HOST ABUNDANCE, JUVENILE SURVIVAL, AND OVIPOSITION PREFERENCE IN BATTUS PHILENOR

MARK D. RAUSHER

Department of Entomology and Section of Ecology and Systematics,
Cornell University, Ithaca, New York 14853

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Many phytophagous insects are highly specific with respect to the plants on which they lay eggs, restricting oviposition to plant species within one family or group of related families (Brower and Brower, 1964; Ehrlich and Raven, 1964; Eastop, 1973), or even to species or groups of species within a particular family or genus (Singer, 1971; Janzen, 1974; Wiklund, 1974, 1975; Benson et al., 1976; Chew, 1977; Ives 1978; Smiley, 1978). Although the proximate cues used for host selection by ovipositing females are known for some highly specific species (Gupta and Thorsteinson, 1960; Singer, 1971; Staedler, 1974; Nishida, 1977; Ichinose and Honda, 1978; Rausher, 1978), little is known about the advantages associated with preferring to lay eggs on some species of plants rather than on others. In this study I evaluate two alternative hypotheses that account for oviposition preference in a butterfly.

Females of the pipevine swallowtail butterfly, Battus philenor, search preferentially at any one time for only one of their two host plants in east Texas (Rausher, 1978). One hypothesis that can explain this search preference is that it ensures that females lay most of their eggs on the plant species on which eggs and larvae have a greater probability of surviving to the adult stage (Chew, 1975, 1977; Feeny, 1975; Gilbert and Singer, 1975; Wiklund, 1975; Smiley, 1978). In some situations, however, the host species on which juvenile survivorship is greater may be rarer than other potential host species. Under such circumstances, the advantage gained by preferentially searching for and ovipositing on the plant species on which juvenile survivorship is greater may be more than offset by the disadvantages associated with searching for the rarer host species. If females have a short life expectancy, for example, they may discover fewer plants and lay fewer eggs before dying if they search preferentially for the rarer host species than if they search preferentially for the more abundant host. Consequently, a second hypothesis that accounts for a specific search preference in ovipositing B. philenor females is that it ensures they search for and lay most of their eggs on the more abundant plant species. Although these two alternatives are not necessarily mutually exclusive, it has been possible to distinguish between them in this study.

METHODS

Experimental Organisms

The pipevine swallowtail, B. philenor (Papilionidae: Troidini), is distributed throughout much of the southern United States and northern Mexico. Throughout its range it feeds exclusively on plants in the genus Aristolochia. In east Texas the two host plants, A. reticulata and A. serpentaria, are small, erect perennial herbs that flower and set seed underground. The two species grow sympatrically in the open longleaf pine uplands (see Watson, 1975, for a description of the habitat) and can be distinguished easily by the shape of the leaves. A. reticulata has broad, ovate leaves, while A. serpentaria has long, narrow, grass-like leaves. Individual plants seldom produce enough foliage to support the complete growth and development of one larva.
The above-ground parts of both plant species die back to the ground at the end of the growing season. Some time in mid-March they begin producing new stems and leaves. The pipevine swallowtail breaks pupal diapause and emerges to form the first adult brood just as the first new leaves are being produced by its host plants. First-brood females are common between about March 15 and April 15 (Rausher, 1979a), during which time they can be observed searching for host plants and laying small clusters of eggs (\(\bar{x} = 2.2\) eggs per cluster). About a week after being laid the eggs hatch and the first-instar larvae being feeding. When a larva has consumed all edible foliage on a plant, it leaves that plant and moves on the ground through the vegetation until it locates another. A searching larva will feed on either species of host plant, regardless of which species it fed on initially (Rausher, 1979a). A larva must often discover and feed on at least 25 different plants to obtain enough food to complete its development. Larval mortality is high during movement between plants, and smaller larvae are less likely to discover new plants than are larger larvae (Rausher, 1979c). Most of the surviving larvae pupate by early May. Beginning around May 5 a second brood of adults emerges and lays eggs until about June 1. The larval offspring of second-brood females feed on many different Aristolochia plants during their growth and development. The larval offspring of second-brood adults enter pupal diapause by late June or early July and do not emerge again until the following spring (see Rausher, 1979a, for a more complete description of the phenology of B. philedor and its host plants).

**Study Site**

This study was performed during March–August, 1977 and March–April, 1978 in an area of open longleaf pine upland habitat at the John Henry Kirby State Forest, located approximately 24 km north of Kountze, Texas, on U.S. Highway 69. Kirby State Forest is an area approximately 1.6 km (1 mi) square, consisting mostly of longleaf pine woods. Although the land was once logged, much of it has not been disturbed for over 40 years. Periodic burning has maintained much of the vegetation characteristic of the open longleaf pine uplands and has excluded many of the species that often invade this habitat when natural fires are suppressed (e.g., elements of the beech-magnolia-loblolly forest community; Watson, 1975).

