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NOTES

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Antipredation and “antimimicry”: wing pattern is supported by behavior in *Archaeoprepona chromus* (Lepidoptera: Nymphalidae: Preponini)

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Abstract: Sagittal movement of the hindwings was observed in the Neotropical butterfly *Archaeoprepona chromus* (Guérin-Ménéville, 1844) (Nymphalidae: Preponini). It was repeatedly initiated by the butterfly in response to an approaching threat (camera), and ceased when the threat was removed. This behavior is akin to the previously described false-head behavior of hairstreak butterflies (Lycaenidae) and supports the deflection hypothesis regarding the function of the underside wing pattern (small eyespots) for this and many similar species. This wing pattern and behavior constitute a tradeoff between escaping attack by cryptic patterning and deflecting attack by drawing attention to less vital parts of the butterfly. The bright colors of the eyes and the proboscis in this species may be an additional defense mechanism, as the head region with the proboscis extended may loosely resemble a snake head, thus repelling, delaying, or further deflecting attacks by avian predators. Observations are discussed in the context of our current knowledge of the evolution of Preponini, bird predation, and the function of eyespots in nymphalid butterflies. Field observations on *Doxocopa cyane* (Latreille, [1813]), conducted in the same site, suggest that defense strategies employed by this similar-looking but only distantly related butterfly can be very different from those employed by *Archaeoprepona*. By examining collections from the broad geographic ranges of these two sympatric species, one can conclude that while they are likely mimetic, there is also an obvious divergence in color of the dorsal reflective patch, which may be imposed by sexual selection.



Fig. 1. *Archaeoprepona chromus* engaged in energetic sagittal hindwing movements which attracted attention to the posterior end of the butterfly and that were repeatedly initiated in response to an approaching stimulus.

