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Genetic differences and phenotypic plasticity as causes of variation in oviposition preference in *Battus philenor*

D.R. Papaj* and M.D. Rausher

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**Summary.** Bradshaw (1965) proposed that phenotypic plasticity would be more common than adaptive genetic variability in species for which environmental fluctuations occur over periods roughly equal to that species' generation time. In an effort to examine this notion, sources of seasonal variation in two components of oviposition behavior in an east Texas population of pipevine swallowtail butterflies (*Battus philenor*) were investigated under natural and seminatural conditions. Variability in a visually-based pre-alighting component involving orientation to leaf shape was primarily due to phenotypic plasticity in the form of adult learning; no seasonally-based genotypic differences in leaf-shape discrimination behavior were observed. By contrast, a chemotactile post-alighting component involving elicitation of oviposition after landing on the host plant was not phenotypically plastic, i.e., not susceptible to learning. In addition, only slight and nonsignificant seasonally-based differences in post-alighting responses to different host species were observed.

**Key words:** Phenotypic plasticity – Genetic variability – Learning – Host-selection behavior – Foraging behavior

Bradshaw (1965) proposed that phenotypic plasticity and genetic tracking (i.e., regular changes in gene frequency at polymorphic loci) are two alternative means by which organisms commonly are adapted to respond to regularly fluctuating environments. He also argued that phenotypic plasticity would tend to be found more often than adaptive genetic variability in species for which environmental fluctuations occur over periods roughly equal to that species' generation time. This argument has recently received some support from more formal analyses (Slatkin and Lande 1976).

The justification for Bradshaw's contentions is relatively straightforward. When successive generations experience alternating environments (i.e., strongly negative autocorrelation of environments: generations 1, 2, 3, 4...n experience environments I, II, I, II, ... respectively), phenotypic plasticity permits the development in most or all individuals of the phenotype with highest fitness each generation. By contrast, genetic change at loci that are maintained polymorphic by temporally-varying natural selection (Hedrick et al. 1976) is maladaptive in the sense that natural selection increases the frequency of genotypes that have high fitness in the current environment but that have low fitness in the environment of the next generation. Thus, at the beginning of each generation a randomly chosen individual has a lower expected fitness in the current environment than a randomly chosen individual from the previous generation would have had in the same environment. Under these conditions, modifier alleles that reduce the effects of genetic variance on the phenotype have a relatively high probability of being selected (Slatkin and Lande 1976), which would have the primary effect of leaving phenotypic plasticity as the more common adaptive response to environmental fluctuations.

An east Texas population of the pipevine swallowtail butterfly, *Battus philenor*, provided an opportunity to examine the validity of Bradshaw's hypothesis. In east Texas, this butterfly has two generations, or broods, per year. The adult females of the two generations differ in the proportional allocation of eggs to each of two larval host plants. First-brood females place most of their eggs on the broad-leaved *Aristolochia reticulata* Nutt. (*Aristolochiaceae*) while second-brood females place most of their eggs on the narrow-leaved *A. serpentaria* Nutt. (Rausher 1980). This seasonal change in allocation is caused by a difference between the broods in two components of the behavioral sequence by which females find and oviposit on hosts (Rausher 1980; Rausher and Papaj 1983).

Host selection by pipevine swallowtail butterflies includes a pre-alighting component in which a female approaches and lands on leaves of a certain shape and a post-alighting component in which an individual responds to contact chemicals on the leaf surface by ovipositing or resuming search flight (Rausher 1978; Papaj 1986a). The east Texas population varies seasonally in the particular shape of non-host leaves on which females tend to land. Brood 1 females land predominantly on non-host leaves of a broad shape similar to that of *A. reticulata*. Brood 2 females, by contrast, alight mostly on narrow leaves like those of *A. serpentaria*. As a result, most first-brood females alight primarily on *A. reticulata*, while most second-brood females alight primarily on *A. serpentaria* (Rausher 1980).