**Determination of Host Preferences**

To determine the proportion of Aristolochia plants discovered and oviposited on that were A. reticulata and A. serpentaria, I observed B. philenor females searching for oviposition sites during the first and second broods in 1977 and during the first brood in 1978. All females were observed within an approximately 32-ha (80 ac) area of open pine woods bounded on two sides by dirt roads and on two sides by fire lanes. Observations were made only on sunny days (less than 50% cloud cover) between the hours of 1000 and 1500. I chose individual females for observation by walking in a circular path through the observation area until I sighted a searching female. The female was then followed for 30 min or until she flew out of the observation area. Once observation of a female had ended, I resumed walking along the circular path until I sighted another female, which I then followed. By remaining about 3 m from a female as she flew slowly over the herbaceous vegetation, I could observe each plant on which she alighted (=discovered) and each act of oviposition. For each discovery and oviposition, I recorded the time from the beginning of observation and the plant species. The proportions of the total egg clusters that were laid on each plant species by first- and second-brood females were compared with a G-test (Sokal and Rohlf, 1969). A similar comparison was performed for the proportion of plants that each species comprised out of the total number of host plants discovered.

Search preference was measured for
brood-1 females (1978) and brood-2 females (1977) by determining the predominant search image formed by females during each brood. Because individual females search preferentially for one leaf shape or the other at any one time, they tend to alight on and lay eggs on one host species to the exclusion of the other. Searching females reveal the shape of the leaf for which they are searching by periodically alighting on and “tasting” plants that are not in the genus Aristolochia. The Response Coefficient of a female measures the fraction of nonhost plants alighted on that have broad leaves and thus measures the degree of search preference for broad-leaved plants. Low values (0.0–0.6) of the Response Coefficient indicate that a female is searching preferentially for host plants with narrow leaves (A. serpentaria), while high values (0.6–1.0) indicate a preference for host plants with broad leaves (A. reticulata; Rausher, 1978).

Response Coefficients were measured as described in Rausher (1978) for brood-2 females in 1977. Because it was not known during the first brood in 1977 that ovipositing females form search images, the Response Coefficient for first brood females was measured in 1978. The frequency distribution of Response Coefficients for brood-1 and brood-2 females were compared with a two-tailed Kolmogorov-Smirnov two-sample test (Siegel, 1956).

**Measurement of Plant Abundance**

The relative abundances of the two host species were estimated during the first week of May, 1977. Five parallel transects, 20 m apart, were laid out across the observation area. At 20-m intervals along each transect I marked a 5 m × 5 m quadrat and counted the number of individuals of each Aristolochia species in the quadrat. A total of 40 quadrats was sampled. The mean densities of the two species were compared with a matched pairs t-test (Sokal and Rohlf, 1969). As a measure of the similarity in spatial distribution of the two plant species within the observation area I computed the Spearman rank correlation coefficient between the numbers of individuals per quadrat of each species.

The quadrat analysis provides a reasonable estimate of the relative abundances of the two host plants available to ovipositing females during early May. Because the two Aristolochia species differ slightly in their leafing phenology and in their susceptibility to being eaten, however, their relative abundances may fluctuate throughout the season. I estimated this fluctuation by marking 100 plants of each species in September, 1976 with colored marking flags. Beginning in early March, 1977 the plants were censused weekly to determine the fraction of plants that had at least one leaf and hence were available for oviposition. From these censuses I constructed a seasonal curve of abundance for each species. The mean density, \( \bar{A}_t \), at any time \( t \) during the season is given by the formula,

\[
\bar{A}_t = \frac{p_t}{p_{n,x}} \times \bar{A}_{n,x}
\]

where \( p_t \) is the fraction of plants that have at least one leaf at a time \( t \), \( p_{n,x} \) is the fraction of plants that have at least one leaf at the May 2 plant census, and \( \bar{A}_{n,x} \) is the mean plant density at the time of the quadrat census. Since the quadrat census was done at a time nearer to the May 2 plant census than to any other, equation (1) is an estimate of absolute plant density throughout the season. The standard error of \( \bar{A}_t \) is

\[
\text{SE}(\bar{A}_t) = \bar{A}_t [CV(p_t)^2 + CV(p_{n,x})^2 + CV(\bar{A}_{n,x})^2]^{1/2}
\]

where \( CV(x) = [\text{Var}(x)]^{1/2}/\bar{x} \).

