Journal of the Lepidopterists' Society
49(4), 1995, 386–396

APOSEMATISM AND MIMICRY IN CATERPILLARS

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ABSTRACT. In the Lepidoptera, described instances of larval mimicry are vastly and curiously fewer in number than those tabulated for adults. This disparity may arise in large part from a lack of pertinent research, rather than actual differences between the two life stages. The evolution of larval coloration and its role in the development of possible larval mimicry complexes represents largely unbroken and fertile ground for study.

Aposematic coloration is a conspicuous characteristic of many larval lepidopterans—so conspicuous, in fact, that Darwin (1871:326) was prompted to remark:

> "... distastefulness alone would be insufficient to protect a caterpillar unless some outward sign indicated to its would-be destroyer that its prey was a disgusting morsel. ... Under these circumstances it would be highly advantageous to a caterpillar to be instantaneously and certainly recognized as unpalatable by all birds and other animals. Thus the most gaudy colors would be serviceable and might have been gained by variation and the survival of the most easily-recognized individual."

Conspicuous in their absence, however, are the mimicry complexes that are associated so frequently with aposematic adult Lepidoptera. Virtually all of mimicry theory as it relates to Lepidoptera revolves around discussions of wing patterns in adults and has done so for over a hundred years (Remington 1963). This bizarre apparent asymmetry in the frequency of mimetic resemblance in larval versus adult stages has been remarked upon, but not satisfactorily accounted for, by several authors (e.g., Sillen-Tullberg 1988, Turner 1984). Recently, Bowers (1993), accepting the notion that this paucity of mimicry complexes among larval lepidopterans was a biologically "real phenomenon" and not a sampling artifact, offered several possible explanations. First, she suggested that visual cues are in general more important to adults than to larvae in that adults rely upon such cues for species recognition during courtship and mating. She also suggested that, while visually orienting vertebrate predators are most important for adult Lepidoptera, larval stages may be more subject to selection by invertebrate predators such as parasitoids, which rely heavily on chemical, rather than visual, cues for host-finding.

Although having at least some theoretical bases from which to draw is advantageous, neither of the explanations offered by Bowers (1993) is wholly satisfying. The reliance by adults upon visual cues for conspecific recognition during courtship and mating would seem to argue against the evolution of mimicry in *adults,* rather than against the evolution of mimicry in *larvae*; mimetic patterns should reduce the efficacy with which potential conspecific mates are recognized. Moreover, there are aposematic moths that apparently rely upon chemical, rather than visual, cues during courtship. Sesiids which resemble stinging hymenopterans rely principally upon long-range female-emitted pheromones in courtship (Greenfield & Karandinos 1979); conspicuously colored and unpalatable *Utetheisa* species (Arctiidae) utilize both long-range female-produced sex pheromones and short-range male-produced aphrodisiacs in a complex, chemically mediated courtship ritual (Conner et al. 1981). In such cases, external appearances appear to result from natural selection exerted by predators, rather than sexual selection exerted by potential mates. As for the relative impact of vertebrate predators, in comparison with invertebrate predators, it is certainly true that parasitoids inflict greater mortality on caterpillar populations than they do on adult Lepidoptera. However, volumes of literature document the enormous appetite of birds for lepidopterous larvae (Holmes 1990). At low insect population levels, birds are capable of reducing numbers of lepidopteran larvae by 80 to 90%; population densities of larval lepidopterans inside exclosures, protected from birds, were as much as 50 to 300% higher than densities outside exclosures, where caterpillars were subject to bird predation. In contrast, Kettlewell (1955) observed only a 40 to 50% reduction in numbers of adult peppered moths as a result of bird predation. Whether mortality due to birds is greater for larvae than for adults is difficult to prove (and in fact may differ among species)—but there are few quantitative studies to suggest that it is substantially lower.

As for the discriminative visual capabilities of invertebrate predators, while chemical cues may be important, there is little evidence to suggest that vision is altogether unimportant. Particularly in host habitat finding, many parasitoids orient to visible signs of caterpillar feeding, such as leaf damage, leaf rolls, or abnormal growths (such as galls) (Berenbaum 1990). There are even studies to suggest that certain invertebrate predators, such as the mantid *Tenodera aridifolia sinensis* (Saussure), use visual cues in establishing learned aversions to aposematic prey (Gelperin 1968, Berenbaum & Miliczky 1984, Bowdish & Bultman 1993). Laboratory studies with artificially painted distasteful prey (the large milkweed bug *Oncopeltus fasciatus* (Dallas)) showed that broken patterns elicited a longer strike delay than did solid color patterns; this response is consistent with previous work on insect vision demonstrating that figural intensity ("edginess") has a substantial effect on insect discriminative abilities and preferences.

