

A tropical horde of counterfeit predator eyes

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We propose that the many different, but essentially similar, eye-like and face-like color patterns displayed by hundreds of species of tropical caterpillars and pupae—26 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 huge and pervasive mimicry complex that is evolutionarily generated and sustained by the survival behavior of a large and multispecific array of potential predators: the insect-eating birds. We propose that 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. Such a mimetic complex differs from various classical Batesian and Müllerian mimicry complexes of adult butterflies in that (i) the predators sustain it for the most part by innate traits rather than by avoidance behavior learned through disagreeable experiences, (ii) the more or less harmless, sessile, and largely edible mimics vastly outnumber the models, and (iii) there is no particular selection for the eye-like color pattern to closely mimic the eye or face of any particular predator of the insect-eating birds or that of any other member of this mimicry complex. Indeed, selection may not favor exact resemblance among these mimics at all. Such convergence through selection 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 harmless prey.

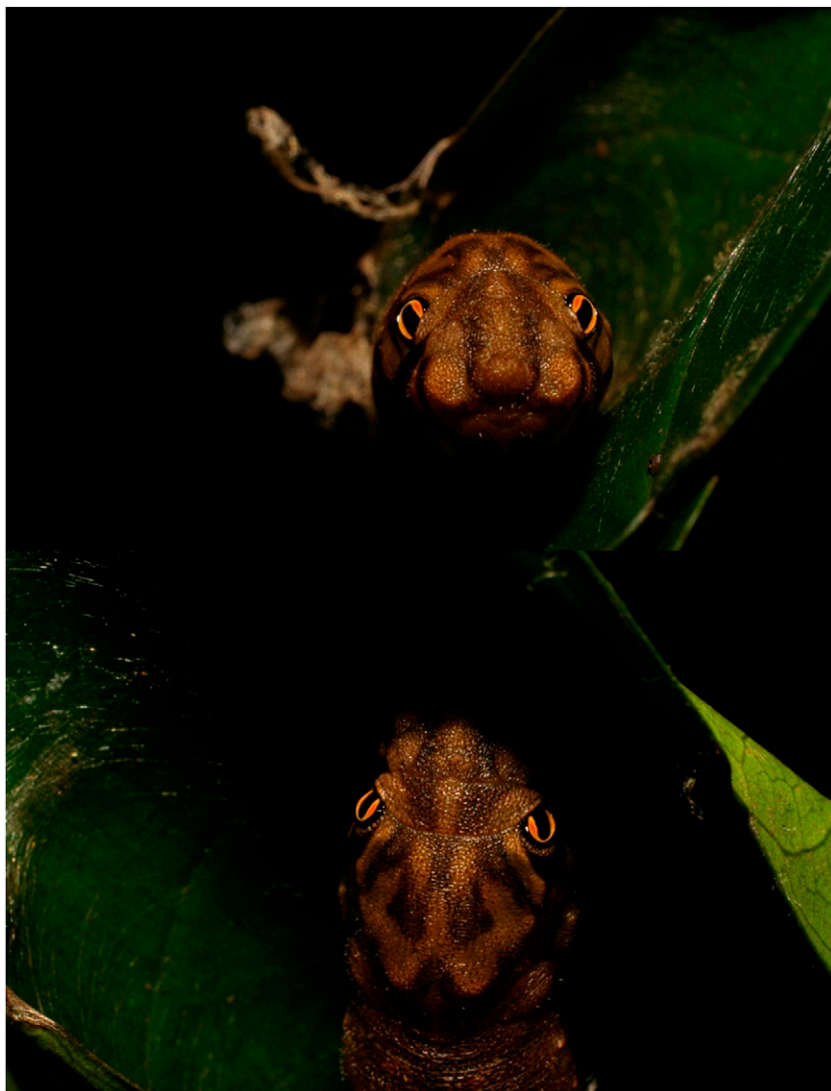


Fig. 1. The 7-mm-wide pupa of *Cephise nuspesez* (23) (Hesperiidae), a Costa Rican skipper butterfly as it appears to a foraging bird that (*Upper*) has poked into the front of the rolled leaf shelter constructed by the caterpillar or (*Lower*) has opened the roll from above. When disturbed, this pupa rotates to present its face to the open end of the leaf roll.

