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Both Palatable and Unpalatable Butterflies Use Bright Colors to Signal Difficulty of Capture to Predators

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Abstract

Birds are able to recognize and learn to avoid attacking unpalatable, chemically defended butterflies after unpleasant experiences with them. It has also been suggested that birds learn to avoid prey that are efficient at escaping. This, however, remains poorly documented. Here, we argue that butterflies may utilize a variety of escape tactics against insectivorous birds and review evidence that birds avoid attacking butterflies that are hard to catch. We suggest that signaling difficulty of capture to predators is a widespread phenomenon in butterflies, and this ability may not be limited to palatable butterflies. The possibility that both palatable and unpalatable species signal difficulty of capture has not been fully explored, but helps explain the existence of aposematic coloration and escape mimicry in butterflies lacking defensive chemicals. This possibility may also change the role that putative Müllerian and Batesian mimics play in a variety of classical mimicry rings, thus opening new perspectives in the evolution of mimicry in butterflies.

Introduction

Butterflies have provided some of the best examples for studies on prey protective coloration. In his pioneer work, Bates (1862) proposed that palatable butterflies (the mimics) imitate the coloration pattern of unpalatable, chemically defended species (the models) to deceive visually hunting predators such as insectivorous birds. Müller (1879) proposed that two or more unpalatable butterflies could also converge on coloration patterns, as such convergence would decrease the costs involved in educating predators to avoid them. Poulton (1890) observed that unpalatable butterflies and other insects usually exhibit bright and contrasting colors and proposed the term aposematic or warning coloration as these colors might signal something unpleasant or dangerous to predators. Within this context, several experiments conducted in the last decades have shown that colors exhibited by unpalatable species such as red, yellow, orange, and black make prey more easily detected, identified, and also more memorable to predators than prey with cryptic coloration (reviewed in Ruxton *et al* 2004, Mappes *et al* 2005).

On the other hand, palatable butterflies that do not mimic unpalatable models were usually assumed to exhibit a cryptic coloration (Cott 1940, Edmunds 1974). In fact, many palatable butterflies actually do. In most cases, however, cryptic coloration is restricted to the ventral surface of the wings, which are usually dull, mottled pale, and/or dark and match the background coloration when perched with closed wings (Fig 1a, g, h). In groups such as the Charaxinae (Nymphalidae) and Coliadinae (Pieridae), several species exhibit amazing similarities to plant parts, especially leaves (Fig 1h). This phenomenon is referred to as masquerade (Skelhorn *et al* 2010), which makes butterflies harder to detect by visually hunting predators when they are perched on vegetation or the ground. Given that crypsis and masquerade lead to concealment, both imply a lack of visual signal from the butterflies to their potential predators (Brown 1988).

