

## EGG RECOGNITION: ITS ADVANTAGE TO A BUTTERFLY

BY MARK D. RAUSHER\*

*Department of Entomology, Cornell University, Ithaca, New York 14853*

**Abstract.** Ovipositing females of the pipevine swallowtail butterfly, *Battus philenor*, detect the presence of eggs laid by other females on their host plants. The presence of eggs on a plant inhibits oviposition by a female that discovers it. The selection pressure responsible for the evolution and maintenance of discrimination against plants with eggs appears to be lower survival from egg to adult of eggs laid on plants already containing eggs than on plants without eggs.

Several authors have proposed that a preference in an ovipositing insect for a particular host plant or group of host plants is the result of natural selection for behaviour that discriminates against plants on which egg and larval survival is poor (Wiklund 1975; Chew 1977; Rausher 1978a, b; Smiley 1978). Although most empirical tests of this proposal have examined preferences for plants of one species over plants of another species, there is reason to suspect that ovipositing insects may also discriminate among plants within one species. Different plants of the same species may differ greatly in suitability for larval growth and survival (Singer 1972; Dixon 1976; Edmunds & Alstad 1978). If such differences are consistent and detectable by ovipositing insects, it is likely that those insects will evolve behaviours that lead to preferential oviposition on plants on which juvenile survival is greatest.

The presence of other herbivores on a plant may render that plant less suitable for juvenile growth and survival than a conspecific plant without herbivores (Dixon 1973; McClure & Price 1975; Mitchell 1975). When the amount of edible foliage per plant is small relative to the requirements of one larva, or when larvae are cannibalistic, it is likely that survivorship from egg to adult of an egg laid on a plant already containing other eggs or larvae will be lower than that of an egg placed on a plant free of herbivores. It may thus greatly benefit an ovipositing female to discriminate among host plants with respect to the presence or absence of other herbivores.

The host plants of the pipevine swallowtail butterfly, *Battus philenor*, in southeast Texas are erect perennial herbs in the genus *Aristolochia* (Aristolochiaceae). Because one plant rarely has enough edible foliage to support the growth of a larva to maturity, each larva must abandon its

first host plant and wander until it discovers another host. Early instar larvae cannot move as far as larger larvae, and it is likely that the probability of discovering another host plant increases with larval size. Females that lay eggs only on plants that do not contain other eggs or larvae may thus maximize the amount of food available to the earliest instars. Their larvae would be larger upon leaving the first host plant than larvae produced by females that oviposit on plants already containing eggs or larvae. The evolution of the ability to discriminate against plants with eggs might therefore be expected in *B. philenor*. In this study I examined this expectation. In particular, I asked the following two questions: (1) is juvenile survival lower for eggs laid on a plant already containing eggs than for eggs laid on a plant not containing eggs? and (2) do females in nature discriminate against plants with eggs and oviposit on egg-free plants with greater frequency than on plants already containing eggs?

### Methods

In southeast Texas, the pipevine swallowtail is bivoltine. The first brood of adults emerges in mid-March and completes egg laying by mid-April. During the first brood, females lay most of their eggs on *A. reticulata* and the remainder on *A. serpentaria*. By the second brood, which begins in mid-May and extends until the end of May, females have switched host preference and lay most eggs on *A. serpentaria*, even though *A. reticulata* is still present.

I studied egg and larval survival of naturally laid eggs during the second brood in 1977 at the Kirby State Forest near Kountze, Texas (Rausher 1978a). By following females I was able to observe them discovering and ovipositing on *A. serpentaria* plants. Each plant on which a female oviposited was marked with coloured flagging and was visited daily to monitor the

\*Present address: Department of Zoology, Duke University, Durham, North Carolina 27706.

disappearance rates of eggs and larvae. A large sample of naturally laid eggs was obtained by this method, but virtually all were laid on plants that did not already have eggs (first-laid eggs). During the daily censuses I occasionally found eggs that had not been on the plant the previous day (second-laid eggs). I monitored the rate at which these eggs disappeared and compared it to the disappearance rate of first-laid eggs. Ideally, a sample of second-laid eggs should have been obtained by following ovipositing females, as was done for the first-laid eggs, but the infrequency with which females oviposited on plants containing eggs precluded this method.

