

## DEMOGRAPHIC CONSEQUENCES OF DISCRIMINATION AMONG CONSPECIFIC HOST PLANTS BY *BATTUS PHILENOR* BUTTERFLIES<sup>1</sup>

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**Abstract.** Ovipositing *Battus philenor* butterflies discriminate among conspecific host plants in the field. Discrimination has no detectable effect on larval growth rates or on predispersal mortality but does appear to enhance larval survival by increasing larval size at dispersal. A comparison of these results with those of a previous study suggests that the effects of discrimination among conspecific hosts on larval survival are similar in magnitude to analogous effects of discrimination between host species. The results of this study suggest that models and discussions of the evolution of host selection behavior that treat plant species as the unit of discrimination may be seriously flawed because they overlook significant aspects of insect behavior.

**Key words:** *Aristolochia*; *Battus*; host discrimination; host selection; larval demography.

Models of the evolution of foraging and host selection by herbivorous insects have traditionally assumed that plant species are the primary category among which insects discriminate (Levins and MacArthur 1969, Jaenike 1978). The same assumption is implicit in virtually all empirical investigations that have examined patterns of host selection by phytophagous insects and that have drawn inferences about the evolution of those patterns (Singer 1971, 1982, Wiklund 1974a, b, 1975, Chew 1975, 1977, Smiley 1978, Rausher 1979, 1980).

Nevertheless, there is no compelling reason for believing that the categories of plants discriminated by herbivorous insects correspond to those erected by plant taxonomists (Janzen 1979). In fact, numerous investigations of agricultural pests have demonstrated that insects can and do discriminate among conspecific plants (Everly 1959, Nishijima 1960, Perron et al. 1960, Cromartie 1975, Ives 1978).

While such discrimination is common, its demographic consequences have seldom been investigated. Yet it is precisely those consequences that are of importance for interpretation of the evolution of host selection behavior. If the pattern of discrimination among conspecific hosts has a minor effect on insect growth rates, survival, and fecundity, compared to the effects of discrimination among host species, then models that incorporate only the latter type of discrimination will likely serve as useful approximations. By contrast, if the effects of conspecific host discrimination on these fitness components are of roughly the same order of magnitude as the effects of discrimination among host species, then models that employ plant species as the primary unit of discrimination may be expected to pro-

vide a woefully inadequate description of how natural selection molds host selection behavior.

The primary objective of this investigation was to determine whether conspecific discrimination among hosts in a phytophagous insect has detectable effects on insect growth rate and survival. We first demonstrate that the experimental animal, the pipevine swallowtail butterfly, *Battus philenor*, discriminates among conspecific host plants when ovipositing. We then examine whether larval growth rates and survival differ for larvae growing on plants accepted and rejected by females. Finally, we compare the magnitude of the effects of conspecific discrimination on survival with analogous effects of discrimination among host species.

### METHODS

Pipevine swallowtail females were observed searching for larval host plants between 15 March and 14 June 1980 in the pine uplands of the John Henry Kirby State Forest in Tyler County, Texas. Females were present in two pulses or broods. During the first brood, females oviposited almost exclusively on *Aristolochia reticulata* (Aristolochiaceae), while second-brood females oviposited primarily on *A. serpentaria* (Rausher 1980). Consequently, two sets of experiments were performed. One set assayed female discrimination among and larval growth on and disappearance from *A. reticulata* during the first brood. The second set, performed during the second brood, assessed discrimination among and larval performance on *A. serpentaria*.

#### *Discrimination among conspecific hosts*

Postalighting discrimination was assessed by comparing morphological characteristics of host plants on which females alighted but did not oviposit (rejected plants) with characteristics of host plants on which females laid eggs (accepted plants). Two observers fol-

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TABLE 1. Characters used for comparing accepted and rejected plants. Numbers in parentheses refer to broods (first or second) in which characters were measured.

| Plant character                  | Time measured             |
|----------------------------------|---------------------------|
| Total leaf area,* initial (1, 2) | Day female alighted       |
| Terminal bud length, initial (1) | Day female alighted       |
| Height, initial (1, 2)           | Day female alighted       |
| Stem diameter (1)                | Day female alighted       |
| Change in leaf area† (1)         | 7 d after female alighted |
| Terminal bud length, final (1)   | 7 d after female alighted |
| Total leaf area, final (2)       | 7 d after female alighted |
| Height, final (2)                | 7 d after female alighted |

\* Sum of individual leaf areas estimated from leaf length and width measurements and a regression of area on length and width.