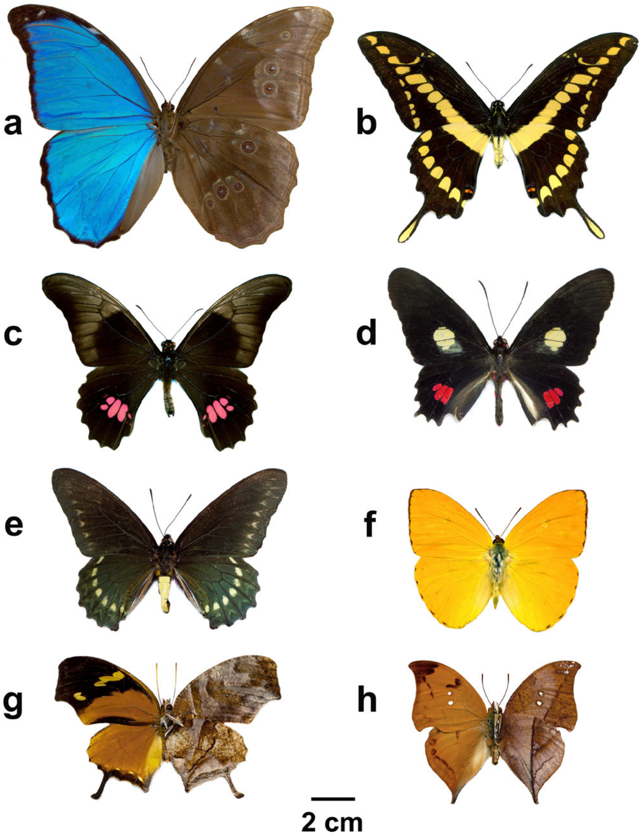

Fig 1 Some butterfly species cited in the text: **a** *Morpho menelaus coeruleus* (Perry), male, dorsal (*left*) and ventral (*right*) views. Like several other *Morpho*, this butterfly performs a kind of flapping flight that makes it hard to capture by birds. The iridescent blue coloration on the dorsal surface of the wing renders this butterfly easily detected at large distance. At rest, they exhibit a predominant cryptic coloration and seem to use eyespots to deflect predator attacks. **b** *Heraclides thoas brasiliensis* (Rothschild & Jordan), male, dorsal view. One of the biggest and easily noticed butterflies in the Neotropical region. As most palatable butterflies, its wings are soft and brittle, allowing the butterfly to escape by losing a piece of the wing when pecked by predators. The prominent tails on the hindwings are believed to attract predator attacks to them, thus avoiding attacks on more vital parts of the body. **c** *Heraclides anchisiades capys* (Hübner), male, dorsal view. Although regarded as a Batesian mimic of *Parides*, this butterfly is much bigger, faster, and occurs in many sites without their models. **d** *Parides anchises nephalion* (Godart) (Troidini), dorsal view. One of the most unpalatable butterflies in the Neotropical region. The *red and white spots* on a dark background is shared with a variety of Müllerian and Batesian mimics. **e** *Battus polystictus polystictus* (A. Butler), male, dorsal view. Although highly unpalatable, this butterfly exhibits a very fast and erratic flight. **f** *Phoebis argante* (Fabricius), male, dorsal view. Fly above the canopy, along the forest edge, roads, rivers, and other open areas where it is easily detected by predators. This butterfly, however, becomes cryptic when it perches on flowers of *Cassia* Linnaeus (Fabaceae), its natural host-plants. **g** *Consul fabius* (Cramer), male, dorsal (*left*) and ventral (*right*) views. This butterfly flies slowly when undisturbed, changing to a fast, evasive flight if threatened. Note the differences in wing pattern between dorsal (mimetic) and ventral wings. **h** *Zaretys strigosus* (Gmelin) (Charaxinae), male, dorsal (*left*) and ventral (*right*) views. Note the amazing similarities of ventral view to dead leaves which include not only leaf shape and colors, but primary and secondary nervures, a small false hole, and parts of the wings apparently "eaten" by herbivores.

Many palatable butterflies, however, show a variety of bright colors on the dorsal surface of the wings which may contrast to each other and/or to the background coloration when they fly or perch with open wings (Fig 1a, b, c, f, g; see Trigo 2000 for a review of defensive chemicals in Neotropical butterflies). Moreover, several palatable butterflies in Papilionidae, Nymphalidae, Pieridae, and Hesperiidae fly in open and sunny habitats that make them easily detected and probably more memorable to predators in a way similar to classical aposematic (and unpalatable) butterflies. However, the question of why so many butterflies evolved bright dorsal wing colors remains somewhat open. One possible explanation is that bright colors evolved in male butterflies through sexual selection (Kemp *et al* 2014, White *et al* 2015), regardless of chemical defenses against predators (or lack thereof). Such phenomenon, however, does not explain how palatable and brilliant colored butterflies could offset the fitness cost of being more visible to a variety of insectivorous birds and other predators that rely on eyesight to find prey (for further details, see Turner 1984, Penz & Mohammadi 2013). In fact, a recent study investigating the role of sexual and natural selection on the color patterns of unpalatable *Heliconius* showed that color patterns preferred by females coincide with those that best advertise unpalatability to predators and that a same color pattern may serve both functions (Finkbeiner *et al* 2014), and probably others like thermoregulation (Kingsolver 1988). Therefore, irrespective of the mechanism (natural or sexual selection), it is possible that bright and/or contrasting colors that evolved in palatable butterflies might signal an unprofitable trait to predators that does not involve defensive chemicals.