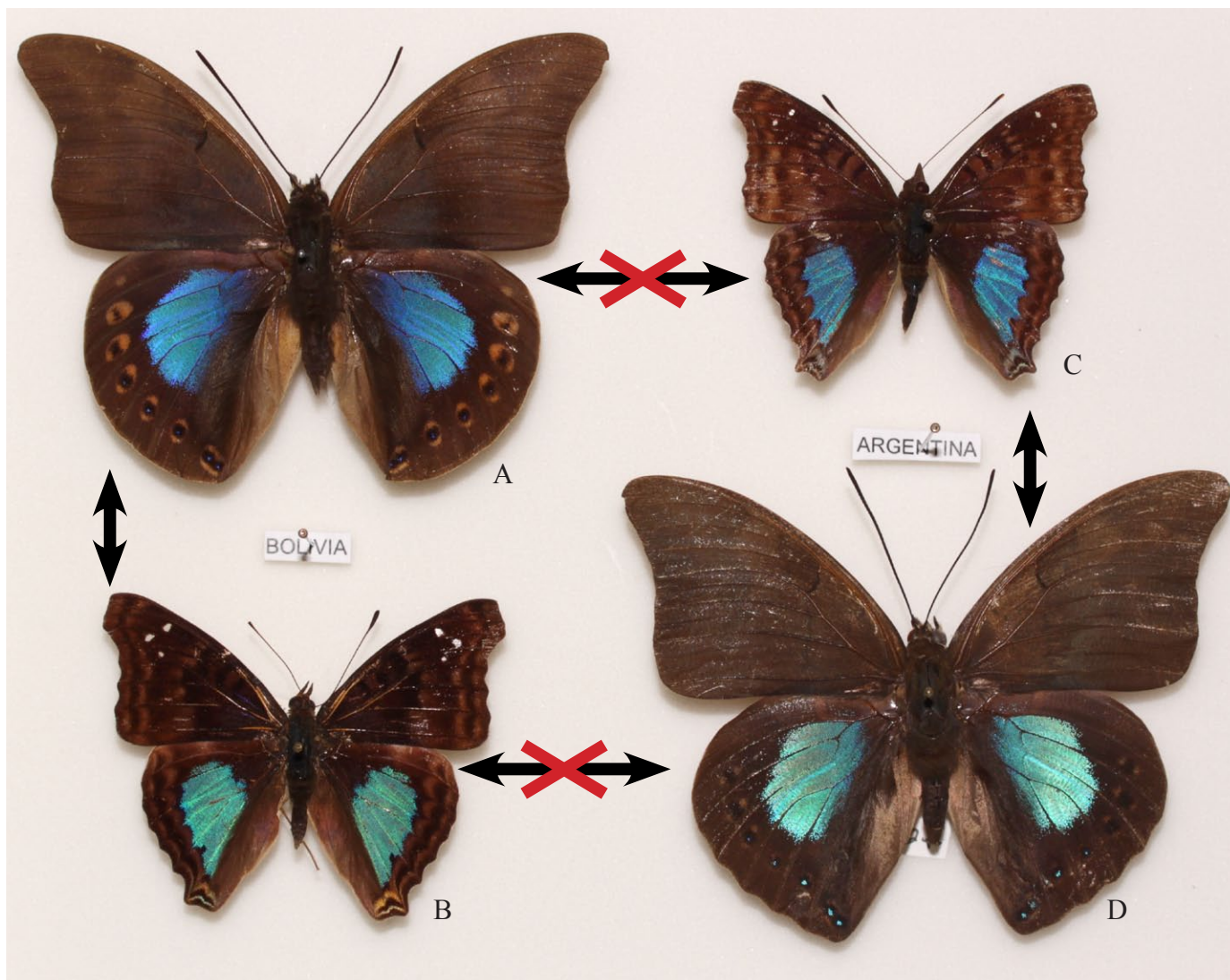


Fig 2. Top: Possible co-evolution of wing patterns in *Archaeoprepona chromus* and *Doxocopa cyane*: (A, B) north of Argentina, *A. chromus* has a blue dorsal hindwing patch and *D. cyane* has a green one, while in Argentina (C, D) they trade colors, with *D. cyane* sporting blue and *A. chromus* green.

Bottom: In nature, these different colors are responsible for differences in visual signals that these butterflies send to conspecifics, perhaps without detracting from them forming an “escape mimicry complex.”



Introduction

From a matador's red cape to a black-tipped tail of a weasel, to luna moth "tails", the deflection of an attack away from a vital part of the body is a common strategy. Cooper (1998), who observed "reactive deflection" in the form of the undulating tail in a skink, suggested that "*Antipredation display is usually directed to predators that have been detected, but might be beneficial when predators are likely to be dangerously close, but undetected. Anticipatory display could be selectively favored if it increased the probability of escape sufficiently to outweigh the increased probability of being detected and captured by a previously unaware predator. This is especially likely if prey have adaptations permitting a high probability of escaping imminent attack by a predator detected within striking distance...*"

Among butterflies, false-head patterns and behavior are present in hairstreaks and some polyommata Lycaenidae. Strong circumstantial evidence exists to back up the old hypothesis that they function as a predator attack deflection mechanism (e.g., Robbins, 1985; Lopez-Palafox et al., 2015). The small size of hairstreaks and the constant reliance on false-head enhancing behavior, consisting of sagittal movements of the hindwings, suggests that this defense perhaps targets invertebrate, rather than vertebrate, predators. Experiments with jumping spiders confirm its effectiveness against these predators (Sourakov, 2013).

For larger butterflies, deflection as a strategy to escape predation has been proposed for a number of species and can be hypothesized for many more, just based on the wing shape and pattern, as for example in African genus *Charaxes*, where the false head is quite obvious (e.g., Swynnerton, 1926; Picker et al., 2004). Using a nymphalid, *Stichophthalma louisa* Wood-Mason 1877, as a model species, circumstantial evidence in the form of beak marks demonstrated that the eyespots deflect birds' attacks (Tonner et al., 1993). In a species of *Pierella* (Satyrinae) that has a conspicuous white hindwing patch, testing the wing strength suggests that these spots serve to deflect predator' attacks, since this species has a much lower tear threshold in the patch region of the wing compared to two species without a patch (Hill and Vaca, 2004). In another example, by adding artificial false head patterns to the wings of white butterflies, Wourms & Wasserman (1985) were able to experimentally demonstrate that the altered butterflies underwent increased mishandling by predatory birds.