**Plant Discovery Rates**

The rate of discovery of host plants was compared for females searching for broad-leaved host plants and females searching for plants with narrow leaves. The second-brood females followed in 1977 were classified as searching for narrow-leaved plants if their Response Coefficient was between 0.0 and 0.6; they were classified
as searching for broad-leaved plants if their Response Coefficient was between 0.6 and 1.0 (Rauscher, 1978). For each female, plant discovery rate was measured as the total number of plants of both species alighted on divided by the total time the female was observed. Discovery rates for the two types of females were compared with a Wilcoxon two-sample test (Sokal and Rohlf, 1969). A similar comparison was made for the brood-1 females followed in 1978.

**Measurement of Host-plant Suitability**

The measure of host-plant suitability used in this study is the rate at which eggs and larvae disappear from host plants. Larvae may disappear from a plant for either of two reasons: they may die while on the plant, or they may leave the plant and begin searching for another. I have shown in a previous paper (Rauscher, 1979c) that small larvae that leave a host plant have a lower probability of discovering another plant, and hence a lower probability of surviving, than do large larvae. Consequently, disappearance of larvae at smaller sizes (i.e., at greater rates) from one host species implies a lower probability of survival for eggs laid on that species, regardless of what fraction of disappearances is due to actual mortality on the plant and what fraction to larvae leaving the original host plant, provided that the spatial distribution of the two host plants is similar.

Disappearance rates for the progeny of second-brood females were measured during late May and early June, 1977 by marking all plants on which observed females had laid eggs. The observed females were the same individuals that were followed for determining host-plant preferences. Each plant on which a female laid an egg cluster was censused daily. At each census the number of eggs or larvae remaining from the previous census, their positions, and the instar of each larva were recorded. Since ovipositing females seldom oviposit on plants on which other eggs or larvae are already present (Rauscher, 1979c), and since small larvae seldom wander onto host plants, individuals present on a plant on one day were assumed to be the same individuals present on the previous day. The censusing of a plant ended when no individuals were seen for two consecutive days. The fraction of individuals remaining on a plant was compared for the two host-plant species at two stages during each instar: once immediately after a molt to the new instar (day 0) and once one day later (day 1; Rauscher, 1979c). Differences in disappearance rates were analyzed statistically with a Kolmogorov-Smirnov two-sample test (Siegel, 1956).

Because very few first-brood females oviposited on *A. serpentinaria* plants, and because those that do lay their eggs very late during the first brood, the rate of disappearance could not be compared for naturally laid eggs and larvae of brood-1 females. The relative suitability of the two host plants for larvae of first-brood females was therefore evaluated by placing out newly hatched first-instar larvae on randomly selected plants of each species and monitoring the rates at which they disappeared. On April 9, 1978 three newly hatched larvae obtained from captive females were placed on the top leaf of each of 30 plants of each host species. The plants were then censused daily as described above. In addition, the disappearance rate of naturally laid eggs and larvae on *A. reticulata* was determined by censuses for the progeny of the first-brood females followed in 1977.

**RESULTS**

**Search Behavior and Host Preference**

Ovipositing females of the two broods distribute their eggs differently with respect to host species. During brood 1 (1977) females placed approximately 84% of their egg clusters on *A. reticulata*. During brood 2, by contrast, females laid only about 17% of their clusters on *A. reticulata* (Table 1). This difference is highly significant (*G* = 74.35, *P* < .001, *G*-test, Sokal and Rohlf, 1969). The seasonal shift
in host plant use is reflected in the fraction of discovered host plants that are \textit{A. reticulata}: 94\% of the plants discovered by brood-1 females are \textit{A. reticulata}, whereas only 45\% of the plants discovered by brood-2 females are this species \((G = 172.21, P < .001)\).

The pattern of search and distribution of egg clusters between host species exhibited by brood-1 (1978) females is very similar to the pattern and distribution exhibited by brood-1 (1977) females. In both cases females laid a similar fraction of their egg clusters on \textit{A. reticulata} \((G = .003, P > .9)\) and alighted on the two host plants in similar proportions \((G = 2.45, P > .1)\). Moreover, when compared with brood-2 (1977) females, the females of brood-1 (1978) distributed their egg clusters differently (88\% on \textit{A. reticulata} vs. 17\% for brood-2 females, \(G = 35.15, P < .001\)) and discovered the host plants in widely disparate proportions (97\% of plants alighted on were \textit{A. reticulata} vs. 45\% from brood-2 (1977) females, \(G = 135.85, P < .001\)).