There are obviously several exceptions to the patterns described above. For instance, the genus *Hamadryas* (Nymphalidae) contains many species exhibiting cryptic coloration on the dorsal surface of the wings, some of which show aposematic coloration on the ventral surface (Jenkins 1983, Chai 1988). Differing from most other Nymphalidae, these butterflies perch on tree trunks with opened wings, which render them cryptic on the trunk. Other exceptions are found in many Satyrini that seem to exhibit a cryptic coloration on both dorsal and ventral surfaces of the wings. These generally live in the dark forest understory and some species seem to be able to fly almost unnoticed by predators (or at least by humans). We may therefore attribute their cryptic color pattern to the low light conditions in their natural habitats (see also Brown 1988). This could be also the case for nymphalid butterflies with transparent wings that also inhabit the understory and, paradoxically, involving both palatable (e.g., Haeteriini, Satyrinae) and unpalatable species (e.g., Ithomiini, Danainae). In addition, there are many cases where palatable butterflies do not exhibit bright or contrasting colors on the dorsal surface of the wings, but this does not imply that they are cryptic (they might exhibit a weak aposematic signal to predators; see Endler & Mappes 2004) or predators cannot associate their colors with unprofitable traits (Ham *et al* 2005).

Here, we argue that palatable butterflies might be using bright colors to advertise difficulty of capture to predators. We review the most common escape tactics of butterflies against insectivorous birds and show evidence based on literature and our own experience on the neotropics that birds do recognize and avoid attacking butterflies with high-escape ability. We also suggest that, depending on the predator involved, unpalatable butterflies may also signal difficulty of capture to predators, and this might change the role that Müllerian and Batesian mimics play in a variety of mimicry rings.

Signaling Difficulty of Capture to Predators

The possibility that predators may associate difficulty of capture to the color patterns of palatable butterflies has been suggested long ago (van Someren & Jackson 1959, Young 1971, Srygley 1994, 1999, Pinheiro 1996). However, few attempts have been made to assess the ability of butterflies to escape predator attacks and, as a consequence, we have no idea on how widespread this phenomenon might be among butterflies.

The first attempt to test butterfly ability to escape attacks by birds was by Chai (1990) who offered a variety of palatable and unpalatable butterflies to caged Rufous-tailed Jacamars (*Galbula ruficauda* Cuvier) (Galbulidae). Later, Pinheiro (1996) released live butterflies close to wild Tropical Kingbirds (*Tyrannus melancholicus* Viellot) (Tyrannidae) to assess their feeding behavior. In both studies, palatable butterflies showed a greater ability to escape bird attacks than chemically defended species. These results were corroborated by investigations on morphology showing that compared to chemically defended species, palatable ones (especially Nymphalidae) have a relatively larger thorax with a larger flight muscle mass, a shorter abdomen that keeps the center of body mass closer to the thorax, and faster, more erratic flight performance (Chai & Srygley 1990, Srygley & Chai 1990a, b, Marden & Chai 1991, Srygley & Dudley 1993, Martins *et al.* 2010; Table 1). Palatable and unpalatable butterflies are also known to differ in wing toughness, the former exhibiting relatively soft, brittle wings that allow escape by losing a piece of the wing after being attacked, and the latter exhibiting tougher wings, that presumably allow butterflies to be captured, smelled, and/or tasted by birds without suffering significant wing damage (Carpenter 1941, Brower 1984, DeVries 2002, 2003). Moreover, many palatable butterflies possess patterns resembling vertebrate-like eyes on the wings (especially Nymphalidae) and prominent tails (most Papilionidae, and some Nymphalidae, Riodinidae, Lycaenidae, and Hesperiidae) (Fig 1b) which potentially divert bird attacks from vital body regions (Robbins 1980, Olofsson *et al* 2010, Pinheiro *et al* 2014, Prudic *et al* 2015; but see also Stevens 2005, Stevens *et al* 2008, Olofsson *et al* 2015 for the possibility that eyespots also intimidate predators). These traits indicate that butterflies lacking chemical defenses have evolved many different ways to escape predator attacks and that visually oriented predators can potentially associate their colors to their difficulty of capture, including any defense they might employ to escape (e.g., flight speed and maneuverability, soft and brittle wings, eyespots, prominent tails, or a combination of such traits).

Further and more suggestive evidence that palatable butterflies signal difficulty of capture is that many elusive, fast-flying species seem to have evolved mimetic relationships with similar (escape Müllerian mimicry) or less evasive (escape Batesian mimicry) butterflies and/or other insects analogous to unpalatable butterflies and their Müllerian and Batesian mimics (Table 2; see Pinheiro & Freitas 2014 for a review of cases included in this table). Escape mimicry has not been fully demonstrated, mostly due to the complexity of phenomena involved and limitations to simulate natural conditions under controlled environments. However, it has been predicted to occur in many other butterflies, skippers (Hesperiidae), which fly very fast and contain numerous cases of color similarities involving both distant and closely related species, plus several other insects (Hespenheide 1973, Holm & Kirsten 1979, Vannin & Guerra 2012), and also birds (Baker & Parker 1979).

