*Journal of Insect Behavior, Vol. 2, No. 1, 1989*

# Mature Egg Number Influences the Behavior of Female *Battus philenor* Butterflies

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*Accepted 29 June 1987; revised 24 August 1987*

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*Although oviposition behavior of butterflies has been studied extensively, physiological parameters that may affect various aspects of female behavior have been overlooked almost completely. The number of mature eggs carried by a female* Battus philenor *greatly affects her behavior at any particular time. Females with many eggs search significantly more for host plants than females with fewer eggs, which tend to rest more. Parameters affecting the number of mature eggs are also studied.*

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**KEY WORDS:** oviposition behavior; reproduction; host plant; *Battus philenor.*

## INTRODUCTION

The behavior of female butterflies, particularly oviposition behavior, is well described in the literature. Most studies have focused on how females respond to host species and host quality (e.g., David and Gardiner, 1962; Ma and Schoonhoven, 1973; Singer, 1971; Chew, 1977; Wiklund, 1975; Jones, 1977; Rausher, 1978; Courtney, 1981; Singer, 1983), to the presence of conspecific eggs, larvae, or egg mimics (e.g., Rothschild and Schoonhoven, 1977; Rausher, 1979; Shapiro, 1980; Williams and Gilbert, 1981), or to variability in microhabitat during oviposition site selection (e.g., Singer, 1971; Rausher, 1979b; Williams, 1983; Grossmueller and Lederhouse, 1985).

Only rarely have there been attempts to link female behavior and repro-

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ductive physiology. This is surprising, since there have been several indications that ovarian dynamics may be important in understanding female behavior, including oviposition behavior. Singer (1982) showed that *Euphydryas editha* becomes less discriminating as the intervals between ovipositions are prolonged. In monarchs, ovarian development is stimulated in reproductively inactive overwintering individuals when they are placed in summer conditions, apparently due to stimulation of corpora allata activity. Environmentally activated hormones may therefore regulate reproductive behavior and migrations in monarchs (Barker and Herman, 1973, 1976; Herman, 1973).

Oviposition behavior of *Battus philenor* females has been studied extensively in an east Texas population (e.g., Rausher, 1978, 1983; Rausher and Papaj, 1983; Papaj, 1986). In a recent study on behavioral shifts in oviposition behavior, we followed many females and recorded their behavior with handheld computers (Rausher and Odendaal, 1987). In the course of the study I noted that females searching for host plants not only shifted preferences between two host plants, *Aristolochia reticulata* and *A. serpentaria*, but often shifted to other behavioral modes such as collecting nectar. Females usually basked for about half an hour in the mornings. The remainder of the day they searched for host plants, oviposited when they found suitable ones, nectared, or rested, usually in the shade on the trunks of pine trees. Therefore, except in the early mornings, most female *Battus philenor* could be grouped at any time during the day into four main behavioral categories: searching for oviposition plants, laying eggs, nectaring, and resting. In this paper ''resting'' is a subjective term, as stationary butterflies may be performing functions such as maturing eggs or digesting food.

It should be noted that searching for oviposition plants is a very distinctive activity (e.g., Rausher, 1978; Papaj, 1986) that cannot be confused with searching for nectar plants. Females searching for ovipositon plants fly low and slowly over the substrate and systematically search an area for hosts by alighting numerous times on hosts and other plants. Females tend to constantly cross their own flight paths by flying in zigzag and circular patterns. When in the nectaring mode, females usually fly fast and directly to a nectar source and, if flowers are sufficiently close, will hop from one flower to another. The question I address here is what external or internal factors may cause shifts among the four main behavioral categories.

To this end, I attempted to determine if ovarian parameters, notably the number of mature eggs carried by females, influenced the relative proportions of females in the four main behavioral categories. Factors that may influence ovarian parameters, such as age, size, fat content, and how many times a female has mated, were also examined.

## MATERIALS AND METHODS

### Study Animals and Site

The pipevine swallowtail is distributed throughout the southern United States and Central America. This study was carried out in the open pine uplands [pine-bluestem savanna of Vogl (1972) and Streng and Harcombe (1982)] of the John Henry Kirby State Forest in Tyler County, Texas. The two host plants, *Aristolochia reticulata* (Aristolochiaceae) and *A. serpentaria*, are small, erect perennial herbs in this habitat. Butterflies were studied during the entire 1986 field season (early March to late May).

