LARVAL PROTECTIVE COLORATION IN SWALLOWTAILS FROM THE FLORIDA KEYS
(LEPIDOPTERA: PAPILIONIDAE)

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ABSTRACT.—Observations of the occurrence of dark and light color patterns in early instar larvae of Papilio species suggest that they may be selected for disruptive coloration, mimicry of bird droppings, or mimicry of lizard droppings, depending upon size of the larval stage and relative occurrence of appropriate models in the species' habitat.

KEY WORDS: immature stages, larval behavior, Papilio.

Early instar larvae of swallowtail butterflies in the genus Papilio are typically dark brown or black with a whitish saddle patch toward the middle of the body and a pale patch on the caudal end. Seitz (1924) noted the occurrence of a saddle patch on larvae in several groups of "Fluted-Papilios." Igarashi (1984: p. 51) stated that the saddle patch is found in at least twelve "fairly advanced" genera of papilionids, so this color and pattern combination seems to be widespread in the tribe Papilionini with its large genus Papilio (more than 200 species divided into a number of subgenera; New & Collins, 1991).

Most authorities have believed that the brown and white patterns of papilionid larvae are protective in nature and that they mimic bird droppings (e.g., Seitz, 1924: p. 29; Klots, 1951; Opler and Krizek, 1984; Scott, 1986). The larvae thus gain protection against predation by their close resemblance to an unpalatable object found in the same habitat. In the present paper, we advance the suggestion that dark and light larval color patterns in certain swallowtails may be selected as a result of at least three possible factors: (1) a role in disruptive coloration, (2) a mimic role with regard to bird dropping models, and (3) a mimic role with regard to lizard dropping models. Differences in the pattern found in respective Papilio species may be related to and selected in response to the relative seasonal abundance of birds versus lizards in the characteristic environment of that swallowtail at the time of the year when its larval stages are active.

In the Florida Keys, three species of Papilio occur in breeding populations: P. cresphontes Cramer, P. andraemon bonhotei Sharpe, and P. aristodemus ponceanus Schaus. Sometimes placed in the subgenus Heraclides, these species share a general similarity in dark brown and yellow-tan adult wing pattern that is relatively cryptic in the sun-dappled tropical hardwood hammock habitat. All three swallowtails feed on the leaves of trees and shrubs of the plant family Rutaceae during the larval stages.

The first instar larva of the Giant Swallowtail (Papilio cresphontes) is dark brown with pale saddle and caudal patches (Fig. 1a). In the Keys, the Giant Swallowtail occurs at the edges of hardwood hammocks and in disturbed sites and urban areas (Minno and Emmel, 1992).

The other similar swallowtail species resident in the Florida Keys have West Indian affinity: these are the Bahama Swallowtail (Papilio andraemon bonhotei) and the Schaus Swallowtail (Papilio aristodemus ponceanus) (Minno and Emmel, 1992). The color patterns of the first-stage larvae of these species are closely similar to one another, but differ strikingly from that of the Giant Swallowtail. Bahama and Schaus Swallowtail larvae are blackish with only the white patch on the caudal end of the body in the first instar (Fig. 1b). These swallowtails have similar ecological requirements and are among the few butterflies that regularly fly in the shade of the tropical hammocks of the Upper Keys.

The early instar larvae of the Schaus and Bahama Swallowtails closely resemble the droppings of Anolis lizards (Fig. 1c). Two species of Anolis, the Green Anole (Anolis carolinensis) and the Brown Anole (Anolis sagrei), are abundant in the tropical hammocks of the Keys. The droppings of these lizards are of the same size, shape, and color of young swallowtail caterpillars. The larger dark brown part of an Anolis dropping is shiny, like the cuticle of a young swallowtail larva, and consists of insect remains (particularly ants). The white uric acid waste product characteristic of reptile and bird feces is always concentrated in a small pellet at one end of the dropping.

Bird droppings, in contrast, are much more variable in size, shape, and coloration (Fig. 1c). Dried bird droppings are dull in appearance, and the white uric acid wastes often cover most of the outer surface. Frequently, when a bird dropping hits a leaf, it splatters, leaving only a white smear of uric acid. During the spring, large numbers of insectivorous birds, such as warblers, pass through the Keys on their way to summer breeding ranges farther north, and during the fall, to wintering grounds in Central and South America. However, relatively few insectivorous birds are present during the summer wet season when swallowtail immatures are most abundant. Summer resident birds in the mangroves and tropical hammocks of the Keys include the Mangrove Cuckoo (Coccyzus minor), Great Crested Flycatcher...
During the second and third instars, both the Bahama and Schaus Swallowtails develop one pale patch on each side in the middle portion of the body, and a small pale patch behind the head, in addition to the caudal patch. In later instars of the Bahama Swallowtail, a saddle patch forms, mostly located on abdominal segments 2, 3, and 4 (Fig. 1d). All Giant Swallowtail instars have the pale saddle patch, and the last instar strongly resembles that of the Bahama Swallowtail (Fig. 1e). In the Schaus Swallowtail, however, the last instar caterpillar has a row of pale spots that coalesce into a line on each side of the body (Fig. 1f). The largest of these pale spots lies on abdominal segments 3 and 4, but the Schaus Swallowtail larva lacks a saddle.
Since droppings of the lizards (and most hammock-inhabiting birds) found in the Keys do not exceed 1 cm in length, early instar larvae of the resident *Papilio* species match the postulated models in size as well as color. However, it is unlikely that the last instar larvae of the Bahama or Giant Swallowtails, which have saddle patches, are bird-dropping mimics. The mature caterpillars of these species range in length up to 4.5 and 5.5 cm, respectively, and are simply too large. It is more likely that this pattern of light and dark areas on large larvae is disruptive in nature.

In many species of *Papilio*, there is a dramatic change in color at the last larval molt from a brown and white pattern to green (Honda, 1981; Miller, 1987:387). This shift seems to occur in species that feed and rest on the leaves of the host. The green color of these large caterpillars, therefore, helps them to blend in with their background. Swallowtail species that retain "bird dropping" patterns into the last instar also feed on leaves, but usually rest on the branches or trunk of the host shrub or tree. The patches of light and dark color on large larvae of the Schaus, Bahama, and Giant Swallowtail seem to visually break up the body outline, especially in the dappled light of the forest. Thus it would appear that the mimetic brown and white patterns of the young larvae also serve the mature caterpillars, but as a disruptive type of protective coloration.

We suggest that the differences between the Giant Swallowtail and the Bahama and Schaus Swallowtails in the coloration of the first instar larvae must be related to the abundance of lizards and birds present. The Giant Swallowtail occurs in many different habitats from tropical to temperate latitudes and probably encounters a wide variety of vertebrate predators throughout its range. In contrast, the Bahama and Schaus Swallowtails are narrowly restricted to West Indian hardwood forests, where *Anolis* lizards seem to be relatively more abundant than insectivorous birds during the breeding season.

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**LITERATURE CITED**

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