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GEOGRAPHIC VARIATION IN CLUTCH SIZE AND A REALIZED BENEFIT OF AGGREGATIVE FEEDING

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Abstract.—We investigated one causal explanation for geographic variation in clutch size and aggregative feeding of the pipevine swallowtail, *Battus philenor*. Populations in California lay larger clutches than those in Texas, and larger feeding aggregations grow at an accelerated rate on the California host plant. Using reciprocal transplant experiments with larvae from California and Texas populations, we found that the benefit of increased growth rate associated with feeding in larger groups occurred only on the California host plant and was observed for larvae from both populations. These results are consistent with the hypothesis that larger clutch size and aggregative feeding are adaptations to characteristics of the California host plant. Future studies on the evolution of clutch size and aggregative feeding of herbivorous insects should consider how these life-history traits affect host plant suitability.

Key words.—Adaptation, clutch size, geographic variation, gregariousness, life-history evolution, plant-insect interactions.

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The adaptive significance of aggregative feeding of Lepidoptera larvae has received a great deal of attention (Sillén-Tullberg 1988; Hunter 2000). Aggregative feeding is of interest to evolutionary biologists because it is usually a consequence of egg clustering by females. Clutch size is an important life-history trait because it represents a proportion of a female's potential fecundity that is invested in a single oviposition event. Numerous hypotheses have been proposed to explain the evolution of large clutch size and subsequent aggregative feeding (Stamp 1980). Nonadaptive explanations posit that large clutch size may be a consequence of female motivational state or egg load when suitable oviposition sites are rare (Courtney 1984; Tatar 1991). Alternatively, many adaptive hypotheses have been proposed for the evolution of aggregative feeding. Aggregative feeding may increase thermoregulatory ability (Bryant et al. 2000), maximize resource use (Le Masurier 1994), circumvent structural plant defenses (Rathcke and Poole 1975), accelerate larval growth due to enhanced plant quality (Fordyce 2003), and function for defense, either through active group defense or enhanced aposematism (Fisher 1930; Stamp 1980).

Two avenues of investigation have commonly been used to infer the adaptive significance and evolutionary history of aggregative feeding. Experimental methods generally consist of manipulating group size of larvae to numbers above or below the naturally occurring densities within a population, and assessing the ecological consequences of group size, such as mortality or growth rate (e.g., Lawrence 1990; Fordyce and Agrawal 2001). Phylogenetic methods of inference compare the degree to which aggregation occurs among lineages as an attempt to reconstruct correlated evolutionary changes in traits presumed to be adaptive (Sillén-Tullberg 1988; Tullberg and Hunter 1996). Using this method, for example, Tullberg and Hunter (1996) concluded that aggregative feeding is more likely to evolve in lineages where larvae are toxic and warningly colored, thus supporting defense as a factor leading to the evolution of this trait.

Here, we exploited interpopulation variation in clutch size and aggregative feeding of the pipevine swallowtail (*Battus philenor*) to determine if one benefit associated with feeding in larger groups, accelerated growth rate, was only realized in a population characterized by a larger clutch size. This system provided us with a unique opportunity to investigate the adaptive significance of aggregative feeding within a taxon, while permitting us to use populations that naturally feed in small or large groups. Here we present results from a reciprocal transplant experiment of larvae from California and Texas. California females lay significantly larger egg clutches and larvae feed in larger groups compared to populations reported in Texas. We hypothesized that aggregative feeding exhibited by the California population of *B. philenor* represents an adaptation unique to the California host plant whereby groups of larvae effectively manipulate the plant quality so as to enhance its suitability for larval development (Fordyce 2003). Specifically we asked the following questions: Do plant characteristics explain the variation in clutch size observed within the California and Texas populations? Is the increased growth rate associated with larger feeding aggregations observed in California a characteristic unique to California larvae, a response unique to the California host plant, or both?

MATERIALS AND METHODS

Species Description and Study Populations

The California populations of *B. philenor* are disjunct from the rest of the species range and sometimes are designated as the subspecies *B. p. hirsuta*. Members of the genus *Battus* are restricted to host plants in the genus *Aristolochia* (Aristolochiaceae) and in California only one host plant species is available to *B. philenor*, the endemic *A. californica* (Racheli and Pariset 1992). The average clutch size observed in California populations, including the focal population at Stebbins Cold Canyon, is 13 eggs per cluster and larvae feed in

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