\begin{table}
\centering
\caption{Number (and fraction of total) of plants discovered and oviposited on by observed females. The number of females observed in each brood was: brood 1 (1977), \(N = 63\); brood 2 (1977), \(N = 45\); brood 1 (1978), \(N = 25\).}
\begin{tabular}{lrrrrrr}
\hline
 & \multicolumn{2}{c}{Brood 1 (1977)} & \multicolumn{2}{c}{Brood 2 (1977)} & \multicolumn{2}{c}{Brood 1 (1978)} \\
 & A.r.* & A.s.* & A.r. & A.s. & A.r. & A.s. \\
\hline
Plants oviposited on & 76 (.84) & 14 (.16) & 11 (.17) & 53 (.83) & 23 (.88) & 3 (.12) \\
Plants discovered & 332 (.94) & 22 (.06) & 91 (.45) & 113 (.55) & 158 (.97) & 5 (.03) \\
\hline
\end{tabular}
\end{table}

\* A.r. = \textit{A. reticulata}; A.s. = \textit{A. serpentina}. 
TABLE 2. G-test analysis of independence of three factors: response to host plant (oviposit vs. not oviposit), plant species, and brood (broods 1 and 2 in 1977). The last row in the table tests the overall independence of the three factors. The first three rows test the independence of the three possible pairs of factors, while the fourth row tests whether the degree of association between two factors varies over different levels of the third. For details of test, see Sokol and Rohlf (1969).

<table>
<thead>
<tr>
<th>Hypothesis tested</th>
<th>d.f.</th>
<th>G</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Response × Plant species independence</td>
<td>1</td>
<td>40.50</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Response × Brood independence</td>
<td>1</td>
<td>2.27</td>
<td>&gt;1, n.s.</td>
</tr>
<tr>
<td>Brood × Plant species independence</td>
<td>1</td>
<td>172.21</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Response × Plant species × Brood interaction</td>
<td>1</td>
<td>5.22</td>
<td>&lt;.05</td>
</tr>
<tr>
<td>Response × Plant species × Brood independence</td>
<td>4</td>
<td>220.20</td>
<td>&lt;.001</td>
</tr>
</tbody>
</table>

The great difference between brood-1 and brood-2 females in the relative proportion of the two host species discovered suggests that brood-1 females tend to search preferentially for *A. reticulata* plants, while second-brood females have a greater tendency to search for *A. serpentina* plants. Examination of the response coefficients of first- and second-brood females confirms this suggestion (Fig. 1). Eighty per cent of the first-brood females sampled had formed search images for broad leaves (Response Coefficient between 0.6 and 1.0) and hence were searching preferentially for *A. reticulata*. By contrast, 80% of the second-brood females sampled had formed search images for narrow leaves (Response Coefficient between 0.0 and 0.6) and were thus searching preferentially for *A. serpentina* (P < .001, Kolmogorov-Smirnov two-sample test).

These results imply that a switch in predominant searching preference occurs between broods 1 and 2. Closer analysis of the behavior of brood-1 females reveals that the switch may actually occur at the very end of the first brood, around the second week in April. In 1977, for example, 99% of the plants alighted on by females before April 8 were *A. reticulata*, as were 98% of the plants oviposited on. After April 8, by contrast, only 52% of the plants alighted on were *A. reticulata*, while no eggs were laid on that species (G = 81.18 for difference of proportions among plants alighted on; G = 56.44 for difference of proportions among plants oviposited on; both differences highly significant, P < .001). In 1978, too few *A. serpentina* plants were alighted on to make statistical comparisons within the first brood possible, but the differences were in the same direction as in 1977: 100% of plants alighted on and 100% of plants oviposited on before April 13 were *A. reticulata*; after April 13, 96% of plants alighted on but only 81% of plants oviposited on were *A. reticulata*. Moreover, all females sighted before April 13 were searching preferentially for *A. reticulata*, while only 70% were searching preferentially for that species after April 13 (G = 4.42, P < .05). During the first three to four weeks of the first brood, then, virtually all of the plants females discover and lay eggs on are *A. reticulata*. During the last week or so of the first brood, though, some females have begun searching preferentially for *A. serpentina* and some eggs are laid on that host. By the time second-brood females emerge, this trend has been completed and females lay most of their eggs on *A. serpentina*.

Brood-1 (1977) females oviposited on 23% of the *A. reticulata* plants on which they alighted (e.g., 76/332 from Table 1). The comparable figure for brood-2 (1977) females was 12%. Brood-2 females thus laid eggs only half as often after alighting on an *A. reticulata* plant as brood-1 females. In contrast, brood-2 females laid eggs three-quarters as often as brood-1 females after discovery of an *A. serpentina* plant (64% vs. 47%). The statistical significance of this seasonal change in post-
alighting oviposition bias can be tested by the interaction term in a 3-way G-test for independence (Sokal and Rohlf, 1969).