Because eggs were not all laid on the same day, eggs and larvae did not all experience identical environmental conditions at corresponding stages of development. As a result, the duration of a given instar is shorter for some larvae than for others. It is therefore biologically unrealistic to compare the fraction of eggs or larvae remaining in the two treatments a certain number of days after an egg is laid. A better method is to compare the fraction of larvae that remain on the plant at a given developmental stage. Moulting is a convenient marker of developmental progress, since it tends to occur at a well-defined size that is independent of previous developmental rate (Wigglesworth 1972). I compared the fraction of larvae remaining on plants in the two treatments at two different stages during each instar. The first stage is immediately following a moult (day 0) and the second is one day after the moult (day 1).

Larval disappearance rates are not necessarily equivalent to mortality rates. If small and large larvae have an equal probability of locating a new host plant, early disappearance may not affect overall larval survivorship. If, on the other hand, the probability that a larva discovers another host plant increases as the larva grows, early disappearance will correspond to low overall survival regardless of whether disappearance is due to death on the host or to dispersal from the plant. To examine the relationship between larval size and the ability to discover new host plants, I set up a  $16 \times 16\text{-m}^2$  grid of food plants (*A. reticulata*) in their natural pine upland habitat at Kirby Forest (see Watson 1975 for a description of habitat). One plant was placed in the ground at the corner of each  $1\text{-m}^2$  square within the grid and all other host plants were removed (Fig. 1). At 09.00 hours

on 2 June 1977, 75 second- and 75 third-instar larvae were released in the centre of the grid, three larvae of each instar at each of 25 release points (Fig. 1). At 0.5-h intervals I examined each host plant in the grid for larvae and removed any I found. Since preliminary experiments indicated that the total number of larvae discovering plants is not different after 24 h than after 6 h, I terminated the experiment at 15.00 hours. Because I performed the experiment when very few second- and third-instar larvae were present in the field, I am confident that all larvae found on the grid plants had been released by me. From the 0.5-h censuses I constructed a cumulative discovery curve for each instar. The curves represent the probability that a larvae discovers a host plant in the grid within a given period of time.

I measured the response of ovipositing females to plants with and without eggs in two ways. If the presence of eggs on a plant decreases the probability that a female will oviposit once she discovers it, the rate at which new eggs appear on plants in the field should be greater for plants with no eggs than for plants with eggs. To test this hypothesis, I performed three separate experiments. In each I located and marked a certain number of *A. reticulata* plants with eggs on them and an equal number of *A. reticulata*

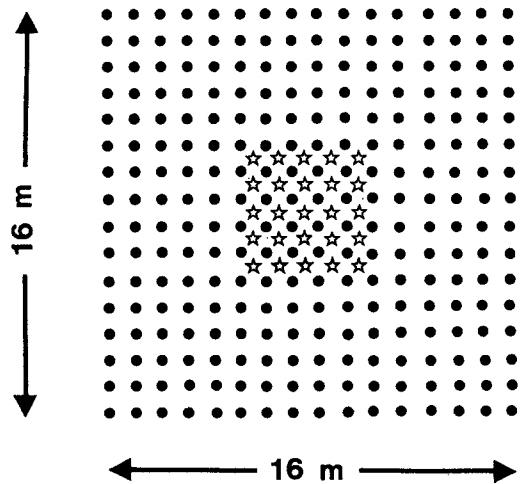


Fig. 1. Grid design for testing relationship between larval size and ability to locate host plants. Each solid circle represents one host plant. Plants were placed in the ground in their natural pine upland habitat with minimal disturbance to the natural vegetation. Each star represents the point of release of three larvae of each instar.

plants without eggs. I attempted to match each plant containing an egg with one of similar size lacking eggs. Because the presence of the vegetation immediately surrounding host plants affects the rate at which females discover them (Rausher, unpublished data), I attempted to make all plants equally 'apparent' (*sensu* Feeny 1976) to searching females by removing the vegetation from an area approximately 0.5 m in diameter surrounding each plant. Four days later I examined each plant for new eggs and compared the fractions of plants having eggs laid on them in the two treatments.