Irrespective of whether the major predators on lepidopteran larvae are invertebrate or vertebrate, that visually orienting predators are important selection agents on lepidopteran larval morphology is attested by the plethora of eucryptic or homotypic forms. Twig and bird dropping mimics are encountered frequently (the latter in two families, the Papilionidae and Nymphalidae). It is difficult to conceive of selection pressure other than that exerted by a visually orienting predator that could give rise to such morphology. Other forms of Batesian mimicry also can be found: fifth instar *Papilio glaucus* L. and *P. troilus* L. larvae bear an uncanny resemblance to green tree snakes. Thus, caterpillars can evolve to match their background, or to resemble animate as well as inanimate components of their environments. Why, then, do they rarely if ever evolve to resemble other caterpillars?

There are at least three alternative explanations to account for the paucity of mimicry complexes in larvae. One explanation is that there are developmental constraints, due to the demands of metamerism (e.g., Zrzavy et al. 1993), on pattern and color formation in larvae. There is no scientific evidence available in support of this notion; rather, work by Turner (1984) with *Bombyx mori* L. mutants suggests that there is an abundance of genetic variability available to lead to the evolution of special resemblance, either to snakes or to toxic caterpillar models. Individuals carrying four mutations—*moricaud*, *zebra*, *multilunar*, and *quail*—according to Turner, turn the silkworm into "a snake mimic not unlike the Elephant Hawk moth caterpillar, with frontally placed eye spots, and an intricate cryptic pink and brown pattern with short diagonal lines along the back." Similarly, individuals carrying two mutations, *multilunar* and *striped*, are aposematically colored: black with orange spots.

A second explanation is that there are differences in the relative advantages of aposematism accrued by caterpillars and adults. Caterpillars are less able than butterflies to tolerate mistakes by naive predators. Unlike butterflies or moths, which possess a large expanse of wing (not all of which is essential for flight), caterpillars have few if any expendable body parts; loss of even a small amount of tissue could be fatal. While they may possess tough cuticle and resist predator damage to some extent (Järvi et al. 1981), their options for escape are far more limited than are those of adults. Restricted to crawling or dropping to the ground as a means of escape, caterpillars are substantially less likely than butterflies or moths to outmaneuver or outdistance their enemies and thus escape. Although falling to the ground may be an effective short-term means of survival, it is a strategy that is not without its own risks; caterpillars must resort to their more labored form of locomotion to recolonize hostplants and risk starvation, desiccation, or discovery in the process. It is interesting to note that chemically protected species with aposematic larval and adult stages frequently have cryptic pupae, presumably because even chemically protected pupae, due to their lack of mobility, rarely survive an encounter with a predator (Wiklund & Sillen-Tullberg 1985, reviewed in Brower 1984).

Butterflies of necessity make themselves conspicuous when they search for mates or for oviposition plants; because conspicuousness is part of their lifestyle, aposematic coloration, legitimately advertising distastefulness, may be of tremendous benefit in avoiding attacks, particularly if there are specific patterns or colors that are innately avoided by predators (e.g., Schuler 1982). Caterpillars, in contrast, do little other than take in food and find a pupation site; neither activity necessarily involves long periods of exposure. In fact, many larval lepidopterans lead a concealed lifestyle; sedentary to the point of immobility, some feed internally in stems, fruits, or roots of plants. In some cases, a concealed lifestyle is complemented by the relatively short period of time spent in the larval stage, as compared to the adult stage. For example, univoltine depressariine oecophorids may spend three to four weeks as larvae, one or two weeks as pupae, and as long as ten months or more as adults (Hodges 1974). The probability of encountering a predator during the larval life stages for such species may be reduced accordingly.