While publications that deal with the subject of false head patterns in butterflies are numerous and the deflection hypothesis, when it comes to butterfly eye spots, has been examined thoroughly (e.g. Stevens, 2005; Vlieger & Brakefield, 2007; Prudic, et al., 2014), the number of observations concerning predator-prey interactions in nature remains limited. Recently, the fact that false-head behavior (sagittal hindwing movements) in hairstreaks is influenced by an approaching predator has been quantitatively demonstrated by Lopez-Palafox, et al. (2015), supporting earlier natural history observations. Their study used a stuffed bird to simulate a predator, but the hairstreaks were in a natural setting, feeding on flowers. Reacting to the stuffed bird appearing in their visual field, 30% of the butterflies stopped moving their wings, suggesting an attempt to escape the predator's attention; 50% initiated or increased the sagittal movement of hindwings, which strongly supports the deflection hypothesis. Meanwhile, Krizek (1998) suggested that the pattern combined with behavior may resemble a "false threatening mouth" and present an intimidating image to a bird.

In the present note, I provide apparently new observations on behavior of a larger nymphalid butterfly, *Archaeoprepona chromus*, which has a wing shape and pattern suggesting a false-head strategy. These observations further support the deflection hypothesis as an explanation of this pattern and of its persistence throughout related Nymphalidae.

Observations on the false-head behavior (sagittal wing movement) in *Archaeoprepona chromus*

Observations were made near San Miguel de Tucumán, Argentina, in November 2015. The butterfly *Archaeoprepona chromus* (Fig. 1), was feeding on mammalian feces, and one can easily observe from the photograph that it is quite cryptic when resting on the ground, resembling a dry leaf and blending in with its surroundings. In fact, I walked by the butterfly without noticing it at first and it did not react to me despite my proximity and the movement and noise I was making. When approached and photographed from a distance of approximately 1 meter, the butterfly maintained a steady demeanor, continuing to "play the cryptic card." However, when the camera (and I) moved to a distance of ca. 0.3 m, the butterfly engaged in energetic sagittal hindwing movements which seemed to attract attention to the posterior end of the butterfly. While the movements were similar to those produced by hairstreaks, they seemed to be more forced, and one-sided, engaging only the wing closest to the threat. When the camera was removed to a

“safe” distance of 1 meter, the butterfly ceased the movements. This was repeated five times with similar results. Each time, the distance to the camera at which the movements were initiated by the butterfly was about the same, suggesting that perhaps the response is hardwired to the butterfly’s visual abilities.

This observation is intended to bring the attention of Lepidoptera behavioral ecologists to the phenomenon of sagittal movement of the hindwings in Preponini. To my knowledge, it has remained unrecorded and provides additional evidence about the function of wing pattern elements in nymphalids. The primary eyespots, according to Monteiro (2015) and references therein, are the underside hindwing ocelli and have been present in butterflies for 90 mya. Hence, while their function may have changed back and forth between deflection, intimidation and sexual selection, they are certainly a prominent and established feature of the butterfly wing pattern. With many non-specialist predators out there eating butterflies, a lot can depend on the specific ecosystem and predator, and what works as an intimidating signal for one predator can work as deflecting for another (e.g., Prudic et al. (2014) showed that large eyespots deflect attacks of praying mantids). Kodandaramaiah et al. (2013) suggested that while the larger eyespots on the hindwings of *Junonia* may be intimidating to predators, the smaller eyespots are there to deflect attacks. The recent phylogeny of Preponini (Ortiz & Willmott, 2013) suggests that evolution has followed the path from mostly cryptic underside patterns, as found in *Archaeoprepona*, to enlargement of some of the ventral eyespots in the *Prepona* clade which may have evolved to intimidate. From there, the *Agrias* clade has evolved, which contains clearly aposematically-colored species. Despite that general trend, just as with *Junonia*, deflection and intimidation are likely to have evolved more than once in Preponini. Experiments with birds on wing-toughness, and assessment of wing damage in natural populations may help to further elucidate this matter.

