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How caterpillars avoid overheating: behavioral and phenotypic plasticity of pipevine swallowtail larvae

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Abstract We tested the hypothesis that larvae of the pipevine swallowtail butterfly, *Battus philenor*, employ behavioral and phenotypic plasticity as thermoregulatory strategies. These larvae are phenotypically varied across their range with predominantly black larvae (southeastern USA and California) and red larvae (western Texas, Arizona) occurring in different regions. Two years of field observations in south Texas indicate that the proportion of red larvae increases with increasing daily temperatures as the growing season progresses. Larvae were also observed to shift their microhabitats by climbing on non-host vegetation and avoided excessive heat in their feeding microhabitat. Larvae of ten half-sib families from populations in south Texas and California, reared under different temperature regimes in common garden experiments, exhibited plasticity in larval phenotype, with larvae from both populations producing the red phenotype at temperatures greater than 30°C and maintaining the black phenotype at cooler temperatures. However, larvae from Texas were more tolerant of higher temperatures, showing no decrease in growth rate in the highest temperature (maximum seasonal temperature) treatment, compared to the California population. In a field experiment, black larvae were found to have higher body temperatures when exposed to sunlight compared to red larvae. These results suggest that microhabitat shifts and the color polyphenism observed in pipevine swallowtail larvae may be the adaptive strategies that enable larvae to avoid critical thermal maximum temperatures.

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Introduction

The rates of physiological processes in ectothermic organisms, including growth and development, are determined in part by environmental temperature (Lyons 1994; Smith and Ward 1995). Many ectotherms possess adaptive behaviors and morphologies that allow regulation of body temperature above or below ambient temperatures. Insects, for example, display a remarkable diversity of strategies for thermoregulation in almost all life stages in response to a variety of environmental factors (Heinrich 1996). These strategies commonly include behaviors and/or phenotypic plasticity that maximize temperature-dependent growth rates and which, therefore, often affect their fitness (Huey and Kingsolver 1989; Nylin and Gotthard 1998). Plastic and behavioral responses, as opposed to fixed or invariant traits, enable insects to respond to seasonal or daily variation in their thermal environments (e.g. Shapiro 1976; Kukal and Dawson 1989; Bryant et al. 2000; Fitzgerald and Underwood 2000; Hazel 2002). Many of the behavioral responses of insects to varying thermal environments involve microhabitat shifts or modifications. For example, in the Lepidoptera, behaviors such as basking (Forsman 2000), gregariousness (Stamp 1980; Bryant et al. 2000) or the construction of shelters (i.e., tents) (Casey et al. 1988; Joos et al. 1988) have been shown to effectively regulate body temperatures.

Many of the plastic responses observed in insects involve pigment changes in seasonally changing thermal environments. Some of the most well-studied examples are found in the Lepidoptera. For example, many butterflies exhibit seasonal polyphenisms in wing-pigmentation patterns (Shapiro 1976). Increased melaninization of the wings of early spring forms of certain butterflies facilitates increased absorption of solar radiation (Watt 1968; Shapiro 1976; Douglas and Grula 1978; Van Dyck