The Responses of Wild Predators to Butterflies

The possibility that butterflies and other prey advertise difficulty of capture to predators and evolve escape mimicry rings is supported by experiments which show that birds learn to avoid prey with an efficient escape mechanism (Gibson 1974, 1980, Hancox & Allen 1991). Brower (1995) nonetheless argued that birds in these experiments quickly lost their aversion to such prey, which contrasts long-term aversion to unpalatable prey obtained in other experiments. If birds were unable to remember prey they have missed, they would continue to pursue prey they are unable to catch. Our observations on wild insectivorous birds showed that experienced individuals avoid attacking butterflies with high-escape ability, indicating they remembered such prey, and also that they use alternative hunting tactics to locate and attack them when they stop flying and perch on a given substrate. This is the case of the Rufous-tailed Jacamar, regarded as the most specialized Neotropical butterfly predator (Chai 1986, Pinheiro 2011), that sight rejects fast-flying butterflies like *Morpho* Fabricius (Morphini) (Fig 1a), *Caligo* Hübner (Brassolini), and many species of *Anteos* Hübner,

Table 1 Morphological traits related to flight pattern and escaping ability in palatable and unpalatable butterflies.

Traits	Palatable	Unpalatable	References
Flight pattern	Fast, unpredictable	Slow, predictable	Chai & Srygley 1990
Body shape	Short, squat	Long, thin	Chai & Srygley 1990
Flight muscle mass	Relatively large	Relatively small	Srygley & Chai 1990a, b, Marden & Chai 1991, Martins *et al.* 2010
Center of body mass (relative to the wing base)	Just posterior	Further posterior	Srygley & Dudley 1993
Wing toughness	Soft, fragile	Tough, robust	Carpenter 1941, Brower 1984, DeVries 2002, 2003
Eyespots and prominent tails	Present	Absent	Olofsson *et al* 2010, Pinheiro *et al* 2014, Prudic *et al* 2015

Phoebis Hübner (Fig 1f), *Aphrissa* Butler, *Eurema* Hübner, and *Pyrisitia* Butler (Coliadinae) even when butterflies fly close (<1 m) to the birds' hunting perches, but attack them when they perch (Campos & Pinheiro unpubl. data). Jacamars are able to detect and capture several cryptic insects perched on vegetation (e.g., moths resting on trunks during the day; Pinheiro *et al* 2004). However, they use at least two additional methods to detect cryptic and probably hard to detect butterflies perched on the vegetation. The first consists of following fast-flying individuals by sight and attacking them if they perch within the birds' visual field. This is also used by many other birds that eat butterflies such as tyrant-flycatchers (Tyrannidae) (Pinheiro 1996, 2003, AVL Freitas pers obs; see also Fitzpatrick 1980, 1981, Gabriel & Pizo 2005), puffbirds (Bucconidae) (Melo & Marini 1999), motmots (Momotidae) (Pinheiro *et al* 2008), and anis (Cuculidae) (Burger & Gochfeld 2001). The second consists of following moving mammals and other big animals that act as beaters and displace butterflies and other insects perched on vegetation which are subsequently detected and attacked (Rand 1953, Dean & MacDonald 1981, Barnett & Shaw 2014). We hypothesize that these behaviors may explain why many butterflies evolved bright coloration on the dorsal surface of the wings, i.e., to advertise difficulty of capture to predators when they are flying or perched with open wings, and a cryptic one on the ventral surface that may prevent detection by predators when butterflies are perched on the vegetation or the ground.

Table 2 Examples of purported cases of escape mimicry in butterflies.