† Estimated as leaf area 7 d after alighting - leaf area on day of alighting.

lowed individual females and marked each host plant on which a female alighted. One observer recorded whether the female oviposited or resumed searching without laying eggs. The other observer inspected the plant for the presence of previously laid eggs. Only plants without such eggs were included in the analysis, since presence of eggs normally deters oviposition, regardless of plant size or quality (Rausher 1979). Observation of a female was ended after 30 min or when she flew out of the study area.

The morphological characteristics measured for each marked plant are listed in Table 1. Measurements were performed on the day on which a female was observed to alight on a plant and again 7 d later. The interval of 7 d was chosen because that is the average duration of the egg stage for *B. philenor*, and experimental larvae were placed out after this time interval.

Statistical comparison of morphological characters was performed using multivariate analysis of variance (MANOVA; Timm 1975). In this analysis, date of observation was considered to be a main effect in addition to female reaction (accept vs. reject), since plant growth produced measurable differences in many of the characters over the course of the experiment. A test of the significance of the main effect of female reaction on plant morphology thus tests whether on any given day accepted plants differ from rejected plants. Such a difference would indicate that the plants females oviposit on do not constitute a random sample of those upon which they alight, and hence that females discriminate among conspecific hosts. Such a difference would not indicate, however, that females "assess" in any sense the particular characters we measured, but only that the cues used for discrimination are correlated with the measured characteristics.

### Larval performance

The demographic consequences of female discrimination were assessed by comparing larval performance on accepted and rejected plants. Seven days after a plant had been alighted on by an observed female, two (first brood) or three (second brood) newly hatched larvae were placed out on the plant. Larvae were obtained from eggs laid by captive females and were assigned randomly to the plants. The number of larvae placed on each plant corresponded to the integer nearest the average egg cluster size for females of a particular brood (i.e., average cluster sizes are 2.2 and 2.6 eggs for first- and second-brood females, respectively).

The lengths of each larva remaining on each plant were measured daily to the nearest 0.5 mm. A separate experiment had shown that larval length and biomass are highly correlated ( $r = 0.91$ ,  $n = 82$ ,  $P < .001$ ) and that our measurement of length was an appropriate index of larval size. Whenever a larva disappeared from a plant we noted whether any edible tissue remained on the plant. Young, edible *A. reticulata* foliage is easily distinguishable from old, inedible foliage by color and texture, while all foliage on *A. serpentina* is edible (Rausher 1981). We could thus assign a tentative cause to the disappearance of each larva. Larvae that disappeared while there was still edible foliage on the plant (category 1, disappearance due to predispersal mortality) were assumed to have died, since previous experiments had shown predispersal mortality to be high and that larvae rarely disperse from a plant while any edible foliage remains (Rausher 1981). Conversely, if a larva disappeared and no edible tissue remained on the plant (category 2, disappearance due to dispersal), we assumed that the larva had dispersed from the plant. Although cause of disappearance may have been misclassified in some cases, we believe the frequency of such misclassifications to be low because of the observed tendency of larvae to disperse only when all edible foliage has been consumed. Moreover, any systematic bias in classification should apply equally to accepted and rejected plants and thus should not influence differences between the two types of plants.

The daily censuses yielded estimates of three characters which influence fitness and population growth rate: larval growth rate, mortality, and size of larvae at dispersal. Larval growth rates on accepted and rejected plants were compared by assessing whether the size of surviving larvae differed on the two types of plants on each day between the 1st and 10th d after larvae were placed on plants. One effect of discrimination on mortality was assessed by comparing, for larvae on accepted and rejected plants, the proportion of larvae disappearing due to predispersal mortality (category 1 disappearance). Finally, the effect of discrimination on mortality incurred during dispersal was assessed by comparing the sizes of experimental lar-

vae measured just prior to disappearance for those individuals presumed to have disappeared from accepted and rejected plants (category 2 disappearance). Since previous studies (Rausher 1979) have demonstrated that the probability that a dispersing larva will discover another host plant is proportional to size at dispersal, a difference in size at dispersal between larvae on accepted and rejected plants reflects a difference in juvenile survivorship.

All statistical analyses of larval size were performed using two-way analysis of variance with female reaction (accepted vs. rejected plants) and date larvae were placed out as main effects. The actual values used in the analyses were the means of the sizes of all larvae on a plant. All values were transformed to logarithms to make the data conform to the normality assumptions of analysis of variance. The GLM (General Linear Models) procedure of Barr et al. (1979) was used.