I also compared the response of females to plants with and without eggs by direct observation of ovipositing females in the field. After a female had discovered a host plant and either laid an egg or resumed search flight without ovipositing, I examined the plant for eggs. Because I could see exactly where the female placed her egg cluster, I could determine which eggs on the plant, if any, she had not laid, and hence whether any eggs were present before she discovered the plant. During brood 1, 1977, I recorded 338 discoveries (all on *A. reticulata*; the few discoveries of *A. serpentaria* plants were ignored in order to eliminate effects due to host plant species), and during brood 2, 1977, I recorded 112 discoveries (all on *A. serpentaria*).

## Results

### Egg and Larval Survival

The overall disappearance rate of eggs and larvae was significantly greater on *A. serpentaria* initially containing eggs than on plants lacking other eggs (Fig. 2). More than twice as many first-laid eggs as second-laid eggs survived to the second and to the third instar. Disappearance rates can also be compared for the egg stage alone and for the larval stage alone. More than 45% of the second-laid eggs disappeared before hatching, whereas the comparable value for first-laid eggs is only 19% ( $G = 16.73$ ,  $P < 0.001$ ,  $G$ -test, Sokal & Rohlf 1969). Of the larvae that hatch, almost twice as many from first-laid eggs as from second-laid eggs survive to the second instar and over 30% more survive to the third instar ( $\chi^2_2 = 6.003$ ,  $P < 0.05$ , Kolmogorov-Smirnov two-sample test, Siegel 1956).

The exact cause of increased disappearance rates of second-laid eggs and larvae is not known, but it is probably a combination of cannibalism and displacement by larvae that hatch from first-laid eggs. Although larvae do not actively seek

eggs, they will consume foliage to which eggs are attached. It seems fairly safe to assume that the eggs are eaten along with the leaf. First- and second-instar larvae are obviously more mobile than eggs and can move out of the way of larger larvae feeding on the same leaf. The presence of larger larvae reduces the amount of leaf material present, however, which probably explains why proportionately fewer second-laid eggs reach second and third instar than reach the first instar (Fig. 2).

Large larvae discover new host plants more quickly than do small larvae. In the larval release experiment, the cumulative discovery curves levelled off for both instars within approximately 4 h (Fig. 3). This fact indicates that most larvae that were going to discover host plants had done so within 4 h. Third-instar larvae were three to four times more likely to discover another host plant than were second-instar larvae. It would thus seem that

