

COMPONENTS OF CONSPECIFIC HOST DISCRIMINATION BEHAVIOR IN THE BUTTERFLY *BATTUS PHILENOR*¹

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Abstract. The hypothesis that pipevine swallowtail butterflies (*Battus philenor*) discriminate among *Aristolochia reticulata* host plants according to their suitability for juvenile survival was investigated under field and enclosure conditions. Butterflies discriminated among host plants differing in leaf quality both before and after landing. Over 3 yr of field observations, the host plants on which females landed and oviposited were smaller, possessed longer buds, and bore a higher percentage of high-quality leaves than host plants on which females landed but left without depositing eggs. Similarly, the host plants on which females landed in those years were not a random sample of the host plants available in the habitat. Plants on which the butterflies alighted bore a higher percentage of high-quality leaves, a lower percentage of low-quality leaves, and longer buds than their nearest neighbors that were not landed upon. These characteristics were associated with differences in expected larval growth and survival. Field and enclosure experiments in which variation in certain plant characters was manipulated independently of variation in other plant characters generally confirmed these results. Enclosure studies suggested strongly that females learned to land on particular host types according to the responses those plants had elicited after previous alightings. The implications of that finding for models of the evolution of pre-alighting and post-alighting components of discrimination behavior are discussed.

Key words: *Aristolochia*; *Battus philenor*; discrimination behavior; host preference; intraspecific variation; leaf quality.

INTRODUCTION

Insect herbivores are not usually distributed randomly over plants within a host species found in a given habitat. While differential survival on different plants (Tilman 1978) is sometimes responsible, such patterns are more commonly generated through discrimination among plants by feeding or ovipositing insects (Whitham 1978, 1980, Journet 1980, Wolfson 1980, Coley 1983, Crawley and Nachapong 1984, Guerin and Städler 1984, Lewis 1984, Service 1984). Such discrimination behavior can be defined broadly as any behavior that results in one plant type being exploited in excess of its relative abundance in the habitat. Nonrandom use of conspecific host plants can arise from any of the following categories of behavioral responses: (1) nonrandom movement patterns in habitats where different host types differ in dispersion (Courtney and Courtney 1982, Kareiva 1982, Stanton 1982); (2) nonrandom rates of contact with alternative host types or with patches of alternative host types (Stanton 1982, Hodgson and Elbakhiet 1985, Myers 1985); and (3) nonrandom selection or handling of host types subsequent to discovery (Kennedy and Booth 1951, Everly 1959, Nishijima 1960, Perron et al. 1960, Ives 1978, Rausher and Papaj 1983, Myers 1985).

Although much effort has been devoted to docu-

menting examples of conspecific host discrimination, less attention has been given to whether and how components of discrimination behavior are adaptive, i.e., whether and how components of discrimination behavior cause individual insects to use plants with characteristics that enhance their fitness. Although nonrandom movement patterns, nonrandom contact, and nonrandom handling presumably evolved so as to increase an herbivore's survival or reproduction over that expected if plants were selected at random, each component may be under the same or different selective pressures. Rausher (1983), for example, offered a paradigm of evolutionary constraints on host-selection behavior by ovipositing herbivorous insects; in this paradigm the nature of natural selection on post-alighting discriminatory responses (category 3 above) was fundamentally different from selection on pre-alighting discriminatory responses (categories 1 and 2 above). Determining how much each class of discrimination behavior contributes to an apparently adaptive pattern of nonrandom host use is, therefore, a prerequisite for understanding the evolutionary processes that bring about and maintain host specificity.

The interaction between the pipevine swallowtail butterfly, *Battus philenor*, and one of its host plants in east Texas, *Aristolochia reticulata*, provides a convenient opportunity to examine these issues. We have already shown (Rausher and Papaj 1983) that the host plants (*Aristolochia* spp.) on which female pipevine swallowtail butterflies (*Battus philenor*) alighted and

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laid eggs differed from host plants on which females alighted and left without ovipositing. In addition, we have shown that this post-alighting discrimination increases the size at which offspring larvae disperse from their initial host plant, compared to the size that would be attained if eggs were laid on a random sample of host plants. Since the probability that a larva survives to reach another host plant depends on its size at dispersal (Rausher 1979), these results imply that discrimination enhances offspring survival. To the question of whether conspecific discrimination behavior is potentially adaptive, we answer in the affirmative, at least with respect to post-alighting behavior.