In addition to inter-brood variation in the pre-alighting response, the post-alighting response, defined as the conditional probability of ovipositing once an individual has alighted, is different for first-brood and second-brood females (Rausher 1980). Second-brood females oviposited on...
an overall smaller proportion of alighted host plants than did first-brood females. The decrease in post-alighting response by second-brood females was greater for A. reticulata than for A. serpentaria, which means that second-brood females are more likely to oviposit on A. serpentaria, relative to A. reticulata, than are first-brood butterflies. This cyclical change in each component of oviposition behavior was interpreted to be an adaptive response to regular seasonal alternation in the relative suitability of the two host species for larval growth and development (Rausher 1980, 1981).

According to Bradshaw's hypothesis, any behavioral differences exhibited by first- and second-brood female pipevine swallowtail butterflies should be due primarily to behavioral plasticity and not to genetic differences between the broods. Behavioral plasticity in the form of adult learning has been described elsewhere for pipevine swallowtail butterflies (Papaj 1986a–c), but the possibility of inter-brood genetic differences had not been examined previously. In this study, we quantify the relative importance of learning and genetic differences as sources of variation in host use by the east Texas population. In doing so, we demonstrate that Bradshaw's prediction is valid for one component of host-selection behavior by pipevine swallowtail butterflies.

Materials and methods
Experimental organisms
The first peak of abundance of adult butterflies in east Texas occurs after Aristolochia reticulata begins leafing out in early March. These Brood 1 individuals are common until the second week in April. Many offspring of Brood 1 adults enter pupal diapause and do not eclose until the following spring. A certain proportion, however, emerge to form the second, smaller brood which begins in the last week of April and ends in early June. All progeny of Brood 2 butterflies presumably diapause as pupae until the following March (Rausher 1986).

Larvae of either brood feed exclusively on two host species, Aristolochia reticulata and Aristolochia serpentaria. Both species are small, perennial hosts which flower and set seed within the leaf litter. Details of the phenology, abundance, distribution, and seasonal change in suitability of each species are provided by Rausher (1980, 1981).

Field variation in searching behavior
Field studies and collection of animals were carried out in March–June of 1980–1982 on a 5-acre tract of pine uplands in the John Henry Kirby State Forest in Tyler County north of Kountze, Texas. This habitat is described in detail in Watson (1979) and Rausher (1980). The particular area in which we observed female oviposition behavior was bounded on two sides by dirt roads and on two sides by fire lanes.

Oviposition behavior was measured and recorded using a procedure similar to Rausher (1980) and Stanton (1982). Between 1000 and 1430 h daily (when butterflies were observed searching for oviposition sites) in May and June of 1980, March–June of 1981, and March–May of 1982, we traversed a circular trail and scanned the entire field site until a searching female was sighted. Females searching for host plants on which to lay eggs are easily recognized by their characteristically slow, fluttering flight and frequent alightings on non-host vegetation. Using a tape recorder and hand-operated triple-unit counter, we followed a searching female butterfly for 10 min or until she flew from the field site. For each female, we recorded the shape of each non-host leaf on which the individual landed using criteria described in Rausher and Papaj (1983). We also recorded alightings and ovipositions on host plants.

For each female, we calculated a Response Coefficient (RC) equal to the fraction of all non-host leaves alighted which were broad as a measure of the pre-alighting response to leaf shape (Rausher 1978; Rausher and Papaj 1983). High RC values (>0.5) denote females that landed predominantly on broad leaves; low RC values (<0.5) denote females that land predominantly on narrow leaves. We used the proportion of alightments on a host species that ended in oviposition to describe the relative post-alighting response to a host species.

Measure of experiential and genetic components of behavioral variation
In these experiments, we attempted to determine the degree to which pre-alighting and post-alighting behavior is phenotypic plastic, i.e. the extent to which prior adult experience with a particular host species alters the tendency of an individual to land and oviposit on different host species.