The results of the 3-way G-test are illustrated in Table 2. The significant Response × Plant species × Brood interaction term indicates that the reduction from brood 1 to brood 2 in the fraction of discovered plants that are oviposited on is greater for A. reticulata plants than for A. serpentina plants. Relative to A. serpentina, then, A. reticulata plants are less acceptable to alighted second-brood females than they are to alighted first-brood females.

The post-alighting response of a female to a host plant is not independent of plant species (Table 2, \( G = 40.41, P < .001 \)). In both brood 1 and brood 2, females lay eggs on a greater fraction of discovered A. serpentina plants than of discovered A. reticulata plants.

The overall post-alighting response of a female to a host plant is independent of brood (Table 2, \( G = 2.17, P > .1 \)). This result means that, despite the seasonal change in the apportionment of egg clusters to the two host species and the different post-alighting response to the two hosts, the fraction of all host plants landed on that females lay eggs on was similar for the two broods (.25 for brood 1 and .31 for brood 2).

Finally, the lack of independence between Brood and Plant species (Table 2, \( G = 172.11, P < .001 \)) indicates that the total number of post-alighting responses (oviposit or leave plant without ovipositing) was apportioned among the plant species differently in the two broods. Since the total number of post-alighting responses is equal to the number of plants discovered, this result confirms the previous finding that brood-1 females discover mostly A. reticulata plants, whereas brood-2 females discover mostly A. serpentina plants.

**Plant Abundance**

The mean density of A. reticulata in early May, as determined by the quadrate censuses, was 9.4 (±1.3) plants per 25 m², while the mean density of A. serpentina was only 0.2 (±0.1) plants per 25 m². The difference between the densities of the two species is highly significant (\( t_{30} = 3.88, P < .001 \), paired sample t-test; an unpaired t-test yields similar results). The relative abundances of the two host species in the observation area appear to be typical of the relative abundances of the two species in the open pine upland habitat throughout east Texas (Rausher, 1979a).

A significant correlation exists between the number of A. reticulata plants per quadrat and the number of A. serpentina plants (Spearman \( r_s = .33, P < .025 \)). This correlation indicates that high densities of A. serpentina plants tend to be found in areas with high densities of A. reticulata, while low densities of A. serpentina tend to be found in areas of low A. reticulata density. The spatial distribution of the two species is thus similar throughout the observation area.

The fraction of plants that have one or more leaves, and are therefore available for oviposition, is always greater for A. reticulata than for A. serpentina (Fig. 2a). The difference is especially marked in March and early April due to differences in phenology between the two plant species. Aristolochia reticulata plants initiate leaf production sooner and over a shorter period than do A. serpentina plants. Consequently, over 90% of all A. reticulata plants have produced one or more leaves by March 28, whereas it is not until April 26 that 90% of all A. serpentina plants have done so. (The values for A. serpentina on April 26 in Fig. 2a is less than .90 because some plants had produced leaves and had been completely defoliated by that date.)

At the time of the May 2 plant censuses, 96% of all A. reticulata plants and 79% of all A. serpentina plants had one or more leaves. Using these values for \( p_{jix} \), the mean plant densities determined by the quadrate census as estimates of \( \hat{A}_{jix} \), the \( p_i \) values shown in Figure 2a, and equation (1), I calculated the density of each host plant species throughout the
season (Fig. 2b). Within the observation area the density of *A. reticulata* is much greater than the density of *A. serpentina* at all times from March through early June, the flight season of *B. philenor*.

**Plant Discovery Rates**

Second-brood females (1977) that were searching for *A. reticulata* plants (Response Coefficient between 0.6 and 1.0) discovered plants at a faster rate than females searching for *A. serpentina* plants (Response Coefficient between 0.0 and 0.6). Females searching for *A. reticulata* alighted on an average of 4.10 (±.97) host plants per 10 min, while females searching for *A. serpentina* alighted on an average of 1.75 (±.19) plants per 10 min. This difference is highly significant (t = 2.9, P < .01, Wilcoxon two-sample test, Sokal and Rohlf, 1969), although it is not as large as the order of magnitude difference in the abundances of the two host species (Fig. 2b) would lead one to expect. Nevertheless, this result demonstrates that the greater abundance of *A. reticulata* plants during the flight period of second-brood females is associated with a greater host-plant discovery rate for females that search preferentially for *A. reticulata*.

First-brood females (1978) that were searching for *A. reticulata* also discovered host plants at a faster rate than females searching for *A. serpentina*. The discov-
ery rates for the two types of females were 8.92 (±.87) and 3.40 (±.81) respectively ($t_s = 2.9, P < .01$, Wilcoxon two-sample test). Although the absolute abundances of the two host species were not measured in 1978, the low seed set and long lifetime of Aristolochia plants in east Texas (Rausher, 1979a, and in prep.) means that the relative abundances were very similar in 1977 and 1978. Moreover, the phenologies of the two species were similar in the two years, with the fraction of A. reticulata plants having at least one leaf always exceeding the corresponding fraction of A. serpentaria plants (Rausher, 1979). Thus, the association between the greater abundance of A. reticulata plants and the greater host-plant discovery rate by females searching preferentially for that plant exists for first-brood females also.