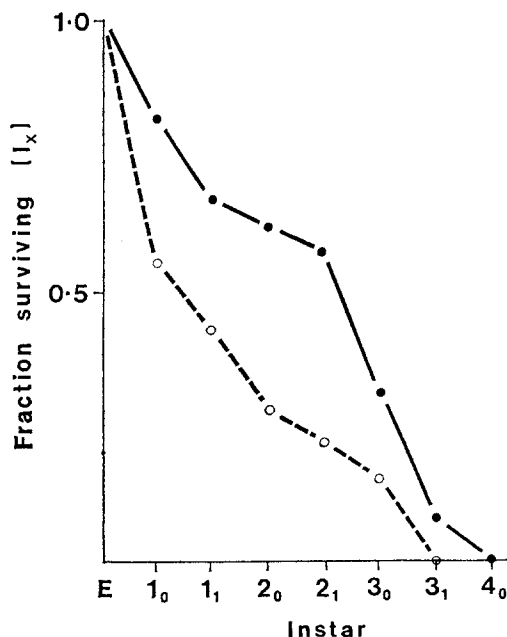


Fig. 2. Fraction of original egg cohort remaining on *A. serpentaria* plant at different stages of development. Subscripts refer to day after moult to indicated instar. Solid circles: eggs laid on plants on which other eggs were not present ( $N = 170$ ). Open circles: eggs laid on plants on which other eggs were present at time of oviposition ( $N = 33$ ). Second-laid eggs and larvae disappear from plants more rapidly than first-laid eggs and larvae ( $\chi^2_1 = 13.78$ ,  $P < 0.001$ , Kolmogorov-Smirnov Two-Sample Test).

small larvae take longer to discover a new host plant and that they are therefore more likely to die of starvation or predation before reaching a new host than are large larvae. My observations on wandering larvae in the field suggest that the caterpillars are unlike many other insects (e.g. Jacobson 1966; Schoonhoven 1972; Yamamoto 1974) in that they do not respond at a distance to chemical odours emitted from their host plants; rather they seem to locate their host plants by wandering randomly until chemoreceptors in the maxillary palpi or antennae contact a host plant. The greater speed and larger size of third-instar caterpillars probably decrease the time that lapses before they 'bump into' a host plant, and hence increase discovery rates.

These results indicate that second-laid eggs have a lower probability of surviving to the adult stage than do first-laid eggs. Disappearance from the host plant can be divided into two stages: disappearance of eggs and disappearance of larvae. The greater rate of disappearance of second-laid eggs as compared with first-laid eggs almost certainly represents increased mortality. The additional eggs that disappear are either eaten by other larvae already on the plant or are knocked off the plant by those larvae, with the larvae hatching from them unable to relocate the plant. On the other hand,

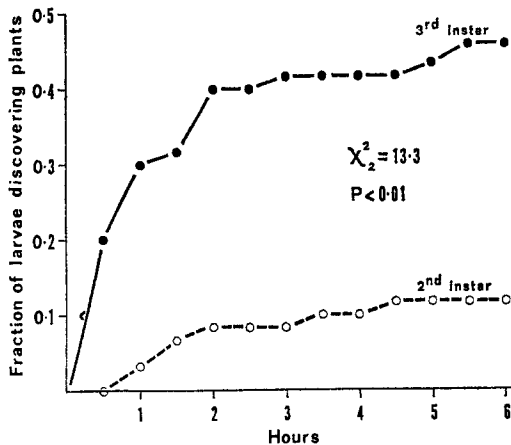


Fig. 3. Larger larvae have a greater probability of locating a new host plant than do smaller larvae. Larvae were placed out in grid of host plants at 09.00 hours. Points represent cumulative fraction of 75 larvae that had appeared on host plants after a given elapsed time. Solid circles: third-instar larvae. Open circles: second-instar larvae. ( $\chi^2 = 13.3$ ,  $P < 0.01$ , Kolmogorov-Smirnov Two-Sample Test).

the increased rate of disappearance of larvae hatching from second-laid eggs may represent either greater mortality while on the plant or earlier dispersal from the host plant. Even if early dispersal accounts entirely for the increased disappearance rate of larvae hatching from second-laid eggs, however, earlier disappearance ultimately leads to a lower larval survivorship to the adult stage. The results depicted in Fig. 3 imply this equivalence of earlier larval disappearance and lower larval survival, since larvae that disappear as early instars are smaller and less likely to survive long enough to discover a new host plant than larvae that disappear at a later stage. The combined effects of greater egg mortality and greater larval mortality of second-laid eggs and the larvae they produce means that females that do not lay eggs on plants that already contain other eggs will have a greater fraction of their eggs survive to the adult stage than females that oviposit on plants containing eggs.

Although disappearance rates were determined only for eggs and larvae on *A. serpentaria*, the results would almost certainly be the same for eggs laid on *A. reticulata*. The average *A. reticulata* plant during the first brood contains no more, and probably less, edible foliage than the *A. serpentaria* plants used in the experiments (Rausher 1978b). Consequently, larval competition for the foliage on a single *A. reticulata* plant would be, if anything, more intense than is indicated by these results.