The individuals in these tests included the second and third generations of adults reared from females originally collected from both broods in Kirby Forest in 1982. The first generation of larvae were initially fed on either or both east Texas Aristolochia species as available. Until transport to growth chambers at Duke University, larvae were reared under normal photoperiod and temperature on the porch of the field station in east Texas. Larvae were subsequently reared to pupation in growth chambers at a photoperiod of 14:10 light:dark and temperatures of 29·15°C day:night on a revised ad libidum diet of various Aristolochia species. This culture regime precluded facultative pupal diapause and all surviving individuals eclosed within two weeks of pupation. Both stocks upon emergence were bred within lines and reared for two more generations.

The second and third generations of larvae were reared only in the growth chambers on an ad libidum diet of primarily A. macrophylla (= durior). The Texas hosts were not represented in the diet of these insects. By feeding larvae on a mixed diet lacking Texas hosts, we hoped to minimize a possible effect of larval induction of adult preference.

Because our larval food plant supply was limited, it was not possible to rear enough individuals to employ a standard full-sib or half-sib mating design (Falconer 1960) for the analysis of genetic variation. Instead, we simply compared the behavioral responses of second- and third-generation offspring of the two broods. Because the two groups of individuals were reared under a common environment in the growth chambers, any maternal effects should be minimized; consequently, any observed differences between the groups should be due primarily to underlying genetic differences.

Genetic drift over the two generations of rearing in the laboratory could have caused the two stocks to diverge. This potential problem was minimized, however, by using 25 mating pairs to found each generation. Using eq. 19 in
Lande (1976), we can calculate the expected differentiation of the two groups due to genetic drift. Assuming a relatively high heritability of 0.5, the expected divergence with 95 percent confidence is less than or equal to 0.2 standard deviations of the mean. Our statistical analyses do not have sufficient power to detect differences of this magnitude. Any differences we can detect with our analyses will be much larger and are likely to be a consequence of initial genetic differences between the two broods.

Assays of pre-alighting and post-alighting responses were performed in a large (15 m x 15 m x 3 m) screened enclosure at the Department of Zoology Field Station at Duke University in Durham, North Carolina. A computer-generated random-number sequence (SAS Institute 1982) was used to distribute equal numbers of six non-host species in a rectangular grid over bare ground in a large (15 m x 15 m x 3 m) screened enclosure. Three species consisted of broad-leaved types (leaf length: width ratios < 2.0) and three species were narrow-leaved types (leaf length: width ratios > 7.0). A list of species and length:width ratios is provided in Papaj (1986a). The leaf shapes of the non-host species encompassed the range of broad and narrow non-host leaves on which females land in the field (Rausher and Papaj 1983). In the resulting 60 m^2 array we also distributed randomly cohorts of 20 individuals of each host species among the non-host plants. All plants were planted in identical 5/8-inch diameter green plastic pots arranged in a rectangular grid within the enclosure. Because the attractiveness of *A. recticulata* as a substrate for oviposition after alightment appears to decline as a plant ages phenologically (Rausher 1981; Papaj and Rausher 1987), we took considerable care to use only plants that had leafed out recently and replaced individuals of both host species regularly.

Flowering *Lantana* sp. and *Verbena* sp. and artificial solutions of honey and water (1:1) were placed at intervals around the perimeter of the array. In addition, all females were fed honey-water solutions by hand at the beginning and end of each day. The butterflies were kept overnight between tests in Duke University laboratory rooms at about 25°C.

Groups of mated female butterflies originating from each brood were released into the array with either *A. recticulata* or *A. serpentaria* available for alightment and oviposition, but never both simultaneously. Plants of the other host species were covered by small cages of fiberglass screen at the beginning and midway during each session, eggs were cleared from the hosts. A regular removal of eggs is desirable because *B. philenor* females recognize eggs and avoid oviposition on plants that bear eggs (Rausher 1979).

Alightings on non-host leaves were pooled over oviposition bouts by a female and the resulting Response Coefficients were arcsin-transformed. A two-way analysis of variance (SAS Institute 1982) with Brood Origin and Host Exposure as main effects was used to detect genetic and learning components of variation in response to leaf shape respectively. The post-alighting response for a given female was measured as the proportion of all hosts alighted on that received eggs. A two-way analysis of variance with Brood Origin and Host Exposure as main effects was used to detect a genetic component of variation in response to host contact.

