Journal of the Lepidopterists' Society
41(3), 1987, 141–144

PREDATION BY *ANOLIS* LIZARDS ON *BATTUS PHILENOR* RAISES QUESTIONS ABOUT BUTTERFLY MIMICRY SYSTEMS

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ABSTRACT. *Anolis* lizards in Texas make supposedly distasteful and poisonous *Battus philenor* adults a component of their natural diet. The lizards appear to suffer no ill effects, and individual lizards will eat *Battus* more than once. We followed individual female butterflies searching for oviposition sites for 90 h and observed 4 instances of predation in the field. We supplemented these observations with field experiments and a laboratory study. Results raise questions about the general importance of lizard predation in the evolution of butterfly mimicry systems.

Additional key words: Papilionidae, aristolochic acid, distasteful butterflies, pipevine swallowtail.

Mimicry is widespread in nature, and studies of predation on butterflies have been prominent in the development of ideas about aposematic coloration (Brower 1958, Brower et al. 1963, Rothschild et al. 1972). Most of these studies have involved examining the behavior of captive predators when offered palatable and distasteful butterflies. There is remarkably little information on predation of adult butterflies in nature, and published field observations deal almost exclusively with attacks of birds on butterflies (Fryer 1913, Rutowski 1978, Wourms & Wasserman 1985). Observations of natural predation by lizards are rare (Ehrlich & Ehrlich, 1982), yet "birds and lizards have long been considered to be the major selective agents responsible for the extreme diversity of unpalatable and mimetic forms of butterflies in nature" (Boyden 1976). When wild *Ameiva* lizards in their natural habitat were fed live butterflies, they quickly became conditioned to avoid unpalatable species (Boyden 1976). Ehrlich and Ehrlich (1982) observed iguanid lizards preying on tropical butterflies, and because different butterfly species seemed to be attacked differently, concluded that their observations supported the assumption that lizards are often strong selective agents in the evolution of butterfly color patterns and behavior.

One classic study of mimicry in butterflies focused on the pipevine swallowtail and its mimics. The larvae feed on plants in the genus *Aristolochia* (Aristolochiaceae). The adults are distasteful to birds (Brower 1958), presumably because they sequester distasteful aristolochic acids and related alkaloids, as do other *Aristolochia*-feeding papilionids (Euwe et al. 1968, Rothschild et al. 1972). These substances are poisonous to

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generalist insects in small quantities (Rausher 1979) and in vertebrates can cause acute renal failure (Hedwall 1961, Jackson et al. 1964). Mimetic species include *Papilio troilus*, dark-form *P. glaucus* females, *P. polyxenes*, and *Limenitis archippus archippus*.

During a field study of *Battus philenor* in the John Henry Kirby State Forest, Tyler Co., Texas, we observed individual females searching for oviposition sites for a total of 90 h from 22 March to 9 May 1985. We observed four instances of predation on *Battus* by lizards, as well as two unsuccessful attempts. These observations and additional experiments cause us to question whether qualities that render butterflies distasteful to birds also render them distasteful to lizards.

Instances of Predation

Our first observation of lizard predation involved an aging *Battus* female that alighted on a host plant and started to deposit eggs. Within seconds of alighting, a large *Anolis* pounced on her from a tree trunk about 0.4 m away, apparently killing her with its first bite, which covered her head and thorax. The lizard consumed the entire butterfly during the next 20 minutes. Getting the wings into its mouth appeared to be the most difficult part; it had to scrape the butterfly many times against a tree trunk using sideways movements of the head to work the wings in. Three other similar instances were also observed. Afterwards, we collected these lizards, and they exhibited no ill effects during 24 h in captivity.

In one case, a basking butterfly escaped when an *Anolis* pounced on it. Another time, a medium-sized *Anolis* jumped from a thin branch onto a stationary copulating pair on a twig about 30 cm below it, collided with them, dislodged the male, and fell about 2 m into the undergrowth below. Before its jump, the lizard was observed to climb slowly from near the pair up to the launching point. Apparently *Anolis* can perceive motionless *Battus philenor*.