caterpillar | mimicry | pupa | insectivorous birds | innate behavior

You are a 12-gram, insectivorous, tropical rainforest bird, foraging in shady, tangled, dappled, rustling foliage where edible caterpillars and other insects are likely to shelter. You want to live 10–20 years. You are peering under leaves, poking into rolled ones, searching around stems, exploring bark crevices and other insect hiding places. Abruptly an eye appears, 1–5 centimeters from your bill. The eye or a portion of it is half seen, obstructed, shadowed, partly out of focus, more or less round, multicolored, and perhaps moving. If you pause a millisecond to ask whether that eye belongs to acceptable prey or to a predator, you are likely to be—and it takes only once—someone's breakfast. Your innate reaction to the eye must be instant flight, that is, a “startle” coupled with distancing. The bird that must learn to avoid what appears to be a predator's eye is not long for this world. Now, a safe few meters away, are you going to go back to see whether that was food? No.

You, like billions of other individuals and hundreds of other species for tens of millions of years, have just been a player in an act of natural selection favoring mutations that lead to the multitudes

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of “false eye” color patterns, “eyespot” patterns, or “facsimiles of eyes” and “faces” adorning tropical caterpillars and pupae (Figs. 1–4, and *SI Appendix*, Figs. S1 and S2). These eyespots are round or oval and mono- or polychromatic, with round or slit pupils. Associated body patterns often suggest other head and facial features, which in turn enhance the eye-like nature of the spots. Depending on the angle of observation and on how much or which part shows, one pattern may even simulate different faces (Figs. 1 and 2). None of these patterns exactly matches the eyes or face of any particular species of predator; but, even when quickly and partially glimpsed, all give the illusion of an eye or face. These false eyes are mimicking the eyes and faces of such predators of insect-eating birds as snakes,

lizards, other birds, and small mammals, as perceived at close range by the insectivorous birds in their natural world. These color patterns—long noticed by field naturalists, evolutionary behaviorists (see especially refs. 1–3), ecologists, taxonomists, ecotourists, and, no doubt, 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 terrestrial vertebrate eyes. Such footprints are scattered across many diurnal vertebrate/prey interactions (e.g., refs. 4 and 5), but here we focus only on those of caterpillars and pupae and the birds that eat them.

Discussion

We postulate that both the frequent occurrence of false eyespots on tropical cat-

terpillars and pupae, and the great taxonomic diversity of their bearers, are powerful indirect evidence that the avian reactions to false eyes are innate. Nevertheless, we expect the reactions to vary interspecifically in connection with the intensity of the bird’s selective regime, the bird’s learning ability and personal history of predator avoidance, and the evocativeness (e.g., ref. 5) of any particular false eye(s) as perceived by the bird in the habitats in which it characteristically forages. The response may also vary intraspecifically with the bird’s microenvironmental circumstances and with experience—for example, light level, proximity, degree to which the false eye or the whole insect is obstructed, what the bird’s neighbors and life have taught it, whether it has recently suffered a near miss, how hungry it is (e.g., refs. 3, 6), size of eyespot (e.g., refs. 5, 7), etc.

The sum of these avian reactions across many tropical circumstances, habitats, and ecosystems is a diffuse selective pressure to which we suggest that innumerable 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 based on aposomatic (warning) colors, cryptic colors, flash colors, and behaviors associated with them. For example, the outcome of innate avoidance of coral snakes by birds (8) may extend to other toxic snakes and to harmless ones (4), to turtles (9), and to both toxic and harmless caterpillars (9). Those species-rich tropical complexes (4) are not our concern here but seem to display the same phenomenon with the same root cause. The 36 species of caterpillars and pupae in Figs. 1–4 and *SI Appendix*, Figs. S1 and S2, are a small and partial representation of the hundreds of species with false eyes and faces encountered in the course of a 30-year, ongoing inventory of ca. 450,000 individuals and >5,000 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>; ref. 10).