In order to examine the reversibility of an effect of host exposure on the pre-alighting response and to detect an effect of host exposure on the post-alighting response, we exposed a group of females from each brood stock to both host species in succession. For each brood stock exposed to either host species, any individuals surviving the exposure regime in the previous experiment were exposed to the alternative host species. These females were then observed as described above.

### Results

**Host-selection behavior and allocation of eggs in east Texas**

The seasonal pattern of allocation of eggs by pipevine swallowtail butterflies to the *Aristolochia* host species in east Texas in 1981 generally resembled 1977 and 1978 data reported by Rausher (1980) with some interesting exceptions. Slightly more egg clusters were placed on *A. recticulata* by Brood 1 females than on *A. serpentaria* (51%; Table 1). Females in the second brood, by comparison, laid only about a third of their egg batches on *A. recticulata* in 1981 and none on *A. recticulata* in 1980. Thus, the population shifted dramatically from a marginal tendency to lay more eggs on *A. recticulata* in the early-spring brood to a clear tendency to lay more eggs on *A. serpentaria* in the late-spring brood.

The relative lack of specificity by the first brood differs from Rausher’s (1980) results for 1977 and 1978 in which significantly more egg clusters were laid on *A. recticulata* than on *A. serpentaria* by Brood 1 females (84% vs. 16% in 1977). This discrepancy in the extent to which eggs were allocated to *A. recticulata* was accompanied by a marked difference in pre-alighting response to leaf shape as well. The overall distribution of response coefficients for each brood is shown in Fig. 1. Brood 2 females searched predominantly for narrow leaves (i.e., most RC’s < 0.5) as reported by Rausher (1980). During the first brood, however, only a slender majority of females were searching predominantly for broad leaves (i.e., most RC’s > 0.5). The latter observation departs strongly from 1978 data in which almost 80% of Brood 1 individuals approached and alighted primarily on broad leaves.

The post-alighting responses by each brood to the two *Aristolochia* host species in 1981 are summarized in Table 2a. After alightment, both broods were much less likely to oviposit on *A. recticulata* than on *A. serpentaria* (0.07 vs. 0.36 overall). Brood 2 individuals, however, were relatively

<table>
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<tr>
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</thead>
<tbody>
<tr>
<td><em>A. recticulata</em></td>
<td>0.0</td>
<td>0.51</td>
<td>0.33</td>
</tr>
<tr>
<td><em>A. serpentaria</em></td>
<td>1.0</td>
<td>0.49</td>
<td>0.67</td>
</tr>
</tbody>
</table>
more likely to oviposit on A. serpentaria than on A. reticulata than were Brood 1 females.

The statistical significance of these differences was evaluated with a three-way G-test of independence (Table 2b). The significant Response × Species interaction confirms that females deposited egg clusters more frequently on A. serpentaria after alighting than on A. reticulata. The lack of a significant Response × Brood × Species interaction (G = 0.82, \( P > 0.05 \)), however, fails to support the hypothesis that Brood 2 females accept A. serpentaria relatively more often for oviposition than do Brood 1 females. Evidence to the contrary was reported by Rausher (1980). Although relative post-alighting response to the two hosts did not differ between the broods, the number of alightments on each species did, however, depend on brood (Brood × Species term; G = 6.67, \( P < 0.01 \)). Brood 1 females alighted proportionately more often on A. reticulata relative to A. serpentaria than do Brood 2 females, confirming the findings of Rausher (1980).

Despite the noted deviations in detail, these data verify several patterns of host-selection behavior and host use reported by Rausher (1980). First, individuals within a brood are variable with respect to leaf-shape search modes. Second, the proportion of females searching primarily for broad leaves is lower for Brood 2 than for Brood 1. Finally, this behavioral shift is associated with a marked seasonal decrease in the proportion of eggs allocated to A. reticulata. Most importantly, this data confirms that the broods did indeed exhibit differences in host use in the year in which we acquired wild females and initiated our brood stocks.