## RESULTS

### *Discrimination by females*

If *Battus philenor* females do not discriminate among conspecific host plants, the plants oviposited on should constitute a random sample of those alighted on, and accepted plants should not differ from rejected plants. In fact, accepted plants in this study did not constitute a random sample. For first-brood females, the overall mean vector of measured plant characteristics differed for accepted and rejected *Aristolochia reticulata* plants (Table 2A). Accepted plants had significantly larger initial and final terminal bud lengths and smaller leaf areas at time of alighting than did rejected plants (Ta-

TABLE 2. Comparison of measured characteristics for accepted and rejected *A. reticulata* plants. A. Multivariate analysis of variance testing for overall difference in measured characteristics between accepted and rejected plants (female-reaction effect). Wilk's lambda criterion ( $\lambda$ ) was used. B. Differences in means of individual characters. Confidence intervals were calculated using Bonferonni procedure (Timm 1975).

| A.                                     |   |           |        |
|--|---|-----------|--------|
| Source                                 | df  | $\lambda$ | P      |
| Date (D)                               | 9   | 0.570     | <.0001 |
| Female reaction (R)                    | 1   | 0.913     | <.0001 |
| D $\times$ R                           | 9   | 0.853     | <.05   |
| Error                                  | 469   | ...       |        |
| B.                                     |   |           |        |
| Character                              | Mean of accepted – mean of rejected plants (95% ci) |           |        |
| Terminal bud length, initial (mm)      | 2.80 ( $\pm 2.37$ )*                                |           |        |
| Terminal bud length, final (mm)        | 2.97 ( $\pm 2.69$ )*                                |           |        |
| Height (mm)                            | -4.40 ( $\pm 9.65$ )                                |           |        |
| Leaf area, initial (cm <sup>2</sup> )  | -2.93 ( $\pm 1.87$ )*                               |           |        |
| Change in leaf area (cm <sup>2</sup> ) | 1.95 ( $\pm 2.65$ )                                 |           |        |
| Stem diameter (mm)                     | 0.11 ( $\pm 0.12$ )                                 |           |        |

\*  $P < .05$ .

TABLE 3. Comparison of measured characteristics for accepted and rejected *A. serpentaria* plants. A. Multivariate analysis of variance testing for overall difference in measured characteristics between accepted and rejected plants (female-reaction effect). Wilk's lambda criterion ( $\lambda$ ) was used. B. Differences in means of individual characters. Confidence intervals were calculated using Bonferonni procedure (Timm 1975).

| A.                                    |   |           |      |
|---------------------------------------|---|-----------|------|
| Source                                | df  | $\lambda$ | P    |
| Date (D)                              | 4   | .341      | NS   |
| Female reaction (R)                   | 1   | .444      | <.05 |
| D $\times$ R                          | 4   | .322      | NS   |
| Error                                 | 14  | ...       |      |
| B.                                    |   |           |      |
| Character                             | Mean of accepted – mean of rejected plants (95% ci) |           |      |
| Height, initial (mm)                  | 14.23 ( $\pm 13.94$ )*                              |           |      |
| Height, final (mm)                    | 15.83 ( $\pm 13.94$ )*                              |           |      |
| Leaf area, initial (cm <sup>2</sup> ) | 18.02 ( $\pm 14.78$ )*                              |           |      |
| Leaf area, final (cm <sup>2</sup> )   | 19.84 ( $\pm 14.81$ )*                              |           |      |

\*  $P < .05$ .

ble 2B). Similar differences were found for second-brood females. Accepted *A. serpentaria* are larger than rejected plants in height and leaf area, both at the time females alight on them and 7 d later at the expected time of hatching (Table 3). These results indicate that first-brood females discriminate among *A. reticulata* plants using some set of criteria correlated with terminal bud size and leaf area, while second-brood females discriminate among *A. serpentaria* plants using criteria correlated with leaf area and height.

### *Effects of discrimination on larval growth and survival*

*Larval growth rates.*—To assess whether growth rates of larvae placed on accepted and rejected plants differed, we compared larval size  $n$  days after larvae were placed out, using a two-way analysis of variance. In this analysis, female reaction (accepted vs. rejected) and date larvae were placed out were the main effects. Because choice of  $n$  is arbitrary, we performed such an analysis for each of the first ten days after larvae were placed on *A. reticulata* (brood 1) and for each of the first 7 d after larvae were placed on *A. serpentaria* (brood 2). After these numbers of days, too few larvae remained on plants to permit a reliable analysis. The results for the separate analyses within a brood are not statistically independent of each other, since size at day  $n$  is correlated with size at day  $n + 1$ ; however, this lack of independence did not cause problems in interpreting the results, since the conclusions were similar for all values of  $n$  examined.