On possible co-evolution of *Archaeoprepona chromus* and *Doxocopa cyane*

While identifying my photos of the above species in the extensive holdings of the McGuire Center for Lepidoptera and Biodiversity, it became immediately obvious that there may be an underlying common trend in the intraspecific variability of the two sympatric species. It has been proposed that the green patches on the dorsal side of Preponini signal to predators “not to bother” with chasing such fast prey (e.g., Miller et al., 2010). The idea that Preponini and Apaturini may form mimicry rings

is not new. For instance, Pinheiro & Freitas (2014) make a compelling case for the existence of “escape mimicry” between *Prepona demophon*, *P. pylene*, and *Doxocopa laurentia* based on their distribution and similarity of dorsal patches. Similarly, the patches of *A. chromus* and *D. cyane* are very similar in shape and the two species are sympatric, which makes one suspect the presence of some sort of mimetic relationships. But while this could be a coincidence, what is unlikely to be a coincidence is that something opposite to a mimicry ring can be observed. North of Argentina, males of *A. chromus* mostly have blue dorsal hindwing patches and *D. cyane* subspecies, such as *D. cyane mexicana* Bryk, 1953 a green one, while in Argentina they trade colors, with *Doxocopa cyane burmeisteri* (Godman & Salvin, 1884) sporting blue and *A. chromus* green (Fig. 2). In photos and videos taken in the field, one can see how these color patches create a sparkling signal on the otherwise bleak background of gravel, leaves, feces and cryptic butterfly undersides. Of the two species, *D. cyane* is the one that frequently “flashes” the patch, while *A. chromus* does so only occasionally. I suppose that in addition to a possible escape-mimicry function that informs birds of the futility of pursuit of such a fast prey, both species may have been driven to diverge from each other in the tone of the patch, as the signal may also be sexual. Having two similar sexual signals in butterflies as common as these two that share the same habitat may have been energetically taxing and led to divergence. In support of the theory that the signal has significance in sexual communication is the fact that blue/green sexual dimorphism exists in *A. chromus* (females of *D. cyane* are mimics of *Adelpha* and hence are completely different from males).

On possible satyric mimicry in *Archaeoprepona chromus*

Cordero (2001) proposed that the ways that false-head patterns function are not by deflection of attack to the posterior end, but the opposite. He suggested that a predator might be determined to attack from the back to avoid being detected; a predator fooled by the pattern could be deflected from the false-head to the real head, thus increasing the chance of being detected by the prey and giving the prey the chance to escape the strike.

While the cryptic coloration and eyespots of *A. chromus* in combination with this behavior described above leave little doubt about their function, the bright-colored eyes and a red proboscis are puzzling as they appear more attractive to predators than if they were monochromatic. One of the possible explanations of the relatively colorful “front end” of *A. chromus* (brightly

colored eyes and red proboscis) may lie in the fact that it loosely resembles a snake head with extended tongue. The checkered pattern at the base of the wing may add to the resemblance, as this pattern may be confused with the pattern on a snake's head (Fig. 3). Snakes, which frequently fall prey to birds, many of which specialize in preying on them, are mostly cryptically-colored, but frequently have brightly-colored (red or blue) tongues that they display to predators when detected (Lilywhite, 2014). Janzen et al. (2010) proposed that in the Neotropics, the numerous snake-head patterns among caterpillars are due to the existence of a large and loosely-associated mimicry complex with snakes, and it is quite possible that this complex also includes adult Lepidoptera. Such imprecise mimicry can be referred to as “aide mémoire” (Rothschild, 1984) or “satyric” (Howse & Allen, 1994; Howse 2014). Castellano and Cermelli (2015) recently suggested an asymmetric distribution of false-negative and false-positive errors in the snake/snake-mimic decision plane, which makes birds very likely to be deceived by the intimidating signals of the snake-mimicking animal, even if substantially different in size from a snake.

