Clutch size in the swallowtail butterfly, *Battus philenor*: the role of host quality and egg load within and among seasonal flights in California

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Summary. Clutch size in the pipevine swallowtail of California (*Battus philenor hirsuta*) varies widely within and among two seasonal flights, early and late spring. Pilson and Rausher (1988) proposed that variation in clutch size in a Texan *B. philenor* population is due to assessment of host quality with subsequent adjustment of clutch size and to differences in motivational state. The assessment hypothesis and a nonexclusive alternative that clutch size is determined by mature egg load were tested for populations in Sacramento, California. Weak and sporadic correlations between host quality and clutch size were found, suggesting that host assessment with adjustment of clutch size is not a strong factor in this population. Clutch size was highly correlated to mature egg load in the early but not in the late spring flight. Yet, females from both flights had similar loads of mature eggs. It is proposed that females lay clutch sizes proportional to egg load, up to a maximum threshold. The threshold may be lowered in the late spring flight in response to changes in overall host quality or to increased egg predation, reducing both the mean clutch size and the correlation between clutch size and egg load. Potential mechanisms for the change in behavior among flights, based on changes in the threshold, are discussed.

Introduction

Numerous butterflies oviposit in clutches of many eggs and exhibit wide variation in the mean clutch size (MCS; Chew and Robbins 1984; Courtney 1984; Stamp 1980). Recent studies have attempted to explain such variation in the pipevine swallowtail butterfly, *Battus philenor*, which lays clutches ranging from 1–7 eggs on *Aristolochia reticulata* in Texas (Pilson and Rausher 1988) and 1–54 eggs on *A. californica* in California (Tatar 1989). This paper evaluates the role of two potential, not exclusive, sources of variation in clutch size within and among seasonal flights of *B. philenor* in California: first, variation in the quality of larval hosts with females assessing host quality and adjusting clutch size and, second, variation in physiological state at the time of oviposition, specifically mature egg load.

The model of host assessment with clutch size adjustment proposes that females assess individual host plants for larval suitability and adjust their clutch size to match that assessment. As individual females encounter hosts of different quality, variation in clutch size is observed. Mangel (1987) demonstrates, with the use of a dynamic programming model, that considerable variation in clutch size can result when females adjust clutch size in response to host quality. A positive relationship between host quality and clutch size has been found in several insects (Godfray 1987 and references therein). For example, clutch size is thought to relate to the quality of host species in the leaf-mining fly *Pegomya* (Godfray 1986), in the heliconiine butterflies (Benson 1978), and in Tephritid fruit flies (McDonald and McInnis 1985; Berrigan et al. 1988). The parasitoid wasp, *Trichogramma*, rapidly assesses host size and adjusts clutch size to this measure of host suitability (Schmidt and Smith 1987a, b).

Variation in clutch size may also result when clutch size is determined or constrained by mature egg load, in addition to or independent of host assessment. The number of eggs laid on a single host correlates to egg load in two species of *Drosophila* (Courtney et al. 1989) and in *Dacus tyroni* (Fitt 1986). Host search and host choice in Pierids (Courtney 1981; Jones 1977) and in *Euphydryas* (Singer 1982) is affected by egg load. In the model of Mangel (1987), whereas variation in clutch size is produced by host assessment and clutch size adjustment, egg load limits the size of potential clutches and determines, through maximization of lifetime reproduction, the optimal clutch size for a given host. Variation in clutch size can also result from variation in egg load.

To evaluate the role of host assessment with clutch size adjustment in producing variation in clutch size of *B. philenor* in Texas, Pilson and Rausher (1988) predicted that the behavior will cause the size of clutches to corre-
late to inferred measures of host quality: oviposition shoot characteristics and the dispersal size of larvae. Pilson and Rausher (1988) found such a correlation and suggested that females assess individual hosts and adjust clutch size, although questions exist regarding the design and interpretation of this study (Tatar 1989; Pilson and Rausher 1989). Pilson and Rausher (1988) further tested the clutch size decision behavior of *B. philenor* females exposed to plants with different characteristics when their motivational states were experimentally controlled by preventing oviposition for various durations. They demonstrated that oviposition-deprived females, when presented with young plants, laid larger clutches than non-deprived females exposed to the same age plants and that deprived females laid larger clutches when presented with young rather than old plants. As well, Odendaal (1989) and Odendaal and Rausher (1990) have shown that clutch size and the time females spend searching for oviposition sites versus other activities is proportional to egg load. These results suggest roles for internal physiological state and for host assessment with clutch size adjustment in determining clutch size in *B. philenor* in Texas (Pilson and Rausher 1988).