Each of these species of immature moths or butterflies has its own evolutionary pedigree. Each has its own degree of retention of traits that have been intensively favored by natural selection in the past and that may not be maintained today by anything more complex than phylogenetic inertia, the absence of an opposing selective force (11), and the multispecific array of insect-eating birds scouring tropical vegetation every day, year in and year out. Once a species has evolved false eyes (or any facial pattern that elicits a fear/flee reaction), those false eyes may barely diminish crypticity



Fig. 2. The 50-mm-long last instar caterpillar of Costa Rican *Ridens panche* (Hesperiidae) at the moment when its leaf shelter is forced open (*Upper*) and a few seconds later (*Lower*), when it presents glowing red false eye spots directed at the invader and glowing lemon-yellow eye spots in the dark of the cavern behind. Both kinds of false eyes are thrust at the leaf roll entrance until the invader leaves.

at a distance, cost next to nothing physiologically, and greatly benefit their bearer in a close encounter with a predator.

These color patterns differ from those of classic mimic/model systems in that their value to the mimic depends not on the closeness of the match to a specific model, but rather on sufficient similarity to an eye and/or face to trigger the fear/flee reaction in an insect-eating bird. How similar is necessary (5) will vary from bird species to bird species and among foraging situations. The ubiquity of this multi-specific mimicry complex argues strongly for the widespread presence of the fear/flee reaction in many species of small birds (or a few quite common ones).

Much contemporary mimicry theory and popular commentary explicitly or implicitly stress the importance of experience, learning, and memory of the potential predator in predator/prey interactions. However, we believe that it generally underestimates the fact that potential predators also innately avoid various aposematic signals and similarities to attributes of their predators, as shown by both experimental study (e.g., refs. 5, 8, 12–16), observation (see especially ref. 4), and our natural history observations, and as sketched out by Blest (3) although subsequently largely ignored for the past half century. When the dominant response of the predator is innate rather than (or as well as) learned, there are major changes in mimicry theory and interpretation of natural history with respect to the relative importance of mimic/model ratios (4), scarcity of models (4, 17, 18), intensity of selection (5, 15), ability to remember (6), etc. Any color, pattern, motion, or sound of a caterpillar or pupa that elicits innate avoidance of a lethal outcome for the bird selectively 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 (5). Although Blest (ref. 3 and references therein) built on these concepts in detail, they have received little attention from the many biologists dealing with mimic/model systems in the tropics, most of whom have focused on the exactness of mimicry among distasteful models and mimics that display diurnally in ostentatious flight.

False-eye color patterns on butterfly wings may serve to deflect a bird’s strike from the actual head of the butterfly (3, 19, 20) instead of startling a potential predator away. However, false-eye color

patterns on butterfly wings can also reduce predation attempts (refs. 5 and 16 and reviews therein). Both of these hypothesized and confirmed processes may be operative at the same time with the same species of prey and different species of predators, but we are concerned here with false eyes and faces on relatively 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. Equally, we are not concerned here with the question of what shape or intensity of an eyespot (5) confers protection at any given moment with any particular bird.

Some first and approximate generalizations about the mimic/model complex of tropical caterpillars and pupae (Figs. 1–4 and *SI Appendix*, Figs. S1–S14) emerge from our observations of their natural history. Taken as a whole, their traits suggest to us the long-term and pervasive operation of natural selection by the species-rich and abundant guild of small vertebrate diurnal predators on caterpillars and pupae in tropical forest. We do not propose alternative hypotheses for this multispecific display by sessile prey because we cannot think of any that are compatible with the collective natural history of the hundreds of species of avian and lepidopteran actors.