### Notes on Dissections

After females were caught they were immediately put on ice or killed to preserve the ovarian state at the time of capture. Like other butterflies, *Battus philenor* typically has eight ovarioles (e.g., Ehrlich and Ehrlich, 1978; Dunlap-Pianka, 1979) coiled up in the posterior abdominal fat tissue, with each ovariole containing a linear arrangement of progressively enlarging follicles. A follicle consists of an oocyte surrounded by nurse cells and enclosed in a follicular envelope. Following the completion of oocyte growth, the follicle cells secrete the chorion, and the mature oocytes ovulate from the follicular envelope into one of the eight branches of the oviduct. In the process of ovulation the follicular envelopes are shed, and they form an orange structure in the ovariole; eggs on the ovipore side of this structure are fully developed, chorionated, and ovulated and ready to be laid. These eggs were counted as mature eggs. Sometimes a few eggs on the other side of the orange structure also appear to have reached their full size but they are not fully chorionated, have not ovulated, and are not counted as mature eggs. Eggs become smaller toward the tops of the ovarioles. Immature ova at the tops of ovarioles are very tiny and difficult to count individually. Counts are presented as the approximate number (within about 5%). Four ovarioles combine into each of two common tubes that finally form the oviduct that ends in the ovipore. Some ovaries were prepared as Fuelgen-stained whole mounts by a modification of the method of King *et al.* (1957) and have been saved in a reference collection.

### Butterflies Observed in the Field

Fifty-two females were collected through the season. Wing wear has been used previously to assess butterfly age in the field (i.e., Watt *et al.*, 1977; Iwasa *et al.*, 1983; Papaj, 1986). For this particular study four wear gradations were used, ranging from 1 for fresh individuals to 4 for old, ragged, scale-bare individuals. Wing length was used as a measure of the size of individuals. The number of mature (developed to full size and chorionated) and immature eggs was counted. Spermatophores contained by nonvirgin females were counted. In cases where several spermatophore fragments were found, they were counted as one spermatophere unless more than one fragment could clearly be identified as a stalk (collum) or the shell-like remains of an older spermatophore (after Ehrlich and Ehrlich, 1978). The fullness of the bursa copulatrix was estimated by examining its contents and rating it on a scale of zero (for completely empty bursae) to three (for full, expanded bursae). The amount of fat in the body cavity was similarly estimated on a scale of zero to three. A simple correlation analysis was run on these characters.

Of these females, 27 were followed at least 20 min before they were collected. Females were searching, ovipositing, nectaring, or resting and, occasionally, being chased by males. A hand-held Radio Shack TRS-80 computer automatically recorded the time and duration, to the nearest second, of each type of behavior. More than 95% of the total observation time corresponded to the four categories of behavior described above. The rest of their time was taken up by basking, avoiding males that attempted to mate with them, avoiding predators (e.g., Odendaal *et al.*, 1987), or flying to other parts of the study site. The number of mature eggs at the beginning of the observation period was calculated for these females by adding any eggs they laid during the observation period to the number they contained when they were dissected.

Of the 27 females observed for at least 20 min, 20% had fewer than 10 mature eggs each and 20% had more than 39 mature eggs. Using these females as representatives of arbitrary extreme categories, I compared the behavior of four females that had fewer than 10 mature eggs ($X = 8.5$; range, 8–9) with that of females that had more than 39 mature eggs ($X = 52.6$; range, 40–72). After arcsin transformations were performed the treatment effect on the relative proportions of time spent resting, nectaring, ovipositing, and searching was studied by multivariate analysis of variance (MANOVA).

## Experimental Procedures

"Full" and "empty" females were obtained by collecting already-mated young females [wing wear rating 1 or 2, meaning 1 to 3 days old (Lederhouse and Odendaal, unpublished data)] in the field and either preventing or encouraging them to lay eggs. Full females were obtained by preventing access to host plants for 36 to 48 h, during which time no oviposition occurred. "Empty" females were obtained by keeping them in cages for 36 to 48 h, then allowing them to oviposit on fresh, young *Aristolochia* for 45 min. As soon as one of these females laid eggs she was placed on another fresh host plant. The first batches often contained more eggs ( > 10) than batches usually observed in the field (Odendaal and Rausher, unpublished data), but the batch size soon decreased to fewer than about five eggs. The tendency to lay wore off after about 30 min, and when a female had been placed on four plants consecutively without ovipositing, she was regarded as empty. Full females were also disturbed by placing them on nonhost plants at a rate similar to that at which host plants were presented to the empty group. Nine empty females were dissected to test this procedure and had significantly fewer eggs than six full ones (empty $X = 7.1$; range, 0–26; full $X = 56.5$; range, 20–122; $P < 0.001$, Mann–Whitney *U* test).

Empty and full females were released in the field and subsequently followed by observers with hand-held computers recording their behavior. Seventeen full females and 12 empty females were followed. After 20 min I again succeeded in collecting five empty ($X = 5.6$; range, 0–18) and four full females ($X = 45.2$; range, 40–52). After arcsin transformations were performed the treatment effect on the relative proportions of time spent resting, nectaring, ovipositing, and searching was again analyzed by MANOVA.

