A horde of tropical counterfeit predator eyes

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ABSTRACT

We propose that the large numbers of different yet functionally similar eye-like and face-like color patterns found on many hundreds of species of tropical caterpillars and pupae – 50 examples of which are displayed here from the dry, cloud, and rain forests of Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica – constitute a gigantic mimicry ring that is evolutionarily generated and sustained by the diverse actions and traits of a gigantic multispecific array of predators: the insect-eating birds. These predators are variously and innately programmed to flee when abruptly confronted, at close range, with what appears to be an eye of one of *their* predators. This mimicry differs from Batesian mimicry as it is classically construed in that (1) it is probably sustained in great part by innate traits rather than by avoidance behavior learned through disagreeable experiences, (2) the harmless and largely edible mimics are much more abundant than are the models, and (3) there is no particular selection for the eye-like color pattern to be a close copy of the eye or face of any particular predator on the insect-eating birds or of any other member of this mimicry ring. Indeed, selection may not favor exact resemblance among these mimics, because that could create a superabundance of one particular false eyespot or face pattern, thereby increasing the likelihood of a bird species or guild learning to associate that pattern with a harmless food item at the moment of encounter.

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You are a 10-gram insectivorous tropical rain forest bird, foraging among the shady, tangled, dappled, rustling foliage in early morning half light. You want to live 10-20 years. You are poking into rolled leaves, peering under leaves, exploring bark crevices, searching behind stems. Abruptly an eye appears, 5 centimeters from your bill. The eye is half seen, obstructed, shadowed, unfocused, approximately round, multicolored, and moving. If you pause a millisecond to ask if that eye belongs to a tasty morsel or to a predator you are - and it only takes once - brunch. Your innate reaction to the eye must be instant flight, a "startle" reaction coupled with distancing. Now, a safe several meters away, are you going to go back into that shady, tangled, dappled and rustling foliage to see if that was a breakfast item? No.

You have just, as have hundreds of other species and billions of other individuals, for tens of millions of years, been a player in an act of natural selection favoring mutations that lead to the multitudes of "false eye" color patterns, "eyespot" patterns, or "facsimiles of eyes" and "faces" decorating tropical caterpillars and pupae (e.g., Figs. 1-6). These eyespots can be round or oval, round or slit pupils, and/or monochrome, and are often accompanied by patterns suggesting other head and facial features, which in turn enhance the eye-like nature of the spots. The patterns may even simulate multiple faces depending on what is visible and how it is oriented (Fig. 1-2). None of these patterns exactly match the eyes or face of any particular species of predator but all give the illusion of an eye or face somewhat seen. In other words, these false eyes are mimicking the eyes and faces of predators of insect-eating birds – snakes, lizards, birds, and small mammals - as perceived by these birds in the real world. These color patterns -- long noticed by field naturalists, evolutionary biologists, behaviorists, ecologists, taxonomists, and even our distant ancestors -- and the birds' reactions to them, are the evolutionary footprints of predator-prey encounters as shallow as today and as deep as the first vertebrate eyes. These footprints are scattered across the remainder of vertebrate-prey interactions, but here we focus only on those on caterpillars and pupae.

Fig. 1. The 7 mm wide pupa of *Cephise nuspesez* (Hesperiidae; Burns 1996), a Costa Rican skipper butterfly as it appears to a foraging bird that (above) has poked into the front of the rolled leaf shelter constructed by the caterpillar or (below) has opened the roll from above.

Fig. 2. The 50 mm last instar caterpillar of Costa Rican *Ridens panche* (Hesperiidae) when its leaf shelter is forced open (above) and a few seconds later (below) to present glowing red false eyespots directed at the invader and glowing lemon yellow eye spots in the dark of the cavern behind.
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The bird's reactions to a false eye are innate but not invariable. It will vary interspecifically -- and thus with its learning ability, the intensity of its selective regime and history for predator avoidance, and the evocativeness of the false eye(s) as that species of bird perceives it in the habitats in which it characteristically forages. The response will also vary intraspecifically with the bird's microenvironmental circumstances (and may be somewhat tempered by experience for some species) – e.g., light level, proximity, how obstructed is the false eye or the whole insect, what its neighbors and life have taught it, whether it has recently experienced a near miss, size of eyespot (e. g., Shirota 1980), etc.