For those species that feed externally, there may be greater benefit in remaining undetected, rather than running the risk of not surviving an encounter with a naive predator. Thus, aposematic patterns in caterpillars may be optimally designed to be "dual signals" (Brown 1988)—cryptic at a distance and aposematic at close range. This apparently paradoxical situation was described by Papageorgis (1975) in relation to mimicry rings among Neotropical butterflies: patterns that at close inspection appear classically aposematic in their natural setting, with natural patterns of shadow, light, and vegetation, are actually cryptic. As Brown (1988) succinctly states, "for an unpalatable but not invulnerable butterfly, this must be a very efficient protection, strongly favored by natural selection." Due to the relatively greater vulnerability of larvae, this strategy logically would be favored even more strongly. The brightly marked green and black larvae of *Pieris brassicae* L., while conspicuous on foliage, are more cryptic on the soil surface than are their uniformly green congeners *Pieris rapae* (Baker 1970). Järvi et al. (1981) argue that the banding pattern of *Papilio machaon* L. larvae is "cryptic at a distance but aposematic at a close distance" and cite previous studies by Windecker documenting the same effect for the black and yellow banded larvae of the cinnabar moth *Tyria jacobaeae* L. (Arctiidae). There may be sufficient selection pressure on caterpillars to maintain dual-purpose markings that there are considerable constraints on the diversity of patterns that are compatible with survival—thus limiting the frequency with which high-fidelity mimetic complexes form.

Although it is not altogether satisfying, the third explanation—that larval mimicry complexes abound but are simply not recognized as such—may turn out to be the most likely. First of all, an enormous number of larval stages, even of well-known Lepidoptera, remain undescribed. Rarely are caterpillars collected for which adult stages are unknown; the reverse is all too often true. Second, although human vision shares many similarities with avian vision, and even insect vision (Land 1992), there are fundamental differences. Humans are very large, very mobile animals and may perceive things in a manner unlike that of any other type of insect predator. It is hardly encouraging that there is not even widespread agreement on whether any particular pattern is cryptic or aposematic (viz., Gould's (1892) assessment of Cameron's (1880) suggestion that the red spots on poplar moth larvae resembled red galls on foliage and hence increased crypsis; see Grayson & Edmunds, 1989). Even when the visual targets are closer to our own body size, as is the case with other mammals, aposematism and crypsis are not so easily distinguished a priori. Godfrey et al. (1987) demonstrated by Fourier analysis of striping patterns that, surprisingly, tigers are cryptic whereas zebras are conspicuous when examined against their natural background. Very little is known about spatial frequency analyzers in birds and even less in insect predators—likely the selective agents that have brought about striping patterns in larvae in the first place. Classifying patterns as aposematic or cryptic may well depend on background (but see Sillen-Tullberg 1985); different plant hosts, with different leaf shapes, may influence the efficacy of background matching or background contrast. Because complete hostplant lists are lacking for most species, a comprehensive picture of the selection pressures leading to a particular pattern also is lacking for most species.