## RESULTS

### Butterflies Observed in the Field

Older females had fewer mature and immature eggs than young females, were more likely to have mated more than once, and had fewer fat reserves (Table I). Larger females had more mature eggs, and the number of spermatophores correlated negatively with the number of mature and immature eggs and positively with the fullness of the bursa copulatrix (Table II).

Unperturbed females with few ( < 10) mature eggs behaved differently than

**Table I.** Descriptive Statistics for Dissected Field-Caught Females[a]

| | Age | Wing size | No. eggs | | No. sperm | Bursa content | Fat |
|---|---|---|---|---|---|---|---|
| | | | Mature | Immature | | | |
| *N* | 52 | 44 | 52 | 52 | 51 | 51 | 50 |
| *X* | 2.44 | 47.29 | 24.71 | 38.92 | 1.39 | 2.31 | 1.98 |
| SD | 1.10 | 3.06 | 17.69 | 13.29 | 0.66 | 1.04 | 1.09 |
| Range | 1–4 | 37–51 | 0–72 | 6–65 | 1–4 | 0–4 | 0–3 |

[a] $N$ = sample size; $X$ = mean; range = min. and max. values.

**Table II.** Simple Correlation Coefficients for Data Summarized in Table I: Age, Wing Size, No. of Mature Eggs, No. of Immature Eggs, No. of Spermatophores, Bursa Copulatrix Content, and Fat Content of Dissected Females[a]

| | Age | Wing size | No. eggs | | No. sperm | Bursa content | Fat |
|---|---|---|---|---|---|---|---|
| | | | Mature | Immature | | | |
| Age | | | | | | | |
| *N* | 52 | 44 | 52 | 51 | 51 | 51 | 50 |
| *r* | 1.00 | 0.19 | −0.33[b] | −0.66[c] | 0.48[c] | 0.25 | −0.75[c] |
| Wing size | | | | | | | |
| *N* | | 44 | 44 | 44 | 43 | 43 | 42 |
| *r* | | 1.00 | 0.36[b] | 0.18 | 0.05 | 0.09 | 0.38 |
| No. eggs mature | | | | | | | |
| *N* | | | 52 | 52 | 51 | 51 | 50 |
| *r* | | | 1.00 | 0.52[c] | −0.34[b] | −0.32 | 0.24[c] |
| No. eggs immature | | | | | | | |
| *N* | | | | 52 | 51 | 51 | 50 |
| *r* | | | | 1.00 | −0.45[c] | −0.30[b] | 0.72[c] |
| No. sperm | | | | | | | |
| *N* | | | | | 51 | 51 | 49 |
| *r* | | | | | 1.00 | 0.47[c] | −0.51[c] |
| Bursa content | | | | | | | |
| *N* | | | | | | 51 | 49 |
| *r* | | | | | | 1.00 | −0.32[b] |
| Fat | | | | | | | |
| *N* | | | | | | | 50 |
| *r* | | | | | | | 1.00 |

[a] $N$ = sample size; $r$ = correlation coefficient.
[b] $P < 0.05$.
[c] $P < 0.001$.

those with many eggs ( $>39$); overall multivariate analysis showed a significant treatment effect on the proportion of time spent by females in different categories (Roy's max. root criterion, $F = 7.06$, $P < 0.025$). The proportion of time spent resting differed significantly between treatments (Table III).

## Experimental Results

For manipulated females there was again a significant overall effect of treatment (Roy's max. root criterion, $F = 19.57$, $P < 0.005$) on the amount of time spent in different categories. The proportion of time spent differed significantly between treatments for searching and resting and to a level of 7% significance for nectaring (Table IV). The number of eggs contained by manipulated females was within the range found in the field (see Table II).

**Table III.** Analysis of Variance of the Proportion of Females Resting, Nectaring, Ovipositing, or Searching for Host Plants for Females That Contained Few (< 10) or Many (>39) Mature Eggs; $N = 8$ and $N = 4$ for "Full" and "Empty" Treatments[a]

A

| | Behavior | | | |
|---|---|---|---|---|
| Treatment | Resting | Nectaring | Ovipositing | Searching |
| Empty | 38.75 | 0.51 | 1.00 | 58.50 |
| SD | 44.22 | 1.00 | 2.00 | 41.55 |
| Full | 4.50 | 1.37 | 11.50 | 82.62 |
| SD | 12.72 | 2.87 | 23.58 | 24.15 |

B

| Behavior | Treatment SS | Error SS | $F$ | $P$ |
|---|---|---|---|---|
| Resting | 1.54 | 1.00 | 6.50 | 0.0289 |
| Nectaring | 0.001 | 0.10 | 0.13 | 0.7267 |
| Ovipositing | 0.09 | 0.78 | 1.16 | 0.3070 |
| Searching | 0.45 | 1.85 | 2.46 | 0.1477 |

[a] Units in A are mean proportions. Treatment df = 1; error df = 10.