The sum of these bird reactions across many tropical circumstances and ecosystems is a diffuse selective pressure to which thousands of species of caterpillars and pupae have variously responded in the evolution of their color patterns. The diffuse nature of the syndrome highlighted here also applies to mimicry of aposematic colors, cryptic colors, flash colors and their associated behaviors. The 50 examples in Figs. 1-6 are only a small fraction of the many hundreds of species of caterpillars and pupae that have been found to bear false eyes and faces during a 30-year ongoing inventory of thousands of species of caterpillars and pupae in the dry, cloud, and rain forest of Area de Conservacion Guanacaste (ACG) in northwestern Costa Rica (http://janzen.sas.upenn.edu; Janzen et al 2009). Each species of immature moth or butterfly has its own history of selection circumstances. Each has its own degree of retention of traits that were intensively selected for in the unknowable past and that may not be maintained today by anything more complex than phylogenetic inertia, the absence of an opposing selective force (Janzen 1985), and the multispecific array of hungry insect-eating birds sweeping through tropical vegetation every day, year in and year out. Once the species has evolved those false eyes (or any facial pattern that elicits a fear-flee reaction), they may cost little, yet benefit their bearer much in an encounter with a predator.   These color patterns differ from those of classical mimic/model systems in that their value to the mimic depends not so much on the closeness of match to a specific model, but rather on simply being enough of a copy of an eye and/or face to trigger the fear-flee reaction in an insect-eating bird because what has just been encountered in its visual field might be a predator.

Figure. 3 ACG caterpillar false eyes and faces (see SI Appendix 1 for names, voucher codes and lateral/dorsal views).

Figure. 4. ACG caterpillar false eyes and faces (see SI Appendix 1 for names, voucher codes and lateral/dorsal views).

Figure. 5. ACG pupa false eyes and faces (see SI Appendix 1 for names, voucher codes and lateral/dorsal views).

Figure. 6 ACG pupa false eyes and faces (see SI Appendix 1 for names, voucher codes and lateral/dorsal views).

Much of contemporary mimicry theory and commentary explicitly or implicitly stresses the importance of experience, learning, and the memory ability of the potential predator in predator-prey interactions, and underestimates the reality that potential predators also innately avoid aposematic (warning) signals and other similarities to predators' attributes (e.g., Smith 1977, Pough 1988, Chew et al 2006, Moeller and Hurwitz 2006, Stevens et al 2007, Kodandaramaiah et al 2009). When innate avoidance is the dominant response of the predator, the relative importance of such factors as mimic:model ratios, scarcity of models, intensity of selection, nature of memory, etc., changes. Anything - motion, pattern, color - that elicits innate avoidance of a lethal outcome for the potential predator favors both the predator and the prey. False-eye and face mimicry need not "exactly" match the real eyes of any particular species of predator in order to be selected for, much as highly effective cryptic behavior and color patterns often do not precisely match the patterns and colors of any particular background. The eyespot and face patterns need only contain features that stimulate predator recognition by small predators themselves.

On the one hand, false eye color patterns on butterfly wings apparently reduce predation attempts (see Kodandaramaiah et al 2009 and reviews therein). On the other hand, when on the wings they may also serve to deflect a bird's strike from the actual head of the butterfly (see Robbins 1981) instead of startling a potential predator away. Although both of these hypothesized processes may be operative, we are concerned here with false eyes and faces on sessile caterpillars and pupae. There is no selective value in deflecting a bird's strike to the site of the false eye on these animals. Furthermore, there is a conspicuous advantage to an adult butterfly or moth if false eyes on the wings generate the same avoidance reactions in a foraging bird (e.g., Kodandaramaiah et al 2009) as we postulate are generated by false eyes and faces on caterpillars and pupae.

For tropical caterpillars (Figs. 2-4) and pupae (Figs. 1, 5, 6) as a whole, there are some first and approximate generalizations about this mimic-model ecosystem. False eyes and faces

* are common on species that live largely concealed in places, often of low and variable light levels, searched by diurnally foraging birds (and small primates) - rolled leaves, silk/leaf tangles, dark shadows under large leaves, crevices in tree bark, etc.,

* appear on (often large) caterpillars or pupae that live fully exposed but with their false eye(s) often hidden in folds of skin until displayed by the caterpillar in reaction to the approach or touch of a "large" object,

* occur on caterpillars and pupae that are otherwise cryptically colored and patterned (rather than ostentatiously aposematic) and therefore are not visible at any significant distance, even when the caterpillar or pupa lives fully exposed,

* are not of any one specific "eye" shape or color but rather range from detailed and exact mimics of snake eyes and scales to a minimal suggestion of paired approximate circles in surrounding face-like patterns; even when approximate, these patterns are sufficiently eye-like and face-like to stimulate visual receptors/mental processes that vertebrate predators have evolved for rapidly recognizing what might be an eye, regardless of how imperfectly seen,