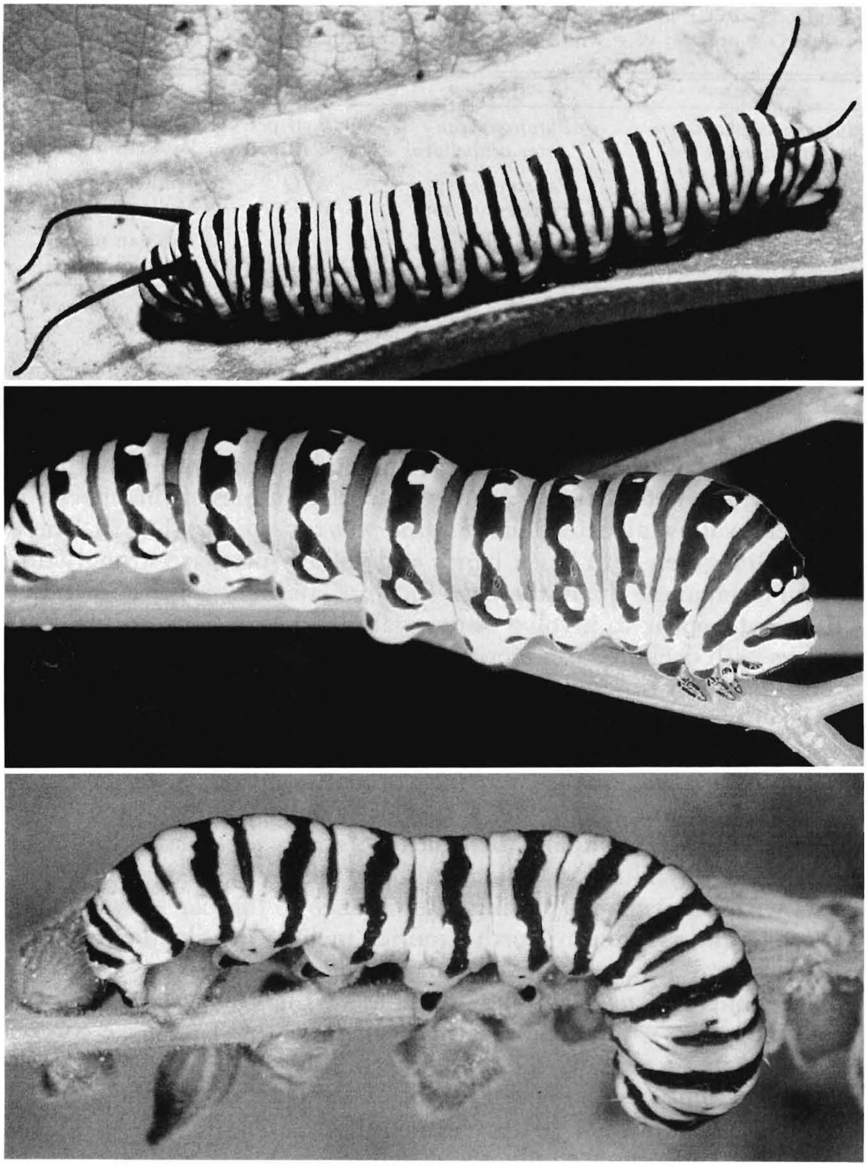
There are several suspected mimicry complexes that have been described in caterpillars; all involve aposematic models that sequester hostplant toxins. Bowers (1993) described several possible examples (Table 1) but for no case have extensive studies been conducted on the palatability of the larvae or on the responses of vertebrate or invertebrate predators to larval morphology under controlled conditions. Identifying additional mimicry complexes may prove difficult; one first step would be to identify aposematic unpalatable models that may serve as the focus for such a complex. One potential model throughout eastern North American oldfields is the aposematic unpalatable species, *Danaus plexippus* L., the monarch caterpillar (Fig. 1). The distastefulness of adult monarchs has been long known to be due to sequestration of

TABLE 1. Putative mimicry complexes involving caterpillars (after Bowers 1993). B = black, O = orange, W = white. See text for elaboration.

Species pair	Hostplants	Color	Mimetic system
Euphydryas phaeton	*Plantago* spp.	O/B striped	Batesian model
Chlosyne harrisii	*Aster umbellatus*	O/B striped	Batesian mimic
Meris alticola	*Penstemon* spp.	B/W/O	Mullerian mimic
Neoterpes graefiaria	*Penstemon* spp.	B/W/O	Mullerian mimic
Papilio memnon heronus	Rutaceae	·	Batesian model
Cerura erminea menciana	·	·	Batesian mimic

emetic cardiac glycosides from asclepiadaceous hostplants (e.g., Ritland & Brower 1991). Similarly, the distastefulness and protective value of the aposematic (black, white, and yellow banded) coloration of the larva have been documented in experimental studies with avian predators (e.g., Jarvi et al. 1981). Among potential mimics of this species is the black swallowtail caterpillar, *Papilio polyxenes* Fabr. (Fig. 2). These caterpillars, green with black bands and yellow spots, are strongly distasteful to Japanese quail; the basis for unpalatability is not known but it does not appear to involve osmeterial gland secretions, in that caterpillars with occluded osmeteria were rejected at frequencies equal to caterpillars with functional osmeteria (Leslie & Berenbaum 1990; see also Järvi et al. 1981). Their European relative, *P. machaon,* almost indistinguishable in larval appearance from *P. polyxenes,* is more distasteful to Japanese quail, *Coturnix coturnix* L., than is the monarch caterpillar *Danaus plexippus,* a species widely acknowledged to be aposematic as well as unpalatable, due to its ability to sequester hostplant cardenolides (Wiklund & Sillen-Tullberg 1985). Co-occurring caterpillars with more than a passing resemblance to the black swallowtail and monarch in northern North America include the clouded crimson *Schinia gaurae* J. E. Smith (Noctuidae), which feeds exclusively on the prairie plant *Gaura* (Fig. 1), a member of the Onagraceae, a plant family not known for toxic secondary metabolites. The three species are sympatric throughout the midwestern states in meadows and prairies. The resemblance between the black swallowtail and the clouded crimson is close but not perfect—they differ dramatically in size, for example, with *S. gaurae* only about half the length of *P. polyxenes* at maturity. Hinton (1974), however, suggested that, due to the "rapid peering" technique of foraging utilized by insectivorous birds, size differences may not necessarily be recognized immediately.