In this paper, we address the question of how discrimination among conspecific plants is adaptive. We examine specifically the hypothesis that female *B. philenor* butterflies increase larval size at dispersal by preferentially accepting *A. reticulata* plants that have large amounts of young, edible foliage and rejecting plants with small amounts. This hypothesis is motivated by previous studies (Rausher 1981) that showed that larvae readily feed on and grow rapidly on young foliage, but grow slowly on and tend to disperse frequently from old foliage. Although our previous study (Rausher and Papaj 1983) concentrated exclusively on post-alighting discrimination, we examine here both pre-alighting and post-alighting components of discrimination among *A. reticulata* plants.

METHODS

Field experiments

Field experiments were performed in 1981–1983 in open pine uplands (the pine–bluestem savanna of Streng and Harcombe 1982) in the John Henry Kirby State Forest in Tyler County, Texas. In these experiments, classification of leaves into young, intermediate, and old foliage was made on the basis of leaf color. Young leaves are tender and light green, while old leaves are tough and dark green. A standard assignment of leaves to age classes by color was achieved by matching leaves to a chart consisting of representative leaves of each of three color categories: A: light green, B: medium green, and C: dark green. These color categories reflect true differences in leaf quality, since larvae reared from hatching on leaves of category A grew faster (Fig. 1; ANCOVA, Leaf Color Effect, $F_{2, 177} = 275.10$, $P < .0001$, $R^2 = 0.85$) and had lower mortality (Fig. 1; binomial test, $P < .05$) than larvae reared on leaves of categories B or C.

Experiment 1.—We asked whether young foliage on an *Aristolochia reticulata* plant is a prerequisite for oviposition by *Battus philenor* females. In 1982, 100 plants were allocated randomly to each of two treatments: Young Foliage Present and Young Foliage Absent. In early April, all plants were clipped above the first node to stimulate production of new foliage. Four weeks later, young foliage was removed from plants in

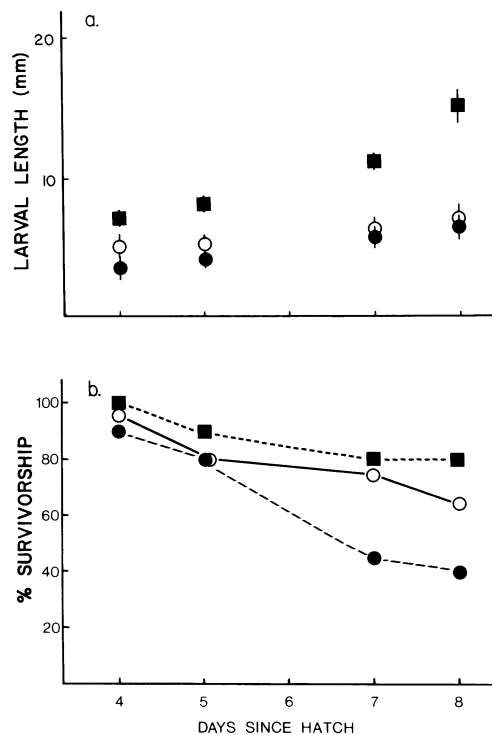


FIG. 1. (a) Change in mean larval length in time since hatch for *Battus philenor* larvae placed on leaves in three color categories: A (light green, ■), B (medium green, ○), and C (dark green, ●). Bars around symbols represent \pm one standard error about the mean. (b) Change in percent survivorship in time since hatch for larvae placed on leaves in the same three color categories. $N = 100$.

the Young Foliage Absent treatment. All plants were checked weekly for the presence of eggs. After each census, eggs were removed because females avoid laying eggs on plants bearing previously laid eggs (Rausher 1979).

Experiment 2.—We asked whether females discriminate among *A. reticulata* plants before alighting. Specifically we compared the cohort of plants alighted on by females over the course of the flight season with a cohort of plants sampled randomly from the habitat and censused periodically throughout the same time period. We reasoned that if ovipositing butterflies discriminate among host plants prior to alighting, then the plants visited by a female should not be a random sample of the plants available in the habitat.