In both broods 1 and 2, none of the female reaction  $\times$  date interaction effects was significant in any of the analyses. Moreover, only 1 of the 17 female-

TABLE 4. Significance levels for tests of the hypothesis that larval lengths did not differ on accepted and rejected plants. "Day measured" refers to number of days after larvae were placed on host plant.  $F$  values are for tests of the female-reaction main effect; all have 1 df associated with the numerator. The tabulated df is associated with the error MS.

| Day measured | Brood 1 |     |     | Brood 2 |     |     |
|--------------|---------|-----|-----|---------|-----|-----|
|              | $F$     | df  | $P$ | $F$     | df  | $P$ |
| 1            | 0.11    | 404 | NS  | 0.01    | 32  | NS  |
| 2            | 0.01    | 364 | NS  | 1.34    | 31  | NS  |
| 3            | 0.43    | 335 | NS  | 1.70    | 29  | NS  |
| 4            | 2.52    | 306 | NS  | 0.03    | 28  | NS  |
| 5            | 2.33    | 267 | NS  | 1.00    | 21  | NS  |
| 6            | 1.56    | 229 | NS  | 4.84    | 12  | .05 |
| 7            | 1.06    | 184 | NS  | 0.82    | 9   | NS  |
| 8            | 0.17    | 140 | NS  | ...     | ... | ... |
| 9            | 1.67    | 103 | NS  | ...     | ... | ... |
| 10           | 0.39    | 68  | NS  | ...     | ... | ... |

reaction main effects was significant (day 6, brood 2), and this effect was just barely significant at the  $P = .05$  level (Table 4). Consequently, these analyses provide no indication that discrimination by females influences larval growth rates. Females do not appear

to be ovipositing selectively on plants on which larval growth rates are above average.

*Overall pattern of larval disappearance.*—Although conspecific discrimination by females does not appear to affect larval growth rate, it does influence the size attained by a larva before it disappears from a plant (Fig. 1A, B). The graphs in this figure are analogous to survivorship curves, except that percent of dispersing larvae remaining on the experimental plants through a given size replaces percent survival through a given age. For brood 1 larvae, mean length at disappearance was greater for accepted plants than for rejected plants (5.94 vs. 4.871 mm, respectively;  $F_{[1,433]} = 3.40$ ,  $P = .06$ ;  $F$  value is for female-reaction main effect in a two-way ANOVA with date as second main effect). Similarly, in the brood 2 experiment, mean larval length at disappearance was greater on accepted than on rejected plants (8.37 vs. 5.93 mm;  $F_{[1,32]} = 4.95$ ,  $P < .04$ ).

These results indicate that discrimination has some overall effect on larval performance. Because disappearance may be due to either dispersal of larvae from their original host or predispersal mortality, however, the differences in disappearance rates depicted in Fig.