In general, the extent to which birds or other predators can generalize markings of aposematic caterpillar prey is unknown. Discriminative powers may vary among species. It may be that caterpillars are con-



FIGS. 1–2. Putative mimicry complexes involving caterpillars. **1.** Top to bottom: monarch, *Danaus plexippus*; black swallowtail, *Papilio polyxenes*; noctuid, *Schinia gaurae*. **2.** Top to bottom: pipevine swallowtail, *Battus philenor*; great spangled fritillary, *Speyeria cybele*. See text for elaboration.

FIGS. 1–2. Continued.

sumed by a greater diversity of bird species (they constitute an important part of the diet of flycatchers, warblers, vireos, chickadees, and a number of other passerines) whereas butterflies generally are consumed only by larger, more agile birds, so a more general resemblance may be a more effective ploy. Because different birds forage using different cues, a generalized resemblance may work most efficiently at deluding the greatest number of birds. While at first glance it may seem that birds foraging for relatively slow-moving caterpillars should be able to discriminate between even subtly different prey items, such a view overlooks the fact that birds foraging for caterpillars do so against a highly heterogeneous background. Viewed against the comparatively uncomplicated background of the sky, adults may be easier to distinguish with precision. Moreover, different caterpillar patterns are more likely to be viewed against different backgrounds (e.g., hostplants) than are butterflies in flight, causing greater resolution problems for birds. Birds notwithstanding, naive freshman entomology students have been known to confuse black swallowtail caterpillars with the only vaguely similar monarch caterpillar *Danaus plexippus* in east central Illinois (personal observation); how representative naive college freshmen are of naive vertebrate predators in general is, though, anybody's guess.

The pipevine swallowtail butterfly, *Battus philenor* L., is the widely recognized model in a large Batesian mimicry complex involving as many as three families of Lepidoptera: Nymphalidae (*Limenitis astyanax* Fabr.), Saturniidae (*Callosamia promethea* Drury), and other Papilionidae (*Papilio polyxenes, Papilio troilus, Papilio glaucus*). As a larva, *Battus philenor* (Figure 2A) is aposematically colored: black with a series of red spots along the abdomen. Similar markings are found on the larva of the great spangled fritillary *Speyeria cybele* Fabr. (Nymphalidae) (Fig. 2). Both species frequent low-lying vegetation in forest understory throughout the eastern United States—*B. philenor* on *Aristolochia* species and *S. cybele* on *Viola* species. It is highly likely that birds or other predators foraging in this forest community could encounter both species (despite the fact that the nymphalid feeds nocturnally). Whether this resemblance represents Batesian or Muellerian mimicry (or, indeed, if it constitutes an example of mimicry at all) has yet to be demonstrated.

Experimental work has proceeded on mimicry in butterflies, yet the paradigms, even as they apply to the most familiar systems, are still being refined (e.g., Ritland & Brower 1991). Studies of caterpillar mimicry are a century behind. There is to date no system for which palatability of putative models and mimics has been assessed against even a single ecologically appropriate predator; for which predator responses to mimetic resemblances have been monitored; and for which there is a demonstrated selective advantage to mimetic pattern for larvae under field conditions. Until such studies are conducted, the differences in defense strategies of caterpillars and adults can never be fully understood.

ACKNOWLEDGMENTS

My interest in mimicry, in swallowtail caterpillars, and, for that matter, in insects in general can all be traced to the course I took from Professor Charles Remington during the second semester of my freshman year at Yale University. Although I entered the course as an entomophobe, I left with a newfound interest and affection for insects. In the years since that class, my appreciation for the astonishing achievements of arthropods has continued to grow, as has my deep appreciation for Charles—for his insights, his encouragement, his patience, and his tremendous ability to inspire and motivate.

As for this particular paper, I thank Jeffrey Birdsley of the Kellogg Biological Station for avian insights, James Sternburg of the UIUC Department of Entomology for photographs and expert advice (in particular, pointing out the resemblance between the great spangled fritillary and the pipevine caterpillar), Steve Passoa of USDA-APHIS Ohio Department of Agriculture for the photograph of the clouded crimson caterpillar, and Lincoln Brower, Terry Harrison, Gilbert Waldbauer, and Arthur Zangerl for valuable comments on the manuscript. This work was supported by NSF DEB 91-19612.

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