Prior to the onset of adult emergence in 1982, we selected randomly 100 *A. reticulata* plants. The number of leaves in each color category for each plant was censused weekly over the time during which butterflies were observed. We followed searching females for periods of up to 30 min in the same field site. Host plants on which females alighted were marked with a surveyor's flag (Blackburn Manufacturing Company). The number of leaves in each color category for each plant was counted.

Experiment 3.—Any nonrandom alighting detected in Experiment 2 could be a consequence of (1) nonrandom movement patterns that bias the likelihood of encountering particular host types, or (2) nonrandom rates of alighting given encounter. In this experiment, we examined mechanism 2.

If *B. philenor* females discriminate among *A. reticulata* plants prior to alighting, then the plants that are alighted on should not be a random sample of the plants within the females' search paths. In practice, it is difficult to define the search path and to identify plants that are refused prior to alighting, unless rejection is accompanied by a measurable behavioral response to such hosts. We reasoned, however, that the host plants most likely to be recognized and rejected by searching females prior to alighting were plants near the host plants on which females alighted. We asked specifically if the plants on which female butterflies alighted differed physically from neighboring plants on which females did not alight.

During the first brood of 1983 we followed searching females for periods of up to 30 min. Host plants on which females alighted were marked with a surveyor's flag. We then matched each *A. reticulata* plant with the nearest congener that was not also alighted on by the same individual butterfly. For both sets of host plants, we measured the length and width of each leaf, the color category of each leaf, and the length of the bud. Leaf area (A) was estimated from a regression of leaf length and width on the areas of a sample of >200 leaves. The regression equation used was: $A = 0.205W - 0.0067L + 0.0072LW - 2.65$, where L is leaf length and W is leaf width ($R^2 = 0.91$; $P < .0001$).

Experiment 4.—In this experiment we examined post-alighting discrimination by *B. philenor*. We asked specifically whether *A. reticulata* plants on which *B. philenor* females alight and deposit eggs have more young foliage than plants on which females alight but fail to deposit eggs.

Individual females were followed during the first broods of 1981, 1982, and 1983. Each host plant alighted on by a female was marked with a surveyor's flag and checked immediately after the butterfly had resumed flight for the presence of eggs. Plants on which a female oviposited were classified as accepted plants. Plants on which a female did not lay eggs were classified as rejected plants. Any plants on which females did not oviposit and that bore previously laid eggs were eliminated from further analysis because *B. philenor* females tend to reject any plant bearing previously laid eggs (Rausher 1979). For each group of plants, we measured leaf area (in 1981 and 1983), leaf number (in 1982), leaf quality (in all years), and bud length (in 1981 and 1983).

Enclosure experiment

In this experiment we again attempted to determine whether the presence of young foliage on an *A. retic-*

ulata plant influences a female's tendencies to alight and oviposit on that plant. We used a large outdoor enclosure in which plant characteristics could be manipulated independently of location and microhabitat. Thus it was possible to dissociate particular plant characteristics from correlated microhabitat characteristics and verify that females were assessing characters inherent in the host plant. By randomizing the distribution of different types of *A. reticulata* plants, it was also possible to distinguish conclusively between nonrandom movement and differential response to encountered plants as causes of nonrandom alighting on conspecific plant types. Finally, we were able to disentangle experimentally the correlated effects of two plant characters, plant size and leaf quality, on discriminatory responses by *B. philenor* females by establishing discrete categories of *A. reticulata* plants.

The *A. reticulata* plants to which females were exposed differed in size and leaf quality: (1) phenologically mature plants of low leaf quality and large leaf area, (2) phenologically young plants of high leaf quality and large total leaf area, (3) phenologically mature plants of low leaf quality and small total leaf area, and (4) phenologically young plants of high leaf quality and small total leaf area. All host plants were collected from the Kirby Forest field site. In early June of 1983, each plant was cut back to the rootstock and transplanted to green plastic pots. Plants bearing young, high-quality foliage were prepared by cutting back the emergent growth to the rootstocks several weeks prior to the experiment in late July. Fifteen plants of each type were distributed randomly (using a computer-generated sequence; Barr et al. 1979) at grid positions within a rectangular array featuring >400 nonhost plants (see Papaj 1986a for a complete description of this array). Midway through the experiment, all host plants were redistributed in a random fashion to ensure that females did not learn the location of preferred plants.

Naive, mated female butterflies were released in the enclosure and allowed to search continuously between 0900 and 1500 over a 3-d period. We counted the number of plants of each age and size category on which females alighted and the number of ovipositions.