Sources of variation in pre-alighting behavior

Under enclosure conditions, pre-alighting search behavior was highly plastic. Ovipositing B. philenor females clearly adopted a search mode for the leaf shape of the host plant species to which they were exposed (Figs. 2 and 3). This highly significant effect of available host type on response to leaf shape (Table 3, Exposure effect) contrasted sharply with the negligible influence of brood origin on overall search mode (Table 3, Brood effect). Thus, the two broods did not differ phenotypically in overall search mode under the conditions of our test. Furthermore, the lack of significance in the interaction term (Table 3, Exposure × Brood effect) indicates that the effect of host exposure on a female’s leaf-shape response did not depend on the brood stock from which an individual originated.

Behavioral plasticity in response to host exposure is probably due to adult learning, an inference supported by the results of exposing females successively to each host species. Females exposed first to one host species and then to the other always adopted a search mode for the second species (Table 4). In fact, switching of search modes occurred in every case but one. Although sample sizes were small, there was no obvious effect of brood origin on tendency to relearn the leaf shape of a particular host species. Individuals from both broods were equally facile in switching from a search mode for either host species to one for the other.
Fig. 3. Difference in response coefficients for Brood 1 and Brood 2 females exposed to *A. serpentaria*. Dotted bars, Brood 1 females; hatched bars, Brood 2 females. In all, 182 trials were recorded for 32 Brood 1 females; 192 trials were recorded for 30 Brood 2 females.

Table 3. Results of two-way analysis of variance of effect on brood origin and plant species to which a female was exposed on the leaf-shape response coefficient in the enclosure arrays

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
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<th>F</th>
<th>p &gt; F</th>
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<tbody>
<tr>
<td>Model</td>
<td>3</td>
<td>11.92</td>
<td>63.27</td>
<td>0.0001</td>
</tr>
<tr>
<td>Brood</td>
<td>1</td>
<td>0.01</td>
<td>0.22</td>
<td>0.64</td>
</tr>
<tr>
<td>Exposure</td>
<td>1</td>
<td>11.48</td>
<td>182.74</td>
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<tr>
<td>Brood × Exposure</td>
<td>1</td>
<td>0.11</td>
<td>1.84</td>
<td>0.178</td>
</tr>
<tr>
<td>Error</td>
<td>107</td>
<td>17.77</td>
<td>...</td>
<td>...</td>
</tr>
</tbody>
</table>

Sources of variation in post-alighting behavior

Brood stocks also did not differ in post-alighting responses in the enclosure experiment. Females overall were slightly more likely to lay eggs upon landing upon *A. serpentaria* than upon landing on *A. reticulata* (Table 5; Exposure effect, $F=3.04$, $p=0.08$), but the bias for *A. serotonin* was not significantly different between brood stocks (Table 5b; Exposure × Brood Origin effect; $F=2.15$, n.s.). Despite the lack of statistical significance, the observed differences in post-alighting response were in the direction predicted under a hypothesis of adaptive genetic differences. Brood 1 individuals oviposited slightly more frequently on *A. reticulata* on which they alighted than did Brood 2 females; Brood 2 individuals laid egg clusters on a higher proportion of *A. serpentaria* on which they landed than did Brood 1 females.

Unlike pre-alighting leaf-shape responses, post-alighting responses were not altered by prior adult experience; exposure to one host species had no significant effect on the probability of laying an egg cluster after landing on the other host species (Table 6; Exposure × Sequence effect; $F=0.47$, n.s.).