### Female Behaviour

When *Aristolochia* plants are exposed to *B. philenor* females, eggs are laid on a greater fraction of plants without eggs than on plants already containing eggs (Table I, experiments A-C). The most reasonable conclusion to be drawn is that females can detect the presence of eggs on a plant and that oviposition is inhibited by such detection. This conclusion is verified by my direct observations of ovipositing females. During both broods 1 and 2 in 1977, once a female had discovered a plant she was much more likely to oviposit on it if eggs were not already present than if eggs were present (Table I, experiments D and E).

When a female *B. philenor* discovers a host plant, she spends up to several minutes climbing about the plant, apparently searching for eggs. Normally she begins at the top of the plant and moves down the stem; when she reaches the ground she flies back to the top of the plant and

moves down the stem again, usually on a different side of the plant. Because eggs are often placed on the underside of a leaf, they cannot be seen by a female until she is below the leaf. A female often explores a plant until she reaches a position that would permit her to see the eggs on it, and then suddenly flies away and resumes searching. While not conclusive, these observations suggest that *B. philenor*, like some other butterflies (Gilbert 1975), detects eggs primarily by vision and not by any associated scent. The importance of vision in host-plant search by *B. philenor* (Rausher 1978a) lends credence to this suggestion.

### Discussion

The newly hatched larvae of many phytophagous insects are able to move only small distances in search of suitable food plants. Host-plant choice exercised by an ovipositing female can therefore greatly influence her success at producing adult offspring. A preference for a particular host plant or group of host plants presumably reflects selection for avoiding plants on which eggs and larvae survive poorly and for accepting plants on which they survive well (Wiklund 1975; Chew 1977; Rausher 1978a, b; Smiley 1978). Differences in suitability for insect growth and survival exist both among plants of different species (Soo Hoo & Fraenkel 1966a, b; Caswell & Reed 1975; Chew 1975; Wiklund 1975; Fox & Macauley 1977; Slansky

& Feeny 1977; Rausher 1978b; Smiley 1978) and among plants within the same species (Singer 1972; Dixon 1976; Edmunds & Alstad 1978). Ovipositing insects should therefore often discriminate both among plant species (e.g. Singer 1971; Chun & Schoonhoven 1973; Bernays & Chapman 1977; Rausher 1978a; Smiley 1978) and also among conspecific plants (e.g. Rothschild & Schoonhoven 1977).

The pipevine swallowtail possesses a suite of behaviours that enable females to lay eggs on the plants on which egg and larval survival is greatest (Rausher 1978a). Most of these behaviours, including those involved in search-image formation, seasonal shift in host preference, and ovipositing only on plants that have some immature foliage, permit females to discriminate among different species of plants. Egg detection and rejection of plants with eggs permit females to select the most suitable plants on an even finer scale, namely among plants within a particular species.

When host plants are abundant and only a small fraction have eggs on them, a female sacrifices little by passing up those that contain eggs, since she soon finds others that are more suitable. When there is extreme competition for oviposition sites, however, a female that rejects plants because of the presence of eggs will lay very few herself. Since second-laid eggs have some chance of producing adult butterflies, a female would produce more successful offspring by not rejecting plants with eggs. It would therefore be reasonable to expect that a female's oviposition response would become less inhibited by the presence of eggs on a plant as the time since her last oviposition increased. While my data do not permit a test of this expectation in *B. philenor*, studies on other insects indicate that oviposition specificity decreases as motivation rises (Singer 1972; Mitchell 1975). This may explain why *B. philenor* females sometimes oviposit on plants with eggs, especially during the second brood, when competition for oviposition sites is intense (Rausher 1978b).