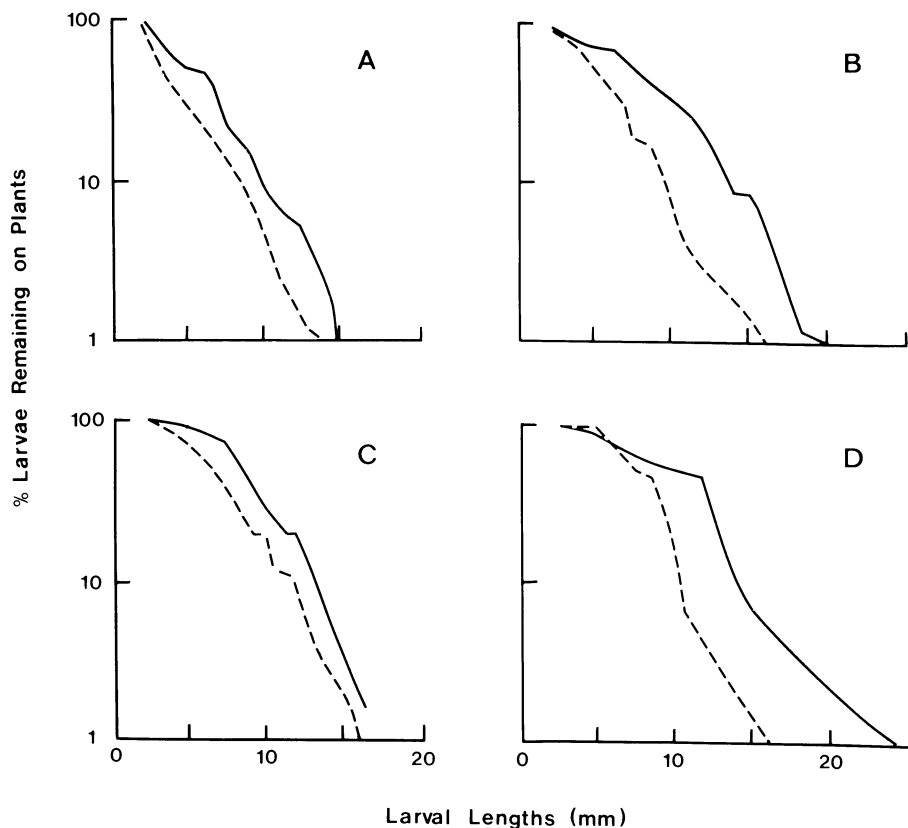


FIG. 1. Percent of larvae remaining on experimental plants as a function of larval size. Curves are analogous to survivorship curves, with percent remaining replacing percent surviving. Solid lines: larvae on accepted plants. Broken lines: larvae on rejected plants. A. All larvae on *Aristolochia reticulata*. B. All larvae on *A. serpentaria*. C. Only dispersing larvae on *A. reticulata*. D. Only dispersing larvae on *A. serpentaria*.

TABLE 5. Likelihood-ratio chi-square analysis of three factors: female reaction to host (accept vs. reject), date larvae placed on experimental plants, and causes of larval disappearance (predispersal mortality vs. dispersal). See text for details.

| Effect                                       | df | $\chi^2$ | <i>P</i> |
|--|----|----------|----------|
| A. Brood 1 ( <i>A. reticulata</i> )          |    |          |          |
| Female reaction $\times$ cause               | 1  | 0.25     | NS       |
| Date $\times$ cause                          | 9  | 24.43    | <.005    |
| Female reaction $\times$ date                | 9  | 107.01   | <.001    |
| Female reaction $\times$ date $\times$ cause | 9  | 18.98    | <.05     |
| B. Brood 2 ( <i>A. serpentaria</i> )         |    |          |          |
| Female reaction $\times$ cause               | 1  | 0.28     | NS       |
| Date $\times$ cause                          | 5  | 39.74    | <.005    |
| Female reaction $\times$ date                | 5  | 10.49    | NS       |
| Female reaction $\times$ date $\times$ cause | 5  | 11.67    | =.05     |

IA, B may be due to underlying differences in either or both processes. The remaining analyses describe preliminary attempts to assess the relative contribution of these two factors to the overall difference in size at disappearance from accepted and rejected plants.

*Predispersal mortality.*—The influence of female discrimination on predispersal mortality was assessed using a three-way likelihood ratio chi-square analysis as described by Fienberg (1970) and Bishop et al. (1975). In this analysis, the three categorical variables were female reaction, date larvae were placed out, and cause of larval disappearance (category 1 vs. category 2). The statistical significance of four different effects can be determined by this type of analysis (Table 5). The female reaction  $\times$  cause effect tests whether the proportion of disappearances due to predispersal mortality (category 1), averaged over all dates, differed for accepted and rejected plants. Consequently, it is the effect of primary interest. The date  $\times$  cause effect tests whether the proportion of disappearances due to predispersal mortality differed on different dates. The female reaction  $\times$  date effect tests whether the proportion of plants alighted on that were accepted differed among dates. Finally, the female reaction  $\times$  date  $\times$  cause three-way effect tests whether the difference between accepted and rejected plants in proportion of disappearances due to predispersal mortality varies from one day to another. Consequently, this effect also provides some indication of whether accepted and rejected plants differ in characteristics that influence larval survival.

For the brood 1 experiment, the female reaction  $\times$  cause effect was not significant (Table 5A). This result indicates that discrimination by females has no overall effect on predispersal mortality; when averaged over all dates, predispersal mortality rates were similar for accepted and rejected plants. By contrast, the three-way effect was significant ( $P < .05$ , Table 5A), indicating that discrimination has some kind of influence

on predispersal mortality. The nature of that influence is best revealed by examining the female reaction  $\times$  cause two-way tables for each date separately.

In the brood 1 experiment there were 10 such two-way tables, corresponding to the 10 dates on which larvae were placed out. For eight of these tables there was no significant lack of independence between female reaction and cause of disappearance. For two tables, however, there was a significant lack of independence ( $P < .05$ ). On the date corresponding to one of these tables, predispersal mortality was significantly higher on rejected plants, while on the date corresponding to the other table, the reverse was true. Thus, it would appear that the effect of female discrimination on predispersal mortality depends on environmental factors that vary from day to day. The number of days on which predispersal mortality is higher on accepted plants appears to be about equal to the number of days on which the opposite is true, and hence the opposite effects tend to cancel each other, leaving no overall influence of discrimination.