Reaction of *Anolis* to Offered Butterflies

Tethered butterflies were presented to *Anolis* in the field. One female and five male *Battus* were allowed to fly past large (>15 cm) perching lizards. In all but one case in which the lizard appeared to be startled by the observer, the butterflies were seized immediately, sometimes by the body, and sometimes by the wings. The bodies but not the wings were eaten because tethers prevented lizards from freely scraping the wings against tree trunks.

Two medium-sized (10–15 cm) lizards were each offered a *Battus* male. One lizard made no attempt to capture it. The second seized the butterfly immediately, but the tether became entangled in a twig; the lizard could not bring the dead butterfly to the ground and eventually abandoned it. We broke the wings of another butterfly near their base, making it unable to fly, and presented it to a large lizard perched on a tree trunk. The lizard immediately seized and consumed it entirely.

Three small (<10 cm) lizards showed no interest in butterflies offered to them. They are almost certainly not large enough to capture and hold a *Battus* even if they tried. None of the lizards that ate butterflies exhibited any adverse symptoms during 24 h in captivity.

Effect of Experience on Subsequent Predation

Clearly, large *Anolis* lizards often kill and eat *Battus philenor* butterflies. It is possible that the predation we observed involved lizards that had not previously consumed a *Battus* adult. The question therefore remained whether eating one would discourage a

lizard from doing so again. To answer this question, we captured two large *Anolis*, placed them in a cage and fed both a *Battus* male the first day, a female the second day, and a male on each of the following two days. The lizards caught all butterflies immediately. Usually, the entire butterfly was consumed. We conclude that either *Anolis* lizards do not learn from experience to avoid *Battus* or the butterflies are not poisonous or distasteful to them.

DISCUSSION

Our observations indicate that *Anolis* lizards readily attack and consume an insect that serves as a model in a large mimicry complex. Qualities that render *Battus* distasteful to birds (Brower 1958) apparently do not render them so to *Anolis*. If this conclusion is applicable to other types of lizards, then lizard predation may have served less often than generally assumed as a major selection pressure causing the evolution of unpalatability or of mimicry.

Three caveats must be added to this suggestion. First, because *B. philenor* is abundant in E Texas, it may constitute a potentially abundant resource for *Anolis*. It is thus plausible that these lizards have evolved to tolerate or detoxify the noxious compounds sequestered by *B. philenor*, and thus may not be representative of all lizards. Second, it is possible that in the year of our study alternative food resources for *Anolis* were scarce, and the lizards preyed on *Battus* despite distastefulness and possible subtle adverse effects. If so, then when alternative resources are more abundant, *Anolis* may exhibit less tendency to consume *Battus*. In such years the distasteful individuals would be protected from lizard predation. This protection would favor the evolution of distastefulness and mimicry. Third, *B. philenor* in E Texas may not be distasteful, perhaps because it does not sequester noxious compounds. Two lines of evidence argue against this hypothesis: both butterflies and host plants contain aristolochic acids (Rausher unpubl. data); and female *Papilio glaucus* occur there predominantly in the black form, indicating that Batesian mimicry there is effective, which implies that *Battus* there is distasteful.

Despite the caveats, we believe our observations suggest that lizards in our study have not been a major selective force in the evolution of mimicry and distastefulness in *Battus philenor*. Our results contrast sharply with those of Boyden (1976), indicating that the influence of lizard predation on the evolution of mimicry systems needs more investigation.

ACKNOWLEDGMENTS

We gratefully acknowledge field assistance by R. C. Lederhouse, and permission from Gary Lacox, Texas Forest Service, to work in the Kirby State Forest. Two anonymous reviewers made useful comments. This research was funded by NSF grant BSR-8406870.

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Received for publication 1 August 1986; accepted 10 April 1987.