Rothschild & Schoonhoven (1977) recently demonstrated that oviposition in three species of butterflies is deterred by the presence of eggs on their host plants in cages in the laboratory. The relevance of their results to field situations is difficult to evaluate, however, since it is not known how the egg loads used in their experimental treatments compare to the egg loads found on plants in nature. They suggest

Table I. Fraction of Host Plants Oviposited on by Female *B. Philenor* According to Whether Eggs Are Already Present on the Plant

Experiment*	Probability of ovipositing on		P**
	Plants with eggs	Plants without eggs	
A	0.029	0.361	< 0.01
B	0.000	0.087	< 0.05
C	0.043	0.170	< 0.05
D	0.024	0.325	< 0.001
E	0.095	0.700	< 0.001

\*A. 35 plants per treatment. B. 46 plants per treatment. C. 47 plants per treatment. D. Females followed during brood 1, 1977; based on 388 plants discovered: 255 without eggs, 83 with eggs. E. Females followed during brood 2, 1977; based on 112 plants discovered: 70 without eggs and 42 with eggs. See text for further details.

\*\*G-test.

that the function of discrimination against plants bearing eggs is to prevent 'overloading' of the plant, a hypothesis that is confirmed in this study of *B. philenor*.

The presence of conspecific individuals on the same host plant lowers the growth and survivorship rates of many herbivorous insects. Large aphid colonies can lead to host plant senescence and the death of recently produced nymphs (Dixon 1973). Since large colonies can be produced from a single aphid in a short period of time, the presence of even one individual on a plant can represent a potent threat to the success of a colonizing individual. For the bean weevil *Callosobruchus maculatus*, the survivorship of the second egg laid on a mung bean, its normal host, is only half that of the first egg laid (Mitchell 1975). For leaf hoppers in the genus *Erythroneura*, reproductive success and juvenile survival is inversely correlated with the number of individuals present on a leaf of the host plant (McClure & Price 1975). Under such conditions, egg-laying females that discriminate against plants containing many herbivores would enjoy a greater reproductive success than females that do not discriminate (Mitchell 1975). When a food plant has much more than enough foliage to support the growth of a larva, it seems less likely that eggs laid by different females will experience severe competition. I would thus expect discriminatory behaviour to evolve primarily in cases involving hosts that are small relative to the requirements of a developing larva or, in the case of aphids, to a developing clone.

Most reported cases of discrimination against the presence of eggs or larvae by insects appear to conform to this expectation. Many species of parasitoids respond to marking pheromones left by females that previously laid eggs on or in a host and do not oviposit, probably because multiple parasitism of hosts often leads to lowered survival of the second parasitoid larva (Price 1970, 1975; Vinson & Guillot 1972; Vinson 1976). Subsequent oviposition by the apple maggot fly, *Rhagoletis pomonella*, is inhibited by a pheromone laid down by a female after she lays an egg in a fruit. When the fruit is small (15-mm-diameter cherries), inhibition is strong and long-lasting, whereas when the fruit is large (55-mm-diameter apples), inhibition is weak (Prokopy 1972). The three species of butterflies studied by Rothschild & Schoonhoven (1977) are all herb feeders. In at least one, the monarch, *Danaus plexippus*,

one larva may be capable of defoliating a milkweed plant, thereby reducing the amount of food available to younger larvae present on the same plant. The food plants of *B. philenor* in southeast Texas are not large enough to support the complete development of one larva. In the Gomez Farias region of Tamaulipas, Mexico, on the other hand, the host plants of *B. philenor* are large, procumbent perennial herbs that can support the complete development of many larvae. Moreover, heavy predation on eggs and young larvae prevents *B. philenor* from defoliating its host plants and thus suppresses any potential competition between eggs laid on the same plant. In this area *B. philenor* does not exhibit any apparent egg recognition behaviour (personal observation). The differences between the behaviours of individuals in the Texas and Mexican populations suggest that discrimination against plants with eggs is an evolutionarily labile behaviour that appears only under certain circumstances. This study demonstrates that strong competition for larval food plants is one such circumstance.

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