Mimicry rings (predominant colors)	Taxa involved	References
Brown and orange stripes	*Catoblepia* Stichel (Brassolini) (several species)	Bristow (1981)
Brown and orange stripes	*Opsiphanes* spp. (Brassolini) *Brassolis* spp. (Brassolini)	Penz & Mohammadi (2013)
Yellow and iridescent blue	*Catoblepia orgetorix rothshildi* Casagrande and Lamas *Caligo atreus* (Kollar) (Brassolinae)	Penz & Mohammadi (2013)
Orange and black stripes	*Dryas iulia* (Fabricius) (Heliconiinae) *Marpesia petreus* Cramer (Biblidinae)	Srygley (1994, 1999)
Green and black stripes	*Philaethria* spp. (Heliconiinae) *Siproeta stelenes* (Linnaeus) (Nymphalinae)	Srygley (1994, 1999)
Brown and yellow	*Adelpha* Hübner (Limenitidinae) (several species) *Doxocopa* Hübner (Apaturinae) (several species)	Srygley (1994, 1999)
Orange sulfur	*Colias eurytheme* Boisduval (Coliadinae) *Arphia conspersa* Scudder (Orthoptera)	Balgooyen (1997)
Bright blue bands	*Archaeoprepona* Fruhstorfer (Preponini) (several species) *Prepona* Boisduval (Preponini) (several species) *Doxocopa* Hübner (Apaturinae) (several species)	Pinheiro & Freitas (2014)
Creamy bands	*Colobura dirce* (Linnaeus) (Nymphalinae) *Colobura annulata* Willmott, Constantino and Hall (Nymphalinae) *Hypna clytemnestra* (Cramer) (Charaxinae)	Pinheiro & Freitas (2014)
Red and blue	*Prepona hewitsonius* (H. W. Bates) (Charaxinae) *Asterope leprieurí* (Feisthamel) (Biblidinae)	Pinheiro & Freitas (2014)

Signaling Difficulty of Capture by Unpalatable Butterflies

Studies on butterfly morphology and flight ability have indicated that palatable butterflies usually fly fast and perform unpredictable aerial maneuvers when threatened, and unpalatable species fly slowly in a predictable way (Chai & Srygley 1990, Srygley & Chai 1990a, b, Marden & Chai 1991, Srygley & Dudley 1993). These studies suggest that unpalatability and escape ability are mutually exclusive and that unpalatable species are easily captured by predators. Although a negative correlation between unpalatability and escaping ability was obtained by Pinheiro (1996), this was only found for nymphalid butterflies where a smaller investment in flight muscles was compensated by a greater investment in fecundity (Marden & Chai 1991). Furthermore, some species in the genus *Battus* Scopoli (Papilionidae) (Fig 1e) were found to be highly unpalatable (Brower 1984, Chai 1990) but are also known to fly fast and perform a variety of evasive maneuvers. Moderately unpalatable Nymphalidae in the genera *Dione* Hübner, *Dryadula* Michener, *Agraulis* Boisduval and Le Conte, and *Eueides* Hübner (Heliconiini), and the highly unpalatable *Danaus* Kluk (Danaini) fly fast and can perform erratic maneuvers. Several insectivorous birds have been reported to attack and feed on these butterflies, especially *Danaus plexippus plexippus* (Linnaeus) that forms large aggregations in Mexico (Fink *et al* 1983, Brower & Calvert 1985), but bird attacks on flying *Danaus* individuals were not observed. In the "Tiger" mimicry ring (Fig 1g), some larger species like *Pterourus zagreus* (Doubleday), *Pterourus ascolius* (C. Felder & R. Felder) (Papilionidae), *Heliconius ethilla* (Godart), *Heliconius numata* (Cramer), *Lycorea halia* (Hübner) (Danaini), and species of *Melinaea* Hübner (Ithomiini) exhibit greater speed and maneuverability than most *Mechanitis* Fabricius, *Hypothyris* Hübner, and *Napeogenes* H. Bates (Ithomiini) which are usually the most abundant butterflies in this ring (Brown & Benson 1974, DeVries 1999, Pinheiro 2007, Pinheiro *et al* 2008). It seems apparent that variation in escape ability occurs in palatable and unpalatable butterflies (Chai 1990, Pinheiro 1996), and that species of both categories could be ranked according to their flight behavior as it relates to predator escape ability.

The possibility that chemically defended butterflies also signal difficulty of capture obviously depends on the predator species involved. Predators such as insectivorous or omnivorous birds not only vary in their tolerance to defensive chemicals (Brower 1984, Exnerová *et al* 2003, Pinheiro 2011) but also in their ability to capture flying insects. Agile birds like jacamars, which are able to catch a variety of palatable and unpalatable butterflies in flight, might associate coloration with unpalatability. Less agile, heavier bodied birds like tyrant-flycatchers, puffbirds, motmots and, especially anis are apparently unable to perform sophisticated and high energy aerial maneuvers, and might associate the same colors with difficulty of capture or even both traits. Whether or not mimetic butterflies signal unpalatability, difficulty of capture or both traits depends on the local assemblage of predators (the signal receivers).