RESULTS

Field experiments

Experiment 1.—*Aristolochia reticulata* plants with young foliage (color category A) received proportionately more eggs than did plants without young foliage (Table 1) on each of four census dates. The Foliage Type \times Eggs interaction term of a three-way log-likelihood chi-square test ($G = 122.30$, $P < .001$) indicates that plants with new foliage were significantly more likely to have eggs laid on them than plants without new foliage. In fact, only 4 of 50 plants without young foliage received eggs during the experiment, compared to at least 48 of 50 plants with young foliage.

Experiment 2.—The *A. reticulata* plants on which females alighted were physically different from a random cohort of plants censused periodically over the entire flight season (two-way MANOVA [Barr et al. 1979] with Plant Category and Date as main effects; Plant Category effect, Wilk's $\lambda_{1,594} = 0.859, P < .0001$). Overall, plants sampled on different dates were physically different (Date effect, $\lambda_{1,594} = 0.383, P < .0001$), reflecting phenological change. In addition, the magnitude of the difference depended strongly on the dates over which the two groups were compared (Plant Category \times Date interaction, $\lambda_{1,594} = 0.859, P < .0001$), with differences becoming more pronounced as the season progressed.

The proportion of high-quality leaves, in particular, differed between plants on which females did and did not alight (Fig. 2b; % Type A Partial ss = 2.99, $P < .001$). Plants on which females alighted generally bore a higher proportion of leaves in color category A than censused plants, a difference that became more pronounced as the flight season progressed. Similarly, the difference between alighted upon and censused plants in proportion of low-quality leaves also differed significantly (Fig. 2c; % Type C Partial ss = 11.83, $P < .001$); again, this difference became more pronounced as the flight season progressed. By contrast, plant size (measured as leaf number) was not a factor in the overall differences between alighted upon and censused plants (Fig. 2a; Leaf Number Partial ss = 0.05, $P > .45$).

Experiment 3.—This experiment corroborates the results of Experiment 2. The *A. reticulata* plants that were alighted on by *B. philenor* females differed physically from neighboring plants that were not alighted on (Table 2). In particular, plants on which females alighted featured a higher proportion of leaves of category A, a lower proportion of leaves of category C, and longer buds than neighboring plants. No difference in leaf area between the two groups of plants was detected. Thus, these results parallel those of Experiment 2 in that categorizing plants as alighted plants and their nearest neighbors does not explain a significant portion of the variance in plant size (measured as leaf number or leaf area), but does explain a significant portion of the variance in two classes of leaf quality. Since females tended to alight on *A. reticulata* plants with proportionately more young foliage than neighboring plants,

