feed on dung and rotting fruits (Brown 1992). Although the species above were not tested for palatability and escape ability, data from Chai (1990), Pinheiro (1996), and Martins *et al* (2010) indicate that *Doxocopa* species are usually palatable and exhibit a good ability to escape bird attacks.

Given that *Archaeoprepona* and *Prepona* are sister genera, it is possible that similarities of color patterns between them are due to common ancestry, and not to mimetic convergence. However, the fact that species in both genera have strongly diverged in the underwing coloration pattern, but not on the upperwing, which we believe could advertise difficulty of capture to predators, suggests that natural selection has promoted monomorphism among species in the two genera, probably by removing individuals exhibiting deviant coloration patterns from their natural populations. In addition, the fact that *Doxocopa* species also potentially participate in this ring strongly suggests that mimetic convergence has evolved at least in the latter. In addition to a strong sexual dimorphism exhibited by many species, *Doxocopa* butterflies show a large variability in coloration patterns and seem to converge on the color patterns of a variety of butterflies such as many *Adelpha* species (see above), some Biblidinae, such as *Diaethria clymena* (Cramer) that is mimicked by *Doxocopa zunilda* (Godart), and other butterflies that also perch on the ground. It is possible therefore that the *Doxocopa* species above have converged on coloration patterns of the *Archaeoprepona* and *Prepona* species, but the mimetic interactions between species in the three genera obviously need further investigations.

The “Creamy bands” ring

Colobura spp. and *Hypna clytemnestra* (Cramer) are commonly found in the Neotropical region. The genus *Colobura* Bilberg is composed by two sibling species: *Colobura dirce* (Linnaeus) and *Colobura annulata* Willmott, Constantino and Hall, which occur together throughout most of their geographical distribution (*C. annulata* does not occur in the Caribean region nor in central and southeastern Brazil where *C. dirce* is abundant). In spite of many differences on the underside wings between *Colobura and Hypna* (*Colobura* spp. exhibit black and white stripes and an eyespot close to tip of the hindwings; *H. clytemnestra* shows silver spots and small tails on the hindwings), these relatively large butterflies share a yellowish creamy band on the upper forewings that make them very similar in flight or perched with the wings opened (Fig 1d–f).

Butterflies in both genera feed on rotting fruits and sap flows and are commonly found in trails and clearings in primary and second-growth forests where their host plants grow up (*Cecropia* spp. and *Croton* spp., respectively; Willmott *et al* 2001, AVLF unpublished). Data obtained with traps containing fermented fruits by DeVries *et al* (2012) in a Costa Rican rainforest showed that *C. dirce* tend to be more abundant in the canopy whereas *H. clytemnestra* was found mostly in the understory. Willmott *et al* (2001) also reported habitat segregation between *Colobura* species, with *C. dirce* living mostly in the understory, and *C. annulata* in the canopy. Our observations on these butterflies in central and southeastern Brazil (where *C. annulata* is absent) showed that *C. dirce* and *H. clytemnestra* may overlap both flight and perching heights. *Colobura dirce* perches head-downward on tree trunks, usually between 2 and 5 m above the ground, and often alternate flight heights from the understory to the canopy. Males of *H. clytemnestra* also perch along trails on leaves or trunks close to the ground and chase passing butterflies (Brown 1992). On different occasions, these butterflies were observed side by side on rotting fruits on the ground.

Whether or not *Colobura* spp. and *H. clytemnestra* would constitute a case of escape Batesian mimicry or escape Müllerian mimicry remains unknown. Both butterflies seem to be palatable to predators (Chai 1990, Pinheiro 1996; palatability data for *H. clytemnestra* are lacking, but the general palatability of the Charaxinae to birds is well known). In addition, at least *C. dirce* seem to exhibit a relatively high ability to escape bird attacks—unsuccessful attacks accounted for 8/26 attacks (31%) by Rufous-tailed Jacamars (Chai 1990) and 1/5 attacks (20%) by tropical kingbirds (Pinheiro 1996). However, the ability of *H. clytemnestra* to escape predator attacks has not been tested, and therefore, both options are possible.

Other possible cases

In addition to many cases of classical Batesian and Müllerian mimicry that remain virtually uninvestigated, there seems to be numerous other potential escape mimicry rings among Neotropical butterflies that deserve attention. Examples include some non-blue *Prepona* (formerly in the genus *Agrias* Doubleday) like *Prepona hewitsonius* (Bates) (Charaxinae) and species of *Asterope* Hübner like *Asterope leprieuri* (Feisthamel) (Biblidinae) which occur in sympatry along most of the Amazon basin (Fig 1g, h), several metalmarks (Riodinidae) that show many similarities of coloration patterns between species in unrelated genera and, especially, among skippers (Hesperiidae) that seem to be faster and more difficult to capture than most butterflies (Sourakov 2009), and remain comparatively much less investigated. In addition, an increasing number of reports suggest that escape mimicry is not restricted to butterflies but involves many other prey insects (e.g., Hespenheide 1973, Balgooyen 1977, Holm & Kirsten 1979, Sourakov 2011, Vannin & Guerra 2012).

Conclusions

Demonstrating escape mimicry in butterflies is obviously a hard task due to the complexity of phenomena involved and difficulties to replicate natural conditions in both laboratory and field experiments. In addition, some purported cases of escape mimicry may not constitute true examples of this form of mimicry as similarities of coloration patterns among species could be due to common ancestry or classical forms of Batesian and Müllerian mimicry. Such alternative explanations, however, do not seem to apply to the cases reported here such as the bright blue bands ring, which constitutes one of the biggest mimicry rings in the Neotropical region, the creamy bands ring, and many other rings involving butterflies, skippers, and other insects that lead us to believe that escape mimicry is a more widespread phenomenon than previously thought. Hopefully, the present paper will encourage future research in this subject, unveiling these and other cases of escape mimicry among butterflies and other insect groups.

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