Can the results of Pilson and Rausher be generalized to other populations of *B. philenor*? In the Sacramento Valley, California, *Battus philenor hirsuta* has two distinct seasonal flights, early spring (March–April) and late spring (May–June), and a weaker third summer flight. The latter flights consist of the proportion of the population (3–39%) that has not diapaused as pupae (Sims and Shapiro 1983). There is large variation in clutch sizes in the early and late spring flights, and MCS among flights differ (Tatar 1989). In this paper I evaluate the relative importance of assessment of individual hosts with clutch size adjustment and of differences in physiological state, i.e., mature egg load, as explanations for variation in clutch size within seasonal flights. The variables were investigated independently in 1989 and together in 1990. Regarding variation in MCS among seasonal flights, I test if differences in the physiological state of females among seasonal flights or if changes in the behavioral response to mature egg load provide a full or partial explanation.

**Methods**

**Clutch size and host characteristics.** The study site, Goethe Park, Sacramento County, is a riparian habitat where *Aristolochia californica* occurs as dense ground cover and as a climbing liana. Thirty hectares of woods are separated by roads and small clearings and constitute the Woods study site. In July 1988 a 2-fa fire burned on the western edge of the site. This area had partially recovered by 1989 and constitutes the Burn study site.

Egg clutches were found by searching *A. californica* plants in the Woods and Burn sites in the early spring (12–22 April, 1989) and in the Woods site in the late spring (2–13 June, 1989). In the Burn site, clutches and hosts were scarce during the late spring census period, although a smaller census was possible at a later date (19–23 June, 1989). Females laid discrete clutches where eggs were generally contiguous. When more than one discrete batch was found on a shoot, the shoot was included when the clutches could be separated by differences in color; the center of eggs darken as they age, and the older of the batches was counted as the clutch size of the shoot.

Correlations of clutch size to measures of host characteristics were sought on two scales: characteristics of the central oviposition shoot and characteristics of hosts within a census cylinder. Measurements were made for both sites in the early spring and for the Woods site in the late spring. A neighborhood of hosts is potentially the scale of female assessment since *B. philenor* females in California inspect hosts in areas ranging from 2 to 15 m² about oviposition sites (personal observation), and larvae leave the oviposition shoot by the third instar and rely on subsequent host discoveries to complete development (Rausher 1979; personal observation). At each located clutch, a 1-m² hoop was centered on the shoot of the clutch. A census cylinder was defined by taking the central oviposition shoot to be the axis of a cylinder, perpendicular to the hoop, with the height of the projected cylinder to be the length of the central oviposition shoot. Seven characteristics of the central oviposition shoot and four characteristics of host plants in the census cylinder were measured (Table 1) as well as the number and size of other clutches in the census cylinder. In the Texas *B. philenor-Aristolochia* system, measures of bud length and leaf number correlate to larval growth (Pilson and Rausher 1988) while bud length and plant height correlate to patterns of host acceptance (Rausher and Papaj 1983). The amount of the wet or dry tissue effects larval growth in *B. philenor* and in the other Lepidoptera (Rausher 1981; Scriber 1984). Host tissue for mass and percent dry matter determination was collected in plastic bags, weighed within 4 h, and dried to constant weight.

The quality of an *Aristolochia* host as an oviposition site was also directly assayed in the field in both flights by the disappearing size of test larvae placed on the plant. In the Texas *B. philenor-Aristolochia* system, 12% of second instar larvae locate hosts 0.5–10 m from a dispersal point in a test grid in 6 h. Third instar larvae are about 4 times as likely to discover new hosts (Rausher 1979). Larger larvae have a greater chance of finding subsequent hosts (Rausher 1979), and size at disappearance is used as the direct measure of host quality. While disappearance from hosts due to predators is evident in Texas (Rausher 1981) and coccinellid larvae successfully attack small *B. philenor* instars in California (Stamp 1986; personal observation), estimates of predation rates relative to dispersal rates in the 1990 study reported hereafter suggest that dispersal is the predominant cause of disappearance. While larval missing from dispersal and predation cannot be distinguished, I assume that rates of predation are low and uniform within a test period so that differences in disappearance size is due to differences in size at dispersal.

In 1989, shoots with clutches that had no contact with other hosts were located in 3-day periods in both seasonal flights. Clutches were counted and removed. Seven days later, five or two newly molted second instars were placed on the early or late spring shoots, respectively. The lengths of remaining larvae were measured daily. The sizes of missing larvae were defined as the largest recorded lengths from the previous day’s measurement at the shoot. For each shoot, the sum leaving size is the total of the sizes of missing larvae. The smaller number of test larvae was used in the late spring because the plants were much smaller. Shoot size was measured by number of leaves in the early spring and by length in the late spring.

**Clutch size and egg load.** In 1989 the role of mature egg load in explaining variation in clutch size within seasonal flights was tested by seeking a correlation between mature egg load and clutch size. Odendaal (1989) defined mature egg load in *B. philenor* as the number of charoninated eggs in the posterior oviduct plus any just oviposited eggs. Females were observed ovipositing and were then captured, killed, and refrigerated prior to dissection. Time of oviposition and number of charoninated eggs, wing length, wing wear, and number of spermatophores, as in Odendaal (1989), were recorded. Observations were made between 0800 and 1600 h over 3–5 days at the peak of each flight. These data also provide esti-