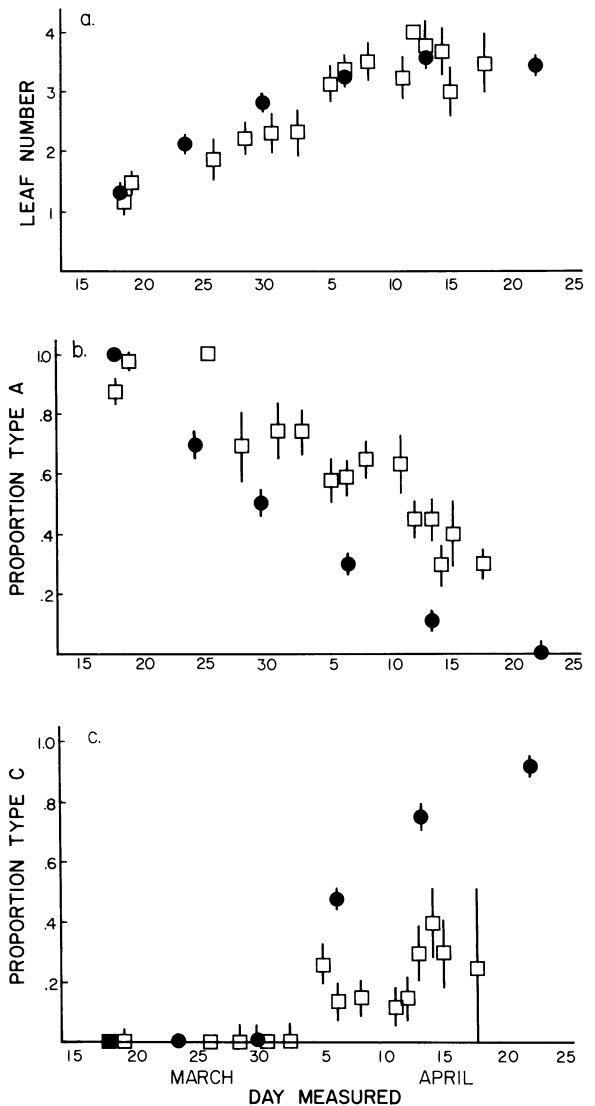


FIG. 2. (a) Temporal trends in *A. reticulata* leaf number for \square plants alighted on by searching *Battus* females and \bullet plants sampled randomly and censused periodically, in east Texas in 1982. (b) Seasonal trends in proportion of *A. reticulata* leaves in leaf color class A (light green) for \square plants on which *Battus* females alighted and \bullet plants sampled randomly and censused periodically. (c) Seasonal trends in the proportion of *A. reticulata* leaves in leaf color class C (dark green) for \square plants on which *Battus* females alighted and \bullet plants sampled randomly and censused periodically. Bars represent \pm one standard error around the mean.

TABLE 1. Results of egg censuses of *Aristolochia reticulata* plants in treatments with and without new foliage in the field in 1981.

Date	Proportion of plants with eggs	
	New foliage	No new foliage
11 May	.21	.02
18 May	.48	.02
25 May	.30	.00
29 May	.13	.00

nonrandom alighting was probably due, at least in part, to differences in the probability with which females approached and alighted on plants of different leaf quality.

Experiment 4.—In all three years of the experiment, *A. reticulata* plants on which *B. philenor* females alighted and laid eggs were physically different from plants on which females alighted but did not lay eggs (Table 3). In 1981, accepted plants were significantly

TABLE 2. Evaluation of paired differences between plants alighted on and their nearest neighbors not alighted on, over time.

Character	Mean difference	MANOVA*	
		t ($H_0 = 0$)	P
Leaf area (cm ²)	-2.19	1.30	>.5
Bud length (mm)	6.26	3.76	<.0002
% leaves type A (light green)	27.10	5.40	<.0004
% leaves type C (dark green)	-14.10	5.41	<.0004

* Results of MANOVA model (Barr et al. 1979) on estimated mean differences with date surveyed as main effect. Test of null hypothesis that the intercept of a MANOVA model for each character is 0. Bonferroni correction was applied to each comparison (Timm 1975).

different from rejected plants (MANOVA, Female Response Effect, $\lambda_{1, 739} = 0.953$, $P < .0001$). Although plants sampled on different dates were physically different (MANOVA, Date Effect, $\lambda_{4, 739} = 0.756$, $P < .0001$), the difference between accepted and rejected plants did not depend on date of sampling (MANOVA, Response \times Date interaction, $\lambda_{4, 739} = 0.969$, $P > .10$). Overall, accepted plants were significantly smaller in leaf area and featured longer buds than rejected plants (Table 3). No apparent differences between accepted and rejected plants in the proportion of leaves in color categories light-green (A) or dark-green (C) was detected in 1981.

In 1982, accepted plants were again different from rejected plants (MANOVA, Female Response Effect, $\lambda_{1, 154} = 0.882$, $P < .001$). Although plants sampled on different dates were again physically different, (MANOVA, Date Effect, $\lambda_{7, 154} = 0.508$, $P < .0001$), the difference between accepted and rejected plants did not

TABLE 3. Comparison of means of measured characteristics for *A. reticulata* plants accepted and rejected after alighting in different years.

Year	Character	(Mean of accepted) - (mean of rejected)	P*
1981	Leaf area (cm ²)	-3.73	<.0004
	Bud length (mm)	3.36	<.02
	% leaves type A (light green)	5.19	>.35
	% leaves type C (dark green)	-0.24	>.99
1982	Leaf number	-0.72	<.001
	% leaves type A	17.37	<.003
	% leaves type C	-1.53	>.50
1983	Leaf area (cm ²)	-2.58	<.002
	Bud length (mm)	2.28	>.10
	% leaves type A	8.37	<.05
	% leaves type C	-0.44	>.80

* Test of the null hypothesis that the differences are equal to 0 (Barr et al. 1979). The Bonferroni correction was applied to each comparison (Timm 1975).