Consequences to Mimicry Theory

The possibility that both palatable and unpalatable butterflies signal difficulty of capture to predators may change the interpretation of how models, Müllerian and Batesian, mimics are expected to perform in "classical" mimicry rings (i.e., those based on unpalatability). As indicated above, Müllerian mimics differ in their ability to escape predator attacks, thus allowing evasive species to become escape models to less evasive ones. This may change the nature of the interaction between them from mutualism in Müllerian mimicry, to parasitism, predicted in Batesian mimicry. However, some Müllerian mimics converge in flight pattern and escape ability. Srygley (1999) showed that mimetic *Heliconius* species pairs were more similar to each other in morphology and flight pattern than to their closest relatives (a phenomenon referred to as locomotor mimicry), and also seem to exhibit similar escape abilities. This, however, may not be the case for other Müllerian mimics involving distantly related species such as in the Tiger ring (see above).

Putative Batesian mimics also need to be compared to their models with regard to escape abilities. They are found in a variety of genera in the Papilionini (*Heraclides* Hübner, *Pterourus* Scopoli, and *Mimoides* K. Brown) (Papilionidae), Melitaeini (*Castilia* Higgins, *Eresia* Boisduval, and *Gnathotriche* C. Felder & R. Felder), Charaxini (*Consul* Hübner) (Nymphalidae), Dismorphiinae (*Dismorphia* Hübner, *Patia* Klots, and *Moschoneura* Butler), and Pierinae (*Perrybris* Hübner, *Charonias* Röber, and *Archonias* Hübner) (Pieridae) (see DeVries 1987, Tyler *et al* 1994 for illustrations). Such mimics are usually smaller and, as expected from mimicry theory, less abundant than their models (Bates 1862, but see Pinheiro 2007). Although flight patterns have not been investigated for most Batesian mimics, *Eresia* spp. and some Dismorphiinae such as *Moschoneura* seem to exhibit slow flight, similar to their *Heliconius* and Ithomiini models. *Consul fabius* (Cramer) (Charaxinae) (Fig 1g) is a particularly interesting example given that it flies slowly when undisturbed (similar to its Tiger models), but it changes to a fast, evasive flight if threatened (CM Penz pers obs). This may not be the case for *Heraclides*, *Pterourus*, *Mimoides* (Papilionidae), which contain many fast and evasive mimetic species. For instance, based on wing color convergence and palatability data, *Heraclides anchisiades* (Hübner) (Papilionini) (Fig 1c) is considered to be a Batesian mimic of *Parides* Hübner butterflies (Tyler *et al* 1994) (Fig 1d). This species is nonetheless much larger, faster, more abundant, and it occurs in many locations where their *Parides* models are not found. A high incidence of beak marks (especially wing tears) in wild individuals from different sites in South America (CEG Pinheiro pers obs) suggests that *H. anchisiades* can potentially educate predators to avoid them because they are difficult to capture. If this is the case, it can be hypothesized that *H. anchisiades* is a mutualistic, escape Müllerian mimic of the highly unpalatable *Parides* at sites where they co-occur, and not solely a Batesian mimic based on the lack of chemical defense. This form of mimicry, which combines two lines of defense against predators, unpalatability and escape ability, remains unexplored yet could help understand the evolution of color patterns in butterflies and other insects. The possibility that the evolution of escape mimicry preceded that of unpalatability has not been fully investigated within the context of classical Müllerian and Batesian mimicry and should be viewed as an important question for future work.

Final Remarks

Here, we suggest that butterflies evolved different types of escape tactics that they signal to predators through aposematic coloration, and such signal is used by both palatable and unpalatable butterflies. This clearly contrasts the classical view on protective coloration where butterflies were classified as aposematic or cryptic depending on the wing colors they exhibit and the utilization or not of defensive chemicals.

Assuming that both palatable and unpalatable butterflies signal difficulty of capture and educate predators to avoid them helps to explain not only the existence of aposematic coloration and escape mimicry in butterflies lacking defensive chemicals, but may also change the mimetic interactions between models, Müllerian and Batesian mimics, in various recognized mimicry rings. In addition, it brings new light on how mimicry might have evolved in butterflies. We hope that future investigations on the evolution of butterfly protective coloration may incorporate the escape tactics of palatable and unpalatable butterflies, thus assessing its effects on various bird predators that attack and feed on butterflies in natural conditions.

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