On the context-dependency of the observed behavior

It is notable that the behavior was observed in the context of solitary feeding and seemed to be absent when the same species was feeding in a group, as this implies that escape-from-predator strategies may vary depending on the context. In this respect it is interesting to note the stark contrast between the behavior of *Archaeoprepona chromus* and *Doxocopa cyane* when feeding in a group setting. *A. chromus* maintained an overall cryptic posture when feeding among conspecifics, and, when threatened, did not display the sagittal wing movement described above. *D. cyane* were constantly on the move, flashing their bright spots as if inviting additional butterflies to partake in the nutrient-rich resource (feces). This may be a strategy employed by an individual butterfly aimed at increasing the group numbers by “inviting” other butterflies and hence reducing the risk to oneself or it could be a manifestation of differences in sexual signaling as discussed above, or both.

Olofsson et al. (2010, 2013), using *Pararge aegeria* and *Lasiommata megera* (two satyrine species with different eyespot pattern) and blue tits, *Cyanistes caeruleus*, showed that the efficacy of deflection of a strike to the eyespots declines when a bird examines the prey for a longer period of time. They also showed that deflection is context-dependent and varies with lighting and background. Other studies (e.g., Van Zandt

Brower, 1958; Pinheiro, 1996), underscore the complexities of analysis of the effectiveness of mimicry in butterflies when it comes to birds as predators, as birds learn quickly, but frequently forget what they have learned and must relearn it. They also vary in their ability to learn patterns and to respond to negative experiences, not only between species but also intraspecifically.

Context-dependent responses in insects have been demonstrated experimentally for a number of species (e.g., Addesso et al., 2014). Therefore it is not surprising if solitary feeding instigates a set of defensive behavioral responses that are different from those found during group feeding. It makes sense that a “safety-in-numbers” strategy should evoke quite different behavior in prey (e.g., wildebeest), as the probability of attack for any given individual diminishes with each additional member of the group and hence confusion of the predator becomes more important than deflecting the attack. For instance, fleeing from the group first may be as advantageous as remaining still, while staying but exhibiting false-head movement might make an individual a selected target of attack. In the case of solitary feeding, however, once the prey is detected, the logical conclusion is that the behavior that optimizes escape – i.e., making a predator strike a fake head instead of a real one – may be favored by selection.

Supplementary materials: Videos

Sagittal hindwing movement in Archaeoprepona chromus:

<https://youtu.be/7wjTssF53XQ>

Red proboscis and feeding, A. chromus:

<https://youtu.be/gE08alYi00I>

Green proboscis and signaling by Doxocopa cyane:

<https://youtu.be/gCSn4LVc2aY>

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- "I'll take spots, then," said the Leopard; "but don't make 'em too vulgar-big. .. 'Now you are a beauty!' said the Ethiopian. 'You can lie out on the bare ground and look like a heap of pebbles. You can lie out on the naked rocks and look like a piece of pudding-stone. You can lie out on a leafy branch and look like sunshine sifting through the leaves; and you can lie right across the centre of a path and look like nothing in particular.'"
- R. Kipling, 1902**



Fig. 3. Head region of *Archaeoprepona chromus* possibly a case of “satyric mimicry” as it may resemble a snake head with tongue extended and thus repel or delay an attack by a bird predator (snake photos are by D. Huth and T. Benson, butterflies by A. Sourakov).



A



B



C

The winners of 2015 ATL photo contest: (A) *Orses itea* (Hesperiidae), (B) *Automeris melanops* (Saturniidae). Both photos are taken by Ricardo Costa in his native São Paulo, Brazil; (C) a caterpillar of nr. *Setosa nitens* (Limacodidae), photo is taken at Sepilok, Sabah, Borneo, by Evgenii Kotelevskii (Saratov, Russia).