TABLE 4. Results of a combined probability test (Sokal and Rohlf 1981) on differences between plants accepted and rejected after discovery, using measurements carried out in more than one year.

Character	df	χ^2	P
Leaf area (cm ²)	4	28.07	<.005
Bud length (mm)	4	12.03	<.025
% leaves type A (light green)	6	20.73	<.005
% leaves type C (dark green)	6	1.76	>.50

depend on date of sampling (MANOVA, Response \times Date interaction, $\lambda_{7, 154} = 0.848$, $P > .10$). Overall accepted plants bore fewer leaves on average and possessed a higher proportion of leaves of color category A than rejected plants (Table 3). No apparent difference between plant acceptance categories in the proportion of leaves of color category C was discerned in 1982.

In 1983, accepted plants were again significantly different from rejected plants (MANOVA, Female Response Effect, $\lambda_{1, 163} = 0.886$, $P < .001$). Although plants sampled on different dates were physically different (MANOVA, Date Effect, $\lambda_{4, 163} = 0.770$, $P < .001$), the difference between accepted and rejected plants did not depend on date of sampling (MANOVA, Response \times Date interaction, $\lambda_{4, 163} = 0.872$, $P > .10$). In 1983, accepted plants were significantly smaller in leaf area and were characterized by a higher proportion of leaves of color category A than were rejected plants (Table 3). Contrary to the 1981 results and those of Rausher and Papaj (1983), differences in bud length between accepted and rejected plants were not significant.

The results of a combined probability test (Sokal and Rohlf 1981: Table 4) on differences between accepted and rejected plants in characters measured in >1 yr generally confirm the findings by Rausher and Papaj (1983): *A. reticulata* plants on which females alighted and oviposited were smaller in leaf area and possessed longer buds than plants on which females alighted but did not oviposit. In addition, accepted plants generally bore a higher proportion of leaves of color category A than rejected plants.

Enclosure experiment.—In enclosure arrays, *B. philenor* females discriminated among plants of discrete sizes and phenological ages both before and after alighting on those plants (Table 5). Young plants received significantly more egg clusters than old plants within a given plant size category (two-way ANOVA, Age effect, $F_{1,55} = 24.46$, $P < .0001$), while large plants in a given leaf-age category received significantly more egg clusters than small plants (Size effect, $F_{1,55} = 25.45$, $P < .0001$). The Age \times Size interaction was not significant ($F_{1,55} = 0.03$, $P > .05$).

Examination of pre-alighting and post-alighting responses indicates that these differences arose from discrimination during both phases of searching behavior.

Alightings were decidedly nonrandom (Table 5). The average number of alightings received by plants of each age and size category pooled over all days were different from those expected if females alighted on each type in proportion to its abundance in the array. Females alighted much more frequently on large than on small plants (two-way ANOVA, Size effect, $F_{1,56} = 35.81$, $P < .0001$). Females also tended to alight slightly more often on young than on old plants within a given size category (Age effect, $F_{1,56} = 4.40$, $P < .05$). Moreover, the number of alightings on plants of each age category was independent of plant size category (Age \times Size interaction, $F_{1,56} = 0.06$, $P > .05$).

When the number of alightings on plants within a size and age category was pooled by day, the proportion of alightings on plants bearing old and young foliage changed over the duration of the experiment (Fig. 3). In particular, large and young plants received proportionately more alightings as time went on; large and old plants received proportionately fewer alightings as time went on. Weak trends were observed for small plants of either age category. A three-way contingency test of independence indicated that the differences in proportions of young and old plants alighted on over time depended on plant size (three-way G test, Day \times Age \times Size interaction, $G = 11.85$, $P < .005$). Possibly as a result of prior experience, females alighted progressively more often on large, young plants and less often on large, old plants. It is unlikely that butterflies were learning the positions of plants with a particular size and age, because the redistribution of pots prior to Day 3 did not diminish the increase in preference for large, young *A. reticulata* over time.