* are usually paired and evolutionarily derived from paired, more or less circular structures (e.g., pupal spiracles) or patterns (but, on occasion, median patterns have given rise to one-eyed mimics), and are not derived from the real "eyes" (actually, stemmata (ocelli)) of caterpillars or the position of real future eyes inside the pupa,

* may be on the head end or the rear end of the caterpillar, and on the front end of the pupa - that part of the prey that a predator is most likely to encounter when investigating the site of caterpillar or pupa concealment, and that resembles in position and shape the most dangerous part of a predator,

* are often moved (at times violently and/or in snake-like fashion) toward a threatening predator upon its close approach or touch,

* may be combined with other colors and shapes that, when viewed from different directions, preserve or enhance the deception (which may include Escher-like transformations and illusions),

* are present in almost all ACG Lepidoptera families that have large caterpillars and pupae, and even some with small ones (e.g., Crambidae, Elachistidae) and are often found on caterpillars and pupae of skipper butterflies (Hesperiidae) and sphinx moths of the genus *Xylophanes* (Sphingidae) (Figs. 1-6),

* are independently evolved in hundreds of taxonomic lineages, though there are species-rich clades in which counterfeit eyes and faces are apparently derived from a single evolutionary event instead of from convergence,

* are also encountered -- though perhaps less frequently -- on extra-tropical species of caterpillars (e.g., *Pterourus*, Papilionidae), though these caterpillars are often subject to predator pressure by insect-eating migrant birds that spend major parts of their lives in the tropics and therefore extend the syndrome described here far outside of the tropics,

* are often overlooked by the casual observer, owing to the plethora of additional caterpillar and pupa colors and patterns (and the many forms of crypsis) that the animals present in "standard" lateral or dorsal views (e.g., see these views of the same immatures as in Figs. 1-6 in SI Appendix 2).

This innate and vision-based mimicry is deeply pervasive and extensive. The great abundance and species richness of caterpillars and pupae in tropical foliage suggest that the foraging insectivorous bird may encounter tens to hundreds of false-eyed individuals per day. There is no reason to postulate that the bird would learn about each species individually and compare it with other predator-mimicking species, or compare its eyes with those of any particular species of potential predator. All these false-eyed species collectively comprise a gigantic mimicry ring that is evolutionarily generated and sustained by the diverse actions and foraging traits of a gigantic multispecific array of predators that is innately programmed to "worry" and flee when it finds itself close to an eye. In contrast to Batesian mimicry, in which the mimics are thought to be significantly rarer than the models, there are probably many hundreds of false-eyed caterpillars and pupae for every vertebrate predator per hectare of tropical forest. This proportion is maintained by the extremely high cost paid by the bird that makes the mistake of pausing when encountering what might be a predator's eye, coupled with the very low price paid by passing up a single potential minimeal of caterpillar or pupa (as they say, the suicide bomber has to win only once, security has to win all the time).

There have been arguments to whether there is mimicry among caterpillars (Behrenbaum 1995). Our conclusion through the on-going caterpillar survey of ACG (Janzen et al 2009) is that essentially all tropical caterpillars that live exposed, and many of those that do not, are visually

mimetic of something – inedible background, some other aposematic or mimetic caterpillar, or a dangerous predator.

The multispecific diversity of caterpillar and pupa false eyes is evolutionarily generated and maintained by the activities of a very heterogeneous array of species of birds (and perhaps some small primates), ranging from fixed-behavior "stupid," insect-eating birds to ones that are "smart" and plastic learners, coupled with strong within-species phylogenetic inertia and anachronisms (i.e., bearing a false eye or face probably has very little negative fitness value). Given that false eyes do not advertise at long distance (as do aposematic colors), only a small number of individuals and species of fixedly (innately) dupable birds may be required to maintain a large array of false eye and face patterns on many species of caterpillars and pupae. These species of birds may evolutionarily drive each of the eye-like and face-like patterns to be something more similar to an eye and/or face without any reference to the false eyes and faces of other, co-occurring species. Each bird is responding to an eye-like or face-like stimulus, even though that stimulus only approximates the real eye or face of any particular species of predator, or the false eye or face of any co-occurring species of caterpillar or pupa. The generally great advantage of false eyes and faces is not seriously diminished by the existence of bird species that can quickly determine that the mimetic caterpillar or pupa is edible. Indeed, it can be postulated that selection may even work against exact resemblance among mimics because that could lead to a superabundance of one particular false eye and/or face pattern, thereby increasing the likelihood of a bird species or guild learning to associate that pattern with a harmless meal at the moment of encounter.

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