doi:10.1111/j.1558-5646.2008.00388.x

ANTAGONISTIC, STAGE-SPECIFIC SELECTION ON DEFENSIVE CHEMICAL SEQUESTRATION IN A TOXIC BUTTERFLY

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Received January 7, 2008
Accepted March 8, 2008

Larvae of the pipevine swallowtail (*Battus philenor*) sequester toxic alkaloids called aristolochic acids from their *Aristolochia* host plants, rendering both larvae and adults chemically defended against most predators. Using a chemically controlled artificial diet, we observed substantial among-family variation in sequestration ability and larval developmental rate in a population occurring in central Texas. Early instar larvae from families that sequester greater amounts of aristolochic acid showed increased survivorship in a field experiment in which cohorts from each family were exposed to natural predators, whereas among-family variation in growth rate did not predict survivorship. Conversely, the aristolochic acid content of adult butterflies was negatively correlated with adult fat content, a fitness correlate. Sequestration ability positively affects the probability of larval survivorship, but at the cost of adult fat content. The costs and benefits of aristolochic acid sequestration vary during the course of the butterfly's development, and these antagonistic selection pressures may explain why variation in sequestration ability persists in wild populations.

KEY WORDS: Aristolochic acid, *Battus philenor*, gregarious feeding, natural selection, trade-offs.

Many herbivorous insects sequester toxic chemicals from their host plants rendering them unpalatable to predators. Such chemical defense has been studied extensively, particularly in the Lepidoptera. Indeed many fundamental evolutionary concepts, such as mimicry, have been based on studies of toxic Lepidoptera and their characteristic aposematic coloration (Bates 1862; Müller 1878; Brower 1958a,b). Slater (1877) and Haase (1893) were among the first to propose that host plants were the source of chemicals responsible for unpalatability, however it was not until the seminal works of Brower (1958a,b) and Rothschild et al. (1970) that the efficacy of plant-derived chemical defenses and chemical sequestration was rigorously examined. Since then, a great deal of knowledge has accumulated concerning the variety of chemical toxins sequestered and the diversity of herbivores capable of sequestration (Duffey 1980; Nishida 2002).

The evolution and maintenance of chemical sequestration as a defensive strategy is different from the detoxification and/or excretion of plant defensive chemicals employed by many nonsequestering herbivores because it is affected by selection pressure from both the first and third trophic levels (Price et al. 1980; Rowell-Rahier and Pasteels 1992; Ode 2006) Selection imposed by the first trophic level can affect traits associated with reducing the toxic effect of the chemical, detoxification, tolerance to the toxin (e.g., target site insensitivity), or intraconverting the toxin to less-toxic forms (Harborne 1993; Holzinger and Wink 1996; Berenbaum and Zangerl 1998; Feyereisen 1999; Glendinning 2002). Selection imposed by the third trophic level (i.e., predators and parasites) should favor concentrations of sequestered defensive chemicals that are generally effective against the spectrum of natural enemies the insect might encounter. The sequestration of