A similar pattern is revealed by the brood 2 experiment (Table 5B). The female reaction  $\times$  cause effect was not significant, whereas the three-way effect was significant, although just barely so ( $P = .05$ ). Analysis of the six two-way female reaction  $\times$  cause tables indicated that four of these tables showed no significant difference in predispersal mortality between accepted and rejected plants. Of the remaining two dates, the table corresponding to one exhibited a significantly ( $P < .05$ ) higher predispersal mortality on accepted plants, while the table corresponding to the other date exhibited an almost significant ( $P = .06$ ) trend in the opposite direction. Thus, as with *A. reticulata*, female discrimination among *A. serpentaria* plants seems to have an effect on predispersal mortality, but the direction and magnitude of that effect appear to differ from day to day. As a consequence, there is no detectable net effect when averaged over many days.

*Larval dispersal.*—The effect of female discrimination on size at which larvae disperse from their first host plant was assessed by comparing maximum size attained by dispersing larvae (disappearance category 2) on accepted and rejected plants. This comparison, shown graphically in Fig. 1C, D, indicates that in both broods, larvae on accepted plants are larger at dispersal than are larvae on rejected plants. Mean size at dispersal in the brood 1 experiment was 8.24 mm on accepted plants and 7.66 mm on rejected plants; for the brood 2 experiment, the corresponding values were 11.81 and 9.23 mm.

The statistical significance of these differences was tested using a two-way ANOVA on size at disappearance, with female reaction and date as main effects. The difference between accepted and rejected plants was significant for the brood 1 experiment [ $F_{(1,226)} = 4.10$ ,  $P < .05$ ], but not for the brood 2 experiment [ $F_{(1,17)} = 0.43$ ,  $P > .5$ ]. While this lack of significance

for the brood 2 data may indicate that the effects of female discrimination on larval size at dispersal differ for females ovipositing primarily on *A. reticulata* and those ovipositing primarily on *A. serpentaria*, the second-brood data are fully consistent with the hypothesis that females discriminate in favor of *A. serpentaria* plants on which larvae grow to greater-than-average size before dispersal. Unfortunately, the small sample size in this experiment probably precluded demonstration of the statistical significance of such an effect. In any case, these data indicate that for *A. reticulata*, and possibly for *A. serpentaria*, discrimination by females among conspecific hosts leads to an increase in the size at which larvae disperse from their original host.

#### DISCUSSION

##### *Conspecific host discrimination and its demographic consequences*

Two major conclusions may be drawn from this investigation: (1) *Battus philenor* females discriminate among conspecific host plants when ovipositing, and (2) discrimination has demonstrable effects on larval survival. Discrimination is indicated by the fact that plants upon which females alight but do not oviposit differ morphologically from those upon which they lay eggs. We wish to emphasize that the morphological characteristics we measured are not necessarily perceived or assessed in any way by females when making a "decision" about whether to oviposit. Nevertheless, the very fact that accepted and rejected plants do differ in some of the measured characteristics indicates that accepted plants do not constitute a random sample of the plants on which females alight, and that those characteristics are at least loosely correlated with the actual cues discriminated by females. We also wish to point out that we have no indication that the cues used to discriminate among *Aristolochia reticulata* plants are the same cues used to discriminate among *A. serpentaria* plants, nor do we know whether observed differences in morphological characters between accepted and rejected plants are in any way responsible for observed differences in larval size at disappearance.

Discrimination among conspecific hosts affects the size at which larvae disappear from host plants in the expected way; larvae grow to larger sizes on accepted plants than on rejected plants. Difference in size at disappearance appears to be almost solely due to differences in the size at which dispersing larvae leave their first plant (compare Fig. 1C, D with 1A, B). Since growth rates and predispersal survivorship do not differ on accepted and rejected plants, these results imply that larvae remain longer on accepted plants and that predispersal mortality rates (probability of dying per unit time) are lower on accepted plants. In effect, the longer residence time on accepted plants compensates for the lower mortality

rate to produce the same predispersal probability of dying as obtains on rejected plants. The ultimate demographic significance of conspecific host discrimination thus appears to depend on how differences in size at dispersal affect subsequent larval survival, since with equal predispersal mortality on accepted and rejected plants, only postdispersal differences in survivorship could produce differences in survivorship over the entire larval stage.

Rausher (1979) has demonstrated that the probability that a dispersing larva will discover another host plant is correlated with larval size. It thus seems reasonable to assume that larvae dispersing from accepted plants would have a greater probability of discovering a new host, and consequently a greater overall probability of survival to the adult stage, than would larvae dispersing from rejected plants. This argument, of course, rests on the assumption that accepted and rejected plants do not differ in proximity to other hosts, but this assumption has been shown by Rausher (1983) to be valid. It seems reasonable to conclude, therefore, that by ovipositing selectively on plants on which larvae grow to larger-than-average sizes before dispersing, females increase the fraction of their offspring that survive to discover new hosts and hence increase overall larval survival. Unfortunately, it has not yet been possible to quantify the magnitude of this overall effect and hence estimate the precise influence of conspecific discrimination on fitness.