Egg and Larval Disappearance

Egg and larval progeny of brood-2 females disappear significantly faster from A. reticulata plants than from A. serpentaria plants (Fig. 3, $P < .001$, Kolmogorov-Smirnov two-sample test). Over five times as many naturally laid eggs hatch and remain on A. serpentaria plants through the third instar as eggs laid on A. reticulata plants. The greater disappearance rate on A. reticulata is due primarily to differences in post-hatching disappearance rates ($P < .001$, Kolmogorov-Smirnov test). Disappearance during the egg stage does not differ significantly for eggs laid on the two host species ($G = 1.29, P > .2$, G-test).

For larvae placed out on host plants during the flight period of brood-1 females, the rates of disappearance on the two species of host plant were very similar (Fig. 4, $P \gg .1$, Kolmogorov-Smirnov test). Although egg disappearance rates could not be compared on the two host species for brood-1 females, there is little reason to expect a difference. The similar rates of disappearance of eggs laid by brood-2 females on the two plant species supports this contention. Thus, the two host plants appear to be equally suitable for the growth and survival of the progeny of brood-1 females. A comparison of disappearance rates for larvae placed out on A. reticulata during the first brood in 1978 with rates for larvae laid naturally on that plant by brood-1 females in 1977 reveals no significant differences ($P \gg .1$, Kolmogorov-Smirnov test). This result suggests that larval disappearance rates were similar for the progeny of brood-1 females in 1977 and 1978 and that therefore the two host plants were equally suitable for the progeny of brood-1 females in 1977 as well as 1978.

The preceding analyses have compared disappearance rates on the two plant
species during the same time period. It is also possible to compare disappearance rates of progeny laid naturally on *A. reticulata* by brood-1 and brood-2 females (Fig. 5). Eggs and larvae of brood-1 females disappear significantly faster than eggs and larvae of brood-2 females (*P* < .025, Kolmogorov-Smirnov test). The suitability of *A. reticulata* plants for egg and larval survival thus decreases from the time when progeny of brood-1 females are developing to the time when progeny of brood-2 females are developing.

It is not possible to compare disappearance rates on *A. serpentaria* for the two time periods in the same way because estimates of disappearance rates could not be obtained for naturally laid progeny of brood-1 females. Nevertheless, it is possible to estimate indirectly the seasonal change in disappearance rate of eggs and larvae on *A. serpentaria*. Progeny laid naturally on *A. serpentaria* by brood-2 females (Fig. 3) disappear more slowly than progeny of brood-1 females laid naturally on *A. reticulata* (Fig. 5), but the difference is not significant (*P* > .05, Kolmogorov-Smirnov test). Since there is also no significant difference between the disappearance rates of larvae on the two host species at the time the progeny of brood-1 females are developing (Fig. 4), it follows that there is no detectable difference between the disappearance rates of brood-1 progeny on *A. serpentaria* and brood-2 progeny on the same plant.

**DISCUSSION**

In east Texas both host-plant abundance and host-plant suitability for juvenile growth and survival appear to influence the way *B. philenor* females apportion their eggs between the two host species, although these two factors differ in importance at different times of the year. Brood-1 females lay most of their eggs on *A. reticulata*. Since larval disappearance rates are similar for the two host species during the period of growth and development of the progeny of brood-1 females, differential survivorship on the two host species is probably not the reason females oviposit primarily on *A. reticulata*. This plant is much more abundant than *A. serpentaria* during the flight period of brood-1 females, however, and the results of this study demonstrate that females searching for the more abundant plant discover host plants at a higher rate than females searching for the rarer plant. It appears, then, that most brood-1 females search for and lay most of their eggs on the more abundant host species.

Two selective advantages may be associated with a searching preference for the more abundant plant species. Because females discover host plants at a higher rate when searching for the more abundant species than when searching for the rarer species, they may lay more eggs per unit time searching. Anecdotal observations on *B. philenor* suggest that adult mortality is high and that therefore females with a higher oviposition rate may lay more eggs before dying. During approximately 40 h of observation time on searching females in 1977, for example, I witnessed two deaths. One female was killed by an anolis lizard as she flew under a shrub to approach a host plant. The other female was grabbed in midair by a dragonfly and eaten. Adults are also captured by robber flies (Asilidae) and web-spinning spiders. A searching preference for the more abundant species may also be
adaptive in that the higher host-plant discovery rate permits females to be more selective in choosing on which plants among those discovered to lay eggs while maintaining a constant rate of oviposition. Both of these possibilities need further study.