Discussion

Behavioral plasticity of pre-alighting behavior

The pre-alighting oviposition behavior of *Battus philenor* females conforms to the expectation that in cyclical environments which alternate every generation, phenotypic plasticity should be the primary means by which individuals exhibit phenotypes appropriate to local conditions. Pre-alighting search in the pipevine swallowtail butterfly is highly plastic, altered readily by a female’s experience with the particular set of host plants available at emergence. Females adopt a search mode for the leaf shape of the host species with which they are experienced and switch search modes when they encounter a host species with a different leaf shape (Papaj 1986a; see Results). Field observations (Rausher 1978; Papaj 1986b) indicate that females often switch search modes after the “accidental” discovery of a host plant with a leaf shape differing from that for which they were searching originally. In short, behavioral plasticity in the form of adult learning can account for the seasonal change in pre-alighting behavior observed in the field.

As predicted, the broods did not differ genotypically in pre-alighting behavior. No differentiation between females originating from the two broods in either overall

Table 4. Effect of reversing exposure on the search mode of *B. philenor* butterflies ovipositing in an enclosure array. All females were initiated exposed to one host species. Results reflect the number of females exhibiting either search mode after presentation of the second host species. Broad-leaf and narrow-leaf search modes defined as in Table 1. Association between final search mode and second host is highly significant (Fisher’s Exact Test, $P<0.0001$)

<table>
<thead>
<tr>
<th>Brood</th>
<th>First Host</th>
<th>Second Host</th>
<th>Final Search Mode</th>
</tr>
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<tbody>
<tr>
<td></td>
<td><em>A. serpentaria</em></td>
<td><em>A. reticulata</em></td>
<td>Broad</td>
</tr>
<tr>
<td>1</td>
<td><em>A. reticulata</em></td>
<td><em>A. reticulata</em></td>
<td>6</td>
</tr>
<tr>
<td>2</td>
<td><em>A. reticulata</em></td>
<td><em>A. reticulata</em></td>
<td>10</td>
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Table 5. A Average proportion ($±1$ s.d.) of landings on *A. reticulata* and *A. serpentaria* plants that resulted in oviposition by female butterflies of early and late spring brood stocks. B Two-way analysis of variance for effect of host exposure and brood origin on the post-alighting responses by *B. philenor* females. Dependent variable is arcsine square-root transformation of the proportion of landings that end in oviposition

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<th>Source</th>
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</tr>
<tr>
<td>Brood</td>
<td>1</td>
<td>0.02</td>
<td>0.26</td>
<td>ns</td>
</tr>
<tr>
<td>Brood × Exposure</td>
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<td>0.20</td>
<td>2.15</td>
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<tr>
<td>Error</td>
<td>71</td>
<td>0.09</td>
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Table 6. A Average proportion (±1 s.d.) of landings on A. reticulata (AR) and A. serpentaria (AS) plants that resulted in oviposition by females of early and late spring brood stocks, according to the order of presentation of host species. B Three-way analysis of variance for effects of host exposure, brood origin, and sequence of presentation on the post-alighting responses by B. philenor females. Dependent variable is arcsine square-root transformation of the proportion of landings that end in oviposition.

<table>
<thead>
<tr>
<th>Host Species</th>
<th>Brood Origin</th>
<th>Order of Presentation</th>
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<th>Mean</th>
<th>Second</th>
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<tr>
<td>AR</td>
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<td>5</td>
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<td>(±0.11)</td>
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<td>2</td>
<td>7</td>
<td>0.27</td>
<td>(±0.33)</td>
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<td>AS</td>
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<td>0.35</td>
<td>(±0.106)</td>
<td>0.37</td>
<td>(±0.022)</td>
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<td>2</td>
<td>8</td>
<td>0.31</td>
<td>(±0.099)</td>
<td>0.33</td>
<td>(±0.183)</td>
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B

<table>
<thead>
<tr>
<th>Source</th>
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<tr>
<td>Sequence</td>
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<td>Brood x Exposure</td>
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<td>0.08</td>
<td>ns</td>
</tr>
<tr>
<td>Brood x Sequence</td>
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<td>0.47</td>
<td>ns</td>
</tr>
<tr>
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<tr>
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<tr>
<td>Error</td>
<td>42</td>
<td>2.24</td>
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</table>

leaf-shape response or learning of leaf-shape response was detected in this study. We note that this result does not mean that there is no genetic variation for pre-alighting behavior or for learning of pre-alighting behavior in the east Texas population. Our procedure, for example, does not provide any information about the amount of genetic variation within each brood.