##### *Comparison of discrimination within and among host species*

Although the precise effect of discrimination on fitness cannot be quantified, it is possible to compare the demographic consequences of discrimination between conspecific hosts with analogous effects of discrimination among host species. In doing so, though, one must bear in mind the crudeness of the comparison, and place major weight on the qualitative, rather than quantitative, aspects of the comparison.

Rausher (1980) demonstrated that brood 2 females discriminate against *A. reticulata* and in favor of *A. serpentaria* when ovipositing. Such discrimination is achieved by two distinct mechanisms: (1) a prelighting search bias, with females tending to alight disproportionately often on *A. serpentaria* (see also Rausher and Papaj, *in press*); and (2) a postlighting response bias, with females exhibiting a greater probability of ovipositing on an *A. serpentaria* plant than on an *A. reticulata* plant once they have alighted. Rausher (1980) also demonstrated that larvae are larger when they disappear from *A. serpentaria* plants than when they disappear from *A. reticulata* plants. The effects of discrimination between host species thus appear to be similar in kind to the consequences of conspecific discrimination. It is instructive to ask whether the magnitudes of these two effects are comparable.

In his previous study, Rausher did not measure lar-

TABLE 6. Comparison of mean stage at disappearance for larvae on preferred and nonpreferred plants. Preferred plants are *A. serpentaria* in the between-host-species comparison, accepted plants in the within-species comparisons. Nonpreferred plants are *A. reticulata* in between-species comparisons. Percent difference is the percent by which mean stage at disappearance on preferred plants exceeds the mean stage at disappearance on nonpreferred plant.

| Type of discrimination                | Mean stage at disappearance<br>( $\pm$ SE) |                        | Per-<br>cent<br>differ-<br>ence |
|---------------------------------------|--|------------------------|---------------------------------|
|                                       | Preferred<br>plants                        | Nonpreferred<br>plants |                                 |
| Between host species                  | 2.78 ( $\pm$ 0.46)                         | 1.71 ( $\pm$ 0.84)     | 38.9                            |
| Among <i>A. reticulata</i><br>plants  | 2.37 ( $\pm$ 0.10)                         | 1.83 ( $\pm$ 0.06)     | 22.8                            |
| Among <i>A. serpentaria</i><br>plants | 2.27 ( $\pm$ 0.09)                         | 1.78 ( $\pm$ 0.11)     | 27.5                            |

val sizes on a daily basis. Rather, he quantified size of disappearance in terms of identifiable stages during the larval period. These stages were operationally identified as the day immediately following a molt to a new instar and the following day. Thus, stage 1 was the day larvae was placed out, stage 2 1 d later, stage 3 the day immediately following the molt to instar 2, etc. In practice, because the duration of instars is normally 2–3 d, and little growth occurs in the 12–24 h prior to molting, these stages represent roughly the end- and midpoints of growth during a particular instar. Moreover, there is a high correlation between log (larval length) and stage ( $r = 0.909$ ,  $n = 496$ ,  $P < .001$ ), indicating that stage is a good measure of size. See Rausher (1979) for further justification for the use of these stages.

In addition to larval length, growth stage was noted for all larvae on the daily censuses during the present study. These data on growth stage were used to derive an empirical relationship between growth stage and larval length (see below) and to compare the effects of conspecific host discrimination with those of discrimination between host species. This comparison is shown in Table 6.

In the earlier study (Rausher 1980), mean stage at disappearance for larvae on the preferred *A. serpentaria* was 38.9% greater than mean stage at disappearance for larvae on the nonpreferred *A. reticulata*. When mean stage at disappearance is converted to mean size, using the regression:

$$\ln(\text{length}) = 0.34(\text{stage}) + 0.76,$$

obtained from the current study, it is found that brood-2 larvae are  $\approx$ 40% larger when they disappear from *A. serpentaria* than when they disappear from *A. reticulata*. From the current study, mean stage at disappearance was 22.8% greater for larvae on accepted *A. reticulata* plants than for larvae on rejected plants. The corresponding difference in mean larval lengths was 23%. Also from the current study, mean stage at

disappearance was 27.5% greater on accepted *A. serpentaria* plants than on rejected conspecific plants, and the corresponding difference in mean larval lengths was 41%.