False eyes and faces:

(i) Are comparatively more common on species of caterpillars and pupae that live in great part concealed in microhabitats that are often of low and variable light levels, and that are searched by diurnally foraging birds—rolled and silked leaves, silk/leaf/dead leaf tangles, dark shadows under large leaves, crevices in tree bark, etc. Because many kinds of insects and spiders hide in such places, they are rich foraging grounds for birds—but with hidden dangers. Consider the caterpillar of the hesperiid (skipper) butterfly in Fig. 2: it is hidden in its silk and leaf shelter during daylight hours, emerging to feed at dusk or night. Its false eyes are exposed when its shelter is torn open; and at that time, it thrusts the “face” of its head out at the intruder instead of retreating or turning away (or simply starting to repair its shelter). This behavior is shared with more than 100 species of ACG skipper butterfly caterpillars and with many species in other families. Again, the skipper butterfly pupa in Fig. 1 spends 2 weeks hidden in a silked, rolled leaf and is visually exposed only when a diurnal predator opens

that shelter. Then the pupa, which is firmly anchored at its base, twists on this anchor so as to project its “face” out of the entrance at the forager.

- (ii) Also occur on (often large) caterpillars or pupae that live fully exposed, but with their false eye(s) often hidden in folds of cuticle until explicitly and ostentatiously displayed by the caterpillar in reaction to the approach or touch of a “large” object. The false eyes in Figs. 3 *B*, *H*, *I*, *K*, and *L* are visible as false eyes only when the caterpillar expands and displays the crucial body part.
- (iii) Usually occur on caterpillars and pupae that are otherwise cryptically colored and patterned (rather than ostentatious); and these mimetic features are not visible at any significant distance, even when the caterpillar or pupa lives fully exposed. For example, the ground colors and patterns of the caterpillars and pupae in Figs. 3 and 4 are generally green, gray, brown, or black, rather than bright red, yellow, or blue.
- (iv) Are not of any one specific “eye” shape or color but rather range from astonishingly detailed mimics of snake eyes and scales (e.g., Fig. 4*H*) to minimal suggestions of paired approximate circles or dots in surrounding face-like patterns (e.g., Fig. 4 *B*, *F*, and *G*). 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 or fractionally seen (see refs. 5 and 15 for elaboration). It is hard to be convinced that the false eyes in Fig. 1 are not real, and we suspect even harder for a small bird when foraging (e.g., see ref. 2 for an extratropical example).
- (v) Are usually paired and evolutionarily derived from paired, more or less circular structures (e.g., pupal spiracles) or patterns. (On occasion, median circular patterns are the evolutionary precursors of one-eyed mimics, especially in caterpillars of Sphingidae and Notodontidae.) False eyes are not derived from real caterpillar “eyes” (stemmata), which are tiny light sensors on the lower “cheeks” of the head, or from the position of future real eyes inside



Fig. 3. Representative ACG caterpillar false eyes and faces (see *SI Appendix, Table S1* for names and voucher codes and *SI Appendix, Figs. S3–S8* and ref. 24 for lateral and dorsal views of the same species of caterpillars).



Fig. 4. Representative ACG pupa false eyes and faces (see *SI Appendix, Table S1* for names and voucher codes and *SI Appendix, Figs. S9–S14* and ref. 24 for lateral and dorsal views of the same species of pupae).

the pupa. The external surfaces of the paired, pupal thoracic spiracles have frequently given rise to pupal false eyespots (e.g., all of the false eyes in Figs. 1 and 4 are evolutionarily modified thoracic spiracles). However, we add that there may be selection to enhance almost any shape and color that can give the hint of eyes (e.g., refs. 5, 15).