Unlike brood-1 females, those of brood 2 lay most of their eggs on *A. serpentaria*. Females are thus not choosing the more abundant plant species. The apparent reason for the change in the apportionment of eggs between the two host species is that in the second brood juvenile survivorship differs on the two host plants. Eggs and larvae disappear at a much greater rate from *A. reticulata* plants. Much of the larval disappearance is due to larvae leaving the host plants in search of others (Rausher, 1979a, and in prep.). Because the two host species have a similar spatial distribution, larvae of a given size are on average equally likely to discover new host plants regardless of the plant species on which they start. The major persistent effect of initial host choice on the probability of larval survival is thus the size at which larvae leave their first host plants. I have shown previously that small larvae have a lower probability of discovering a new host plant than do larger larvae (Rausher, 1979c). Since larval offspring of brood-2 females on *A. reticulata* leave their initial host plant earlier, and hence at a smaller size, than larvae on *A. serpentaria*, eggs placed on *A. reticulata* have a lower probability of surviving to reach a second host plant than eggs placed on *A. serpentaria*. Consequently, brood-2 females that place most of their eggs on *A. serpentaria* will have a greater fraction of their eggs survive to the adult stage than females that place more eggs on *A. reticulata*. As long as the increase in juvenile survival probability that is associated with ovipositing on *A. serpentaria* more than compensates for the disadvantages associated with searching for the less abundant host plant, natural selection will promote the evolution of behaviors that ensure brood-2 females lay most of their eggs on *A. serpentaria*. This situation has apparently been realized in east Texas.

Between broods 1 and 2 the disappearance rate of eggs and larvae on *A. reticulata* increases, while the disappearance rate on *A. serpentaria* remains about the same or may even decrease (e.g., Fig. 5). These different seasonal trends are due primarily to differences in the mature leaves of the two host-plant species (Rausher, 1979a). The mature leaves of *A. reticulata* are tough, poor in nutrients, and are not eaten by larvae unless they are starved. Moreover, few new leaves are produced by *A. reticulata* plants after the initial spring flush of foliage. By the time of the second brood, then, most of the leaves present on *A. reticulata* plants are tough and inedible, and a smaller amount of edible, immature foliage is present than during brood 1. Consequently, the progeny of brood-2 females on *A. reticulata* eat less and are smaller when they deplete the edible foliage on their initial host plant and begin searching for other plants than are the progeny of brood-1 females on *A. reticulata*. This earlier departure accounts for most of the seasonal increase in disappearance rates. The mature leaves of *A. serpentaria*, by contrast, remain tender and edible. The progeny of brood-2 females on *A. serpentaria* thus have at least as much edible foliage on their initial host plant as the progeny of brood-1 females on the same plant and disappearance rates do not change markedly over the season (Rausher, 1979a, and in prep.). The seasonal shift in apportionment of eggs between host plants therefore ultimately reflects a seasonal change in the relative nutritional quality of the foliage of the two host plants.

Although for *B. philenor* in east Texas both plant abundance and plant suitability for juvenile growth and survival appear to influence oviposition behavior, plant suitability appears to be the dominant influence. During the second brood, females search preferentially for and lay most of their eggs on the plant species on which eggs and larvae survive best, even though it is the rarer host. Only when
there is no difference in juvenile survivorship on the two species, as is true for the progeny of first-brood females, does host-plant abundance appear to influence searching preferences and oviposition. This finding suggests that advantages associated with high rates of oviposition are smaller for *B. philenor* than the advantages associated with laying eggs on the plant species affording greater juvenile survivorship. Otherwise, females would be expected to search preferentially for and oviposit primarily on *A. reticulata* during brood 2. Studies on other butterflies, however, have shown that oviposition preferences are not well correlated with host-plant suitability (Wiklund, 1975; Chew, 1977; Rausher, 1979b). In these cases differences in larval survivorship on different host species may influence overall reproductive success less than factors, such as differences in host-species abundances, that affect the rates at which females discover and lay eggs on different host plants. If so, there is little reason to expect a strong correlation between host-plant suitability and oviposition preferences in these species.