These comparisons indicate that the effects of discrimination among conspecific hosts on larval demography, as measured by size or stage at disappearance, are comparable in order of magnitude to analogous effects of discrimination among host species. Moreover, most of the difference in size (or stage) between larvae disappearing from conspecific accepted and rejected plants is due to differences in the size at which larvae disperse. Although we presently have no solid evidence, it seems reasonable to suppose that the same is true of the difference between host species in larval size at disappearance. If this assumption is valid, then it would appear that the effects of conspecific and interspecific host discrimination on size at dispersal, and hence on overall larval survival, are similar in magnitude.

This conclusion suggests that it may often be inappropriate to treat food plant species as the unit of discrimination in discussions of the evolution of foraging and oviposition behavior, as has usually been done in the past (e.g., Levins and MacArthur 1969, Wiklund 1974a, b, 1975, Chew 1975, 1977, Gilbert 1978, Jaenike 1978, Rausher 1979, 1980). The fact that many other species discriminate among conspecific host plants (Everly 1959, Nishijima 1960, Perron et al. 1960, Ives 1978, Rausher et al. 1981) suggests that plant categories of evolutionary importance to phytophagous insects are not necessarily congruent with those recognized as species by biologists. Failure to recognize the actual plant categories discriminated by phytophagous insects may lead to erroneous conclusions about host-selection behavior.

Such distinctions could be important, for example, in testing predictions about how female insects alter oviposition behavior in response to changes in the relative abundances of different host plants. By analogy with foraging theory (Pyke et al. 1977), one might predict that an increase in the abundance of a preferred host species would lead to a lowered probability of ovipositing on a less-preferred host species. However, if females discriminate among conspecific host plants, a change in the overall abundance of a preferred host species might be a poor indicator of change in the abundance of categories of plants within that species that are accepted by females. Thus an increase in that plant species' abundance that is solely due to an increase in the abundance of plants in categories discriminated against by females would probably not be perceived as a "relevant" change by females, and hence would not lead to a change in behavior. An investigator who failed to recognize the distinction between the two types of conspecific plant, those discriminated against and those preferred by females, might then note an increase in abundance of the host

species and the failure of females to alter their behavior and conclude erroneously that those females do not conform to the predictions of foraging theory.

Several recent studies (Wiklund 1974, 1975, Chew 1975, 1977) have tested the hypothesis, derived from foraging theory (Pyke et al. 1977), that oviposition behavior in phytophagous insects evolves in such a way that the preference ranking of different host species corresponds to the ranking of hosts by suitability for insect survival and fecundity. In general, the results of these studies have not conformed well with expectations of theory. While explanations for these deviations from expectation have been offered in the original papers and elsewhere (e.g., Rausher 1983), the results of this study suggest that those deviations may in part be artifacts of a failure by investigators to recognize categories of conspecific plants distinguished by insects.

Because fitness may differ for insects reared on different categories of conspecific plants, as is suggested by the results of this investigation, failure to recognize these categories could lead to biased estimates of the suitability of a particular plant species. Consider, for example, a hypothetical situation in which a butterfly species oviposits on two plant species in a habitat. Suppose further that within each plant species, females discriminate among two categories of plants which can be designated as acceptable and unacceptable. The butterfly thus "recognizes" four different categories of plants: species I-acceptable (I-A), species I-unacceptable (I-U), species II-acceptable (II-A) and species II-unacceptable (II-U). Now suppose (1) all four categories are equally abundant, (2) fitness on plants in these categories is described by the relationship  $I-A > II-A > II-U \gg I-U$ , and (3) females have a higher probability of ovipositing on I-A than on II-A plants. Then the behavior is exactly what is predicted by foraging theory. However, an investigator who failed to recognize the distinction between acceptable and unacceptable conspecific plants and who measured both preference and larval survival on a random sample of plants from each species would find that mean survival would be higher on species II (because of 2 above), while the butterflies would seem to prefer species I. The investigator would thus conclude erroneously that the predictions of foraging theory were not upheld by this butterfly species. We suspect that this type of confusion may explain some of the anomalous results obtained in previous investigations of the evolution of host preference.

While the specific factors that contribute to differential offspring survival (e.g., predispersal mortality due to predators, parasitoids, or microclimatic factors; dispersal mortality) may differ for other insect species, we expect that in other insects oviposition preferences among different categories of conspecific host plants will also exhibit correlations with host suitability for larvae and that differences among conspecific hosts

will be as important as differences between host species in shaping oviposition preferences. For the purposes of modelling the evolution of oviposition behavior, studies that define precisely the categories of plants discriminated by phytophagous insects and that assess the demographic consequences of discrimination are sorely needed.

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