- (vi) Are usually on the head end or the rear end of the caterpillar, and on the front end of the pupa. These are the parts that a predator is most likely to see when probing the site of caterpillar or pupa concealment and that resemble in position and shape the most dangerous part of a predator's predator. Not emphasized in Fig. 3 (but see Fig. 3*A* and *F*) is the fact that these caterpillars often strike a sinuous pose with the body at the same time the head or front bearing false eyespots is thrust at the intruder.
- (vii) Are often combined with other colors and shapes that, when viewed from different directions, preserve or enhance the deception. This may include Escher-like illusions and transformations. For example, the same false eyes and associated facial patterns of the pupa in Fig. 1 give the illusion of two different faces, depending on whether they are viewed from above or from the front.
- (viii) Are present in almost all ACG Lepidoptera families with large caterpillars and pupae (2–10 cm in length), and even in some families (e.g., Limacodidae, Crambidae, and Elachistidae) with quite small caterpillars (only 1–2 cm in length). Although a 1–2-cm, generally green to brown caterpillar inside a tangle of silk and leaves might seem impossibly small for a snake mimic, the frontal false eyes coupled with highly sinuous movements may well elicit a flight reaction by a small bird operating largely on reflexes in close quarters.
- (ix) Have independently evolved in numerous taxonomic lineages. However, there are also species-rich clades within, for example, the Hesperidae and the genus *Xylophanes* of the Sphingidae, in which the counterfeit eyes and faces of caterpillars and pupae (Figs. 1–4 and *SI Appendix*, Figs. S1 and S2) apparently stem phylogenetically from a single evolutionary event instead of through convergence.

- (x) Are also encountered—although less frequently—on extratropical species of caterpillars (e.g., *Pterourus*, Papilionidae; *Xylophanes*, Sphingidae). However, these caterpillars are often subject to predator pressure by insect-eating migrant birds that spend major parts of their lives in the tropics (and often evolutionarily originated there) and therefore may extend the syndrome envisioned here far outside of the tropics and into habitats that are less rich in predators on small birds than are many tropical ecosystems.
- (xi) May be 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 *SI Appendix* for the lateral and dorsal views of the same caterpillars (*SI Appendix*, Figs. S3–S7) and pupae (*SI Appendix*, Figs. S8–S14) as in face and rear views in Figs. 3 and 4 and *SI Appendix*, Figs. S1 and S2].

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 (more at low to medium elevations than at elevations above 1,500 m, which have fewer species of large caterpillars and leaf-rollers). There is no reason to postulate that the bird would learn about each species individually and mentally compare it with other predator-mimicking species, or compare its false eyes with those of any particular species of potential predator.

Conclusion

We postulate that all of these false-eyed species collectively constitute an enormous mimicry complex that is evolutionarily generated and sustained by the diverse actions and foraging traits of a large and multispecific array of avian predators that are innately programmed to instantly flee when in startlingly close proximity to the eye of another species, or to something that resembles such an eye. As stated at the outset, the bird that must learn to avoid an eye is not long for this world. In contrast to classical Batesian mimicry—in which the mimics are generally thought to be significantly rarer than the models—there are 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 foraging bird that makes the mistake of pausing when encountering what might be an eye of one of its predators, coupled with the low price paid by passing up a potential morsel.

There have been arguments as to the existence of mimicry among caterpillars (see review in ref. 21). Our conclusion through the ongoing caterpillar survey of ACG is that essentially all tropical caterpillars that live exposed, and many of those that do not, are visually mimetic of something—an inedible background or object (22), some other aposematic or mimetic caterpillar, a dangerous predator, or some combination of these.

The multispecific diversity of caterpillar and pupal false eyes is evolutionarily generated and maintained by the activities of a heterogeneous array of species of birds (and perhaps some small primates). These range from fixed-behavior (“stupid”) birds to ones that are “smart” and plastic learners. Only a moderate 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 as they perceive it, without any reference to the false eyes and faces of other co-occurring caterpillar species. We suggest that each bird is responding to an eye-like or face-like stimulus, even though that stimulus is only an approximation of 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 some species of birds that can quickly determine that the mimetic caterpillar or pupa is edible (see ref. 6). 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.

We wish to emphasize that, in highlighting the role of innate avoidance of threats by potential predators in this analysis and discussion of mimicry, we do not intend to diminish the one-to-one and one-on-one approaches inherent in many Batesian and Müllerian experimental mimicry studies. Rather, we wish to broaden our understanding by recognizing that when the avoidance is innate, various assumptions, hypotheses, tests, and