Post-alighting responses were also nonrandom. Young plants received egg clusters more often after a female alighted than did old plants, and large plants in a given age category always received egg clusters more often after a female alighted than did small plants (Table 5). Plant phenological age had a tremendous effect on the proportion of alightings that resulted in oviposition (two-way ANOVA; Age effect, $F_{1,56} = 24.62$, $P < .0001$). The post-alighting acceptability of a plant did not, however, depend on the size of the plant (Size effect, $F_{1,56} = 1.30$, $P > .05$). Finally, the effect of plant age on the proportion of alightings that ended in oviposition did not depend significantly on the size of the plant (Age \times Size interaction, $F_{1,56} = 2.11$, $P > .05$).

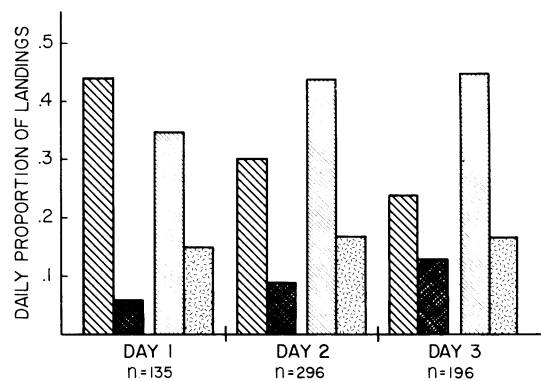


FIG. 3. Proportions of all alightings on categories of *A. reticulata* plants distributed randomly in equal numbers in an enclosure array, over three consecutive days of observation. ▨ old and large plants; ▩ old and small plants; □ young and large plants; ▤ young and small plants.

DISCUSSION

Leaf quality and juvenile performance

A previous study (Rausher and Papaj 1983) showed that females of the pipevine swallowtail butterfly, *Battus philenor*, discriminate adaptively among conspecific host plants in east Texas. Experimentally placed larvae were larger when dispersing from *Aristolochia reticulata* and *A. serpentaria* plants on which females oviposited than when dispersing from plants on which females alight but did not oviposit. Because larger size at first dispersal increased the probability that a larva lived to discover another host plant (Rausher 1979), this oviposition behavior presumably increased larval survival above that expected if females accepted all plants with equal probability.

The difference in size at dispersal between accepted and rejected plants probably did not reflect a difference in intensity of predation (Rausher and Papaj 1983). The finding that females tend to alight on and oviposit on *A. reticulata* plants with a greater proportion of young foliage suggests a more likely adaptive mechanism by which a female's progeny benefit from such discrimination behavior. Rausher (1980, 1981) reported that larvae dispersed sooner from old than from young leaves presented in laboratory assays. Moreover, larvae grew more slowly on old leaves than on young leaves in laboratory assays. A similar difference in larval growth rates on the three leaf color types was ob-

TABLE 5. Number of egg clusters and alightings, and proportion of alightings that ended in oviposition, for *A. reticulata* plants of discrete size and phenological age categories ($\bar{X} \pm 1$ SD). For each age and size, $N = 15$.

Plant size	Plant age	No. egg clusters	No. alightings	Proportion ovipositions
Large	Young	7.47 \pm 5.13	17.20 \pm 9.65	0.405 \pm 0.117
	Old	3.20 \pm 1.86	13.40 \pm 6.57	0.233 \pm 0.142
Small	Young	2.86 \pm 1.70	7.20 \pm 4.68	0.407 \pm 0.204
	Old	0.73 \pm 0.80	3.93 \pm 2.05	0.156 \pm 0.168

served in the laboratory assay (Fig. 1). It seems reasonable to infer that the higher proportion of young, high-quality leaves on acceptable plants permitted larvae to disperse at larger sizes from plants on which females laid eggs than from plants on which females did not lay eggs.

Pre-alighting and post-alighting components of discrimination behavior

While numerous studies have demonstrated that herbivores discriminate among leaves of different ages (Rockwood 1974, Denno et al. 1980, Spires 1981, Colley 1983), few have examined the behavioral components of such discrimination (but see Ives 1978, Rausher and Papaj 1983, Myers 1985). Preference for plants with proportionately more young foliage was a consequence of both pre-alighting and post-alighting components of discrimination behavior. With respect to pre-alighting behavior, *B. philenor* females in the field alighted on a group of *A. reticulata* plants that was not a random sample of the host plants available in the habitat. Although nonrandom alighting of this sort could be attributed to nonrandom movement patterns that bias the likelihood of encountering particular host types, our study indicates that nonrandom rates of alighting on encountered host plants were at least partly responsible.