The radical seasonal shift in the apportioning of eggs between host species suggests that during at least one of the two broods each year females lay a greater fraction of eggs on the preferred species than would be expected from the relative abundances of the two plant species. For second-brood females, this suggestion is doubtless true, since, as I have shown here, these females lay most of their eggs on *A. serpentina* even though this plant species is much less abundant than *A. reticulata*. It is more difficult to evaluate whether first-brood females place a greater fraction of their eggs on *A. reticulata* than would be expected from the relative abundances of the two host species. In both 1977 and 1978, females during the first three to four weeks of brood laid 98–100% of their egg clusters on *A. reticulata*. During this period, *A. reticulata* plants made up greater than 90% of the host plants in the study area (Fig. 2). Because the relative abundance of *A. reticulata* changed during the first brood, however, it is not possible to compare these two figures statistically. Nevertheless, I have shown elsewhere that in early April, the probability that an *A. reticulata* plant will be oviposited on is significantly greater than the probability that an *A. serpentina* plant will have eggs laid on it (Rausher, 1979a, and in prep.). This finding suggests that, during most of the first brood, females lay a greater fraction of their eggs on *A. reticulata* than would be predicted from the relative abundances of the two host species.

Preferential oviposition and the seasonal change in apportionment of eggs between the two hosts appears to be accomplished by a combination of preferential searching and discriminatory post-alighting response. During the first brood most females form search images for broad leaves. Because search image formation biases host-plant discovery in favor of plants with leaves of the shape being searched for (Rausher, 1978), first-brood females tend to discover primarily *A. reticulata* plants. This bias is to some extent compensated by an opposite bias in post-alighting response: females oviposit on a greater fraction of discovered *A. serpentina* than of discovered *A. reticulata* plants. It is impossible at this point to say whether this second bias is an actual chemotactile preference for *A. serpentina* independent of female motivation state, or whether it simply reflects the fact that females searching for *A. reticulata* discover plants at a higher rate than females searching for *A. serpentina* and are simply being more “choosy” about the individual plants they lay eggs on while maintaining a constant rate of oviposition. In either case, however, the apparent post-alighting bias in favor of *A. serpentina* does not fully compensate for the searching bias; brood-1 females lay eggs primarily on *A. reticulata*.

During the second brood most females form search images for narrow leaves. Consequently, host-plant discovery is biased in favor of *A. serpentina*. In this case the apparent post-alighting response
bias reinforces the discovery bias in favor of *A. serpentaria*. Moreover, the significant Response × Plant species × Brood interaction (Table 2) indicates that, after alighting, brood-2 females are relatively less likely to oviposit on *A. reticulata* as compared to *A. serpentaria* than are brood-1 females. This change in post-alighting response bias cannot be explained by increased discovery rates of *A. reticulata* relative to *A. serpentaria* since, if anything, *A. serpentaria* is relatively more abundant during brood 2 than during brood 1 (Fig. 2b). A likely explanation for the change in post-alighting response bias is that females do not lay eggs on *A. reticulata* plants that have only tough, mature leaves. Young leaves must be present on a plant for oviposition to occur (Rausher, 1979a). During brood 1, most *A. reticulata* plants have young leaves and are therefore acceptable for oviposition; by the time of brood 2, however, very few *A. reticulata* plants have young leaves (Rausher, 1979a, and in prep.). The mature leaves of *A. serpentaria*, on the other hand, remain tender and acceptable for oviposition. Thus, the fraction of *A. reticulata* plants that can elicit egg-laying decreases from brood 1 to brood 2 relative to the fraction of *A. serpentaria* plants that elicit egg-laying.

The mechanism that causes a majority of brood-2 females to adopt search images that differ from those adopted by a majority of brood-1 females is not known. It is evident, though, that the change in predominant search image formed is largely responsible for the seasonal change in egg distribution by females. Search images are not perfect, however. Females searching preferentially for one host-plant species occasionally alight on plants of the other host species (Rausher, 1978). The seasonal change in post-alighting response bias appears to be a secondary mechanism that prevents brood-2 females that “accidentally” alight on an *A. reticulata* from laying eggs on that plant. The combined operation of search image formation and chemotactile response should thus be viewed as an adaptive mechanism that enables females to respond to seasonal changes in host-plant suitability.

**Summary**

Two hypotheses about the factors governing the evolution of oviposition preferences in phytophagous insects were examined using the pipevine swallowtail butterfly, *Battus philenor*, in east Texas. Both host-plant abundance and host-plant suitability for growth and survival of the juvenile stages influence female searching preferences and the proportion of eggs laid on each of two host species. At times during the season when juvenile survivorship is similar for eggs laid on the two host species, females lay most of their eggs on the more abundant species. When juvenile survivorship is dissimilar, however, females lay most of their eggs on the species on which juvenile survivorship is greater, even though it is the rarer host species. For *B. philenor* in east Texas the selective advantages associated with searching for the more abundant host plant appear to be smaller than the advantages associated with searching for the host that affords greater juvenile survivorship. Preferential oviposition is accomplished by search image formation and post-alighting response. The combined operation of these two behaviors is an adaptive mechanism that enables females to respond to seasonal changes in host-plant suitability.

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**Literature Cited**


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