Likewise, we are not suggesting that learning in the east Texas population evolved in response to regular fluctuation in the host environment. In fact, even individuals in populations without apparent fluctuations in host environment learn readily to discriminate among host leaf shapes in enclosure presentations (Papaj 1986c). The evolutionary origin of learned discrimination behavior is therefore unclear and apparently unrelated to present patterns of environmental variability. Our results do, however, indicate that genetic differences between broods in host-selection behavior have not arisen in response to current environment fluctuation.

Lack of inter-brood differences in post-alighting behavior

Rausher (1980) suggested that inter-brood variation in post-alighting responses to each host species was a secondary mechanism, in addition to seasonal changes in leaf-shape search modes, for the shift in host use. Rausher remarked that because Brood 2 females that occasionally alighted on A. reticulata laid eggs less frequently on that species relative to A. serpentaria than did Brood 1 females, the post-alighting response might be an adaptation that enabled females to respond to seasonal variation in host suitability.

Our 1981 field results (Table 3; Response × Brood × Species term) indicated, however, that a Brood 2 female was no less likely to oviposit on an A. reticulata on which she alighted relative to A. serpentaria than a Brood 1 female, although the latter certainly alighted on A. reticulata at the higher rate owing to her broad-leaf search mode. The discrepancy between 1977 and 1981 results is probably illusory. Reanalysis of 1977 data using improved contingency tests yielded the same statistical result reported for 1981: Brood 1 and Brood 2 females did not exhibit significantly different post-alighting oviposition responses (Rausher, unpublished data). On the basis of field data, we cannot conclude that there are consistent differences between broods in the relative post-alighting response to each host species. As such, we obviously cannot infer that seasonal variation in post-alighting responses contributes adaptively to the shift in egg allocation.

Not surprisingly, brood stocks did not differ significantly in post-alighting response to each host species under enclosure conditions. In addition, the probability of laying an egg cluster after alighting on a given host species was not phenotypically plastic; specifically, the post-alighting response was not affected by prior adult experience with particular host species, although sample sizes were admittedly small.

Is phenotypic plasticity molded by host abundance or suitability?

Both the relative abundance and suitability of the two host species varies seasonally in ways that could potentially induce females of different broods to search preferentially for different species (Papaj and Rausher 1983). In the early spring, both host species are equally suitable for larval survival, but A. serpentaria is much less abundant. Assuming naive individuals alight on host plants in proportion to their abundance, most females apparently learn to search for the broad leaves of the more abundant A. reticulata because the rate of host alightment is higher in this search mode. By late spring, the suitability of A. reticulata for juvenile growth and survival relative to A. serpentaria falls sharply and the disparity in abundance is diminished somewhat (Rausher 1980, 1981; Papaj, unpubl. data). Either a change in abundance or suitability or both could promote adoption of narrow-leaf search modes.

The fact that a Brood 2 female was no less likely to oviposit on an A. reticulata on which she alighted relative to A. serpentaria than a Brood 1 female might at first suggest that butterflies are not responding behaviorally to the change in host suitability. If true, it would be likely that the change in relative host alightment rate and not the change in relative host suitability causes the switch in predominant search mode observed in east Texas.

Unfortunately, little if anything about the importance of temporal changes in host suitability in inducing changes in searching behavior can be deduced from field studies. In east Texas, the seasonal change in relative suitability of the two Aristolochia species is confounded with the change in their relative density. Since host density clearly influences the post-alighting response of females to hosts of a particular species (Rausher 1983a), simultaneous changes in the relative density and suitability of the two host species renders the relationship between post-alighting response and host suitability difficult, if not impossible, to interpret.
from field data. Resolving whether behavioral plasticity is molded principally by host abundance or suitability awaits the development of behavioral assays in which each factor is manipulated independently.

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