In the field, the *A. reticulata* plants on which females alighted differed physically from their nearest neighbors. Although it is difficult to prove that searching females actually encountered but did not alight on neighboring plants, it would be more difficult yet to defend a mechanism by which movement patterns could produce this result. Consistent differences between plants alighted on and the nearest plants not alighted on could conceivably have arisen if the distribution of acceptable and unacceptable plants was spatially patchy and if contact with acceptable plants increased turning rates and/or decreased search speed so that females alighted mostly on acceptable plants near each other.

This possibility would warrant further scrutiny if plants alighted on by a given female were generally closer to each other than to the nearest plants that did not receive alightings. Most neighboring plants, however, were located within 3 m of plants alighted on and females frequently covered a straight line distance of tens of metres between oviposition events, during which flight they alighted regularly on host plants (D. Papaj, *personal observation*). Thus, neighbor plants for a given female were generally intermingled with plants alighted upon.

In the enclosure, females alighted proportionately more often on large plants than on small plants and more often on young plants than on old plants. Consequently, the group of plants with the most young foliage was alighted on most frequently by searching females. Because groups of plants of different sizes and phenological ages were distributed randomly in equal

numbers, this pattern of nonrandom alighting probably reflects pre-alighting discrimination behavior that is not a consequence of movement patterns and is consistent with field results.

Post-alighting responses by *B. philenor* females followed a similar pattern. In the enclosure, females oviposited more often after alighting on young foliage than after alighting on old foliage. In the field, the pattern was more ambiguous, but consistent with the interpretation that females preferred plants with young foliage. As with pre-alighting responses, plants accepted after alighting bore a greater proportion of younger foliage than plants rejected after alighting. Pre-alighting and post-alighting preferences were thus correlated in this insect.

Evolutionary constraints on discrimination behavior

If correlations between pre-alighting and post-alighting components of conspecific discrimination behavior are common, models for the evolution of discrimination behavior that assume independence between pre-alighting and post-alighting components may be inappropriate. Arguments derived from foraging theory (Jaenike 1978, Rausher 1983), for example, contended that pre-alighting and post-alighting discriminatory responses by ovipositing insects could be subject to very different selective pressures. The order in which host types are preferred in responses made after alighting on a host plant was expected to be correlated with her progeny's expected survivorship on alternative host types. Pre-alighting preference ranking, by contrast, was expected to evolve in a manner that optimized the product of juvenile survivorship and the female's overall egg-laying rate.

Our results suggest a constraint, namely learning (defined here as a change in behavior with experience), under which correlations among components of discrimination behavior might be expected. The frequency with which *B. philenor* females alighted on particular kinds of conspecific plants was apparently modifiable through experience (Fig. 3). Although females first alighted on large plants in each age category in proportion to their abundance, they eventually alighted significantly more often on large, young plants. Experienced females thus adopted a pre-alighting preference ranking of young over old plants that resembled the post-alighting preference ranking.

Learning to choose conspecific host plants may thus cause post-alighting preference rankings to resemble pre-alighting preference rankings, regardless of differences in selective pressures on individual components. If so, post-alighting discrimination behavior may not be well correlated with juvenile survivorship. Natural selection may actually set post-alighting responses to different host types such that the pre-alighting responses will be altered through experience in a way that increases egg-laying rate. Contrary to the predic-

tion that ovipositing females will order the post-alighting preference ranking according to the order of suitability for juvenile fitness, natural selection may order post-alighting responses to alternative host types according to the product of egg-laying rate and juvenile survivorship.

Very little is actually known about the relationship between post-alighting discrimination among conspecific host types and juvenile survivorship (save for Rausher and Papaj [1983] which supports the predicted correlation, and Mackay [1985], which does not). Nevertheless, at the level of host species, the rank order of post-alighting preference has not been well correlated with the suitability of these species for juvenile survivorship (Wiklund 1975, Rausher 1983, Singer 1983, and references within). While these discrepancies have been attributed variously to inappropriate laboratory measures of larval performance (Rausher 1983), lack of recognition of conspecific discrimination (Rausher and Papaj 1983), and even to evolutionary lag (Singer 1983, Mackay 1984), the dynamic interaction between pre-alighting and post-alighting discrimination behavior may provide another explanation. The failure to consider behavioral mechanisms such as learning could potentially engender erroneous conclusions about the adaptiveness of behavioral preference.

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