**Table IV.** Analysis of Variance of the Proportion of Females Resting, Nectaring, Ovipositing, or Searching for Host Plants for Manipulated Females That Were "Full" and "Empty"; $N = 17$ and $N = 12$ for Full and Empty Treatments[a]

A

| | Behavior | | | |
|---|---|---|---|---|
| Treatment | Resting | Nectaring | Ovipositing | Searching |
| Empty | 83.41 | 2.16 | 1.66 | 12.75 |
| SD | 25.40 | 5.70 | 2.67 | 22.09 |
| Full | 34.05 | 11.41 | 3.47 | 51.05 |
| SD | 40.57 | 16.60 | 9.93 | 38.51 |

B

| Behavior | Treatment SS | Error SS | $F$ | $P$ |
|---|---|---|---|---|
| Resting | 3.41 | 6.29 | 14.63 | 0.0007 |
| Nectaring | 0.19 | 1.47 | 3.55 | 0.0705 |
| Ovipositing | 0.00 | 0.68 | 0.00 | 0.9832 |
| Searching | 2.08 | 5.02 | 11.18 | 0.0024 |

[a] Units in A are mean proportions. Treatment df = 1; error df = 27.

# DISCUSSION

Insect behavior is extremely variable. Studies on sources of behavioral variation have concentrated primarily on behavior associated with locating and selecting host plants, and they point to either of two causes (for review, see Rausher, 1985). Individuals are genetically different with respect to a particular behavior studied, or they may differ because they have experienced different environments as either adults or juveniles. Rausher (1985) notes that although it is often possible to determine experimentally whether behavioral variation is genetic or environmental in origin, it is seldom clear what determines the relative proportions of individuals in a population that exhibits a particular behavioral phenotype. The work described here shows that, in addition to genetic and environmental causes, physiological parameters need to be taken into account in interpreting female behavior.

The number of mature eggs a female *Battus philenor* carries influences her behavior. Females with many eggs are likely to spend a larger proportion of their time searching for hosts to oviposit on than females with fewer eggs. One intuitive explanation is that females carrying many eggs that are ready to be laid will devote their time to finding the most favorable localities and oviposit them as soon as possible. Female *Battus philenor* apparently need to spend considerable time locating and selecting host plants (e.g., Rausher, 1980; Rausher and Papaj, 1983; Rausher and Odendaal, 1987), and there may be a premium on locating suitable hosts quickly, as the presence of other females' eggs inhibits oviposition (Rausher, 1979). Time constraints have been mentioned for several species (e.g., Hayes, 1981; Courtney and Duggan, 1983; Kingsolver, 1983; Murphy *et al.*, 1983). On the other hand, females with none or only a few eggs ready to be laid will probably spend their time acquiring energy and nutrient resources for somatic maintenance and egg growth and will spend less time searching for plants on which to lay their eggs.

Various physical parameters are important in *Battus philenor* female reproductive physiology. Females eclose with no mature eggs and a limited number of undeveloped oocytes, unlike *Heliconius*, which continue to manufacture new oocytes when sufficient nutrients are available (Dunlap-Pianka, 1979). Larger *Battus philenor* females have more eggs. Older females have fewer mature and immature eggs and may possibly respond differently to "egg load." The relationship of such parameters to the influence of egg load needs to be investigated, since they may help explain behavioral variation between individuals of different ages. Older females will, on average, have mated more than younger females. The number of spermatophores correlates negatively with the number of mature and immature eggs, presumably because older females have more spermatophores. There apparently is some advantage in mating more than once for *Battus philenor* females, and the effect of subsequent matings on ovarian development and "egg load" is under investigation.

Ovarian dynamics, particularly the development of mature eggs, may form a bridge between environmental sources of variation and its phenotypic expression. Environmental conditions are known to affect ovarian development (e.g., Stern and Smith, 1960; Barker and Herman, 1976; Gossard and Jones, 1977). If the number of mature eggs influences behavior in other species as strongly as it appears to in *Battus philenor*, then female reproductive physiology may be a pathway between environmental parameters and behavioral phenotypes that cannot be ignored by insect behavioral ecologists.

## ACKNOWLEDGMENTS

Mark Rausher introduced me to the *Battus philenor* system, gave statistical advice, and commented on the manuscript. Zenon Cano and Carlos Cordero assisted in the field. Helen Dunlap-Pianka painstakingly explained the finer points of butterfly ovarian dynamics to me. Gary Lacox and the Texas Forest Service facilitated our work in the Kirby State Forest. This work was sponsored by NSF Grant BSR 8406870.

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