

Individual Variation in Oviposition Preference in the Butterfly, *Colias eurytheme*

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Summary. We examined intra-population variation in oviposition preference in the pierid butterfly, *Colias eurytheme*. Females' preferences were tested in the laboratory, using two-way choice tests between the potential hosts, alfalfa and vetch. There were consistent differences in oviposition preference among females within a population. Larval and adult experience had little or no effect on females' preference. These results suggest that the intra-population variation in oviposition preference is genetically based, but the results of experiments designed to estimate the heritability of oviposition preference were not conclusive. We suggest that intra-population variation in host selection characters may play a key role in shifts to new host plants.

Introduction

Selection of a host plant for oviposition by a female insect can be crucial in determining the success of her offspring. Oviposition choice is especially important in insects which have immature stages which are relatively immobile. Many recent studies have emphasized the importance of oviposition preference (e.g., Singer 1971; Wiklund 1975; Jones 1977; Chew 1977; Ives 1978; Rausher 1978, 1979; Stanton 1979, 1980) but in most studies the variation among individual females within a population has not been examined in detail (but see Singer MS). Intra-population variation in oviposition preference would have important consequences for resource utilization patterns, and could play a key role in shifts to new host plants (Tabashnik 1981).

Three mechanisms which could cause variation in oviposition preference within a population are: (1) larval conditioning, (2) adult conditioning and (3) genetic variation. (1) Larval conditioning: The Hopkins Host Selection Principle (Hopkins 1917) states that a female's oviposition preference is biased in favor of the plant species she fed upon as a larva. If there are differences among females in the species of plant which they fed upon as larvae, this mechanism would be expected to cause differences among females in oviposition preference. (2) Adult conditioning: Adult females may form "search images" (Stanton 1975; Rausher 1978) for plant species based on their experience, and females' preferences may be otherwise affected by exposure to particular plant species. If different females are exposed to different species of plants, this mechanism could lead to differences among females in oviposition preference. (3) Genetic variation: Theories of insect-plant coevolution suggest that there

should be genetic variation within insect populations in characters which control host selection and utilization (e.g., Ehrlich and Raven 1965; Feeny 1976). Oviposition preference is one example of such a character, and genetic variation among females could cause differences among females in oviposition preference. These three mechanisms are not mutually exclusive; any combination of them could contribute to variation in oviposition preference within a population.

To examine the variation in oviposition preference within a population, we developed a simple behavioral assay for testing the pierid butterfly, *Colias eurytheme* Boisduval. Before the introduction of alfalfa (*Medicago sativa* L.) into California about 125 years ago, *C. eurytheme* probably used a variety of native legume species as larval host plants (Stern and Smith 1960; Berube 1972; and references therein). Some evidence suggests that native vetches (*Vicia* spp.) were the primary host plants of *C. eurytheme* before alfalfa was introduced (Berube 1972). *C. eurytheme* was able to switch from native legume hosts to alfalfa, and it has become a major pest of alfalfa (C.D.F.A., 1978 and 1979). This butterfly species was originally limited to the western portion of North America, but with the removal of forests and the introduction of alfalfa it rapidly expanded its range and is now found throughout much of North America (see Hovanitz 1950; Stern and Smith 1960; and references therein).

In California, the primary larval host plant of *C. eurytheme* is alfalfa, but other legumes, including *Vicia* species, are also recorded as hosts (Shapiro 1974). Do all *C. eurytheme* females show a strong preference for their primary host plant, alfalfa? In this study, we addressed this question by testing the oviposition preference of wild *C. eurytheme* females in choice tests with alfalfa and vetch. We also evaluated the relative importance of larval conditioning, adult conditioning and genetic variation as potential causes of variation in oviposition preference.

Materials and Methods

Study Organism

The biology of *C. eurytheme* has been studied extensively in the field and laboratory (e.g., see Stern and Smith 1960; Watt 1973, 1977; Hoffman 1978; Silberglied and Taylor 1978; Graham et al. 1980; and references therein).

The wild *C. eurytheme* females used in this study were caught in alfalfa fields near Tracy, California in June and October, 1978; May and September, 1979; and June, 1980. All females used in the experiments had little or no visible damage to their wings (condition ratings 2 or 3; see Watt et al. 1977). Larvae reared in the laboratory were the F₁, F₂, or F₃ offspring of the wild *C. eurytheme* females

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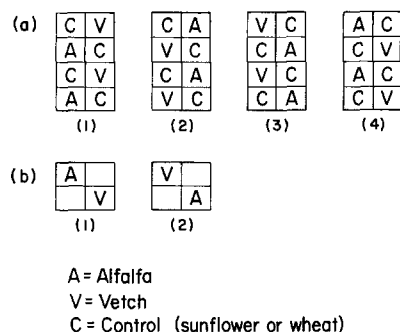


Fig. 1a, b. Positions of plants in cages. a Behavioral assay design A. b Behavioral assay design B

from Tracy. Larvae were reared on vetch (*Vicia*, "Lana Woolypod Vetch," Ferry-Morse Seed Co.) or alfalfa (*Medicago sativa* L. var. *caliente*, Ferry-Morse Seed Co.) at a photoperiod of 16 h light: 8 h dark, 25° C day: 21° C night.

Behavioral Assay

These plants were used in the behavioral assays: alfalfa and vetch (same varieties as described above), sunflower (*Helianthus*, "Mammoth," Burpee Seed Co.) and wheat (*Triticum*, "Fremont Hard Red Spring," Ecology Action Inc.). Plants were grown from seed in the laboratory in plastic freezer containers ("pots") (7.5 cm × 8.5 cm × 8.5 cm) filled with vermiculite.

We fertilized the alfalfa by soaking the pots in dilute ORTHO-GRO® Liquid Plant Food 12-6-6 (1 ml: 200 ml water) for 30 min on the third day after planting. We used seedling densities which resulted in approximately equal total fresh weight per pot for each plant species: alfalfa, 4-6/pot; vetch, 8-10/pot; sunflower, 6-8/pot; wheat, 5-10/pot. In the first replicate (June 1978), we noted that the plants changed as they aged during the course of the experiment. In particular, the vetch tended to droop after a few days. To eliminate this aging effect, seeds were planted on a staggered schedule in all of the later replicates so that females received plants of the same age on successive days.

We used two behavioral assay designs, referred to as Design A and Design B. Design A (2 replicates: June and October 1978): Females were placed individually in screen cages (30 cm × 42 cm × 28 cm) with 8 pots containing plants. Each cage had 2 pots of alfalfa, 2 pots of vetch, and 4 pots of "control" plants. In the June 1978 replicate, sunflower (2 pots) and wheat (2 pots) were used as controls. In October 1978 only sunflower (4 pots) was used. In both June and October 1978, we used 4 configurations of test plants (Fig. 1a). The initial configuration for each female was chosen at random, then the configuration was changed each day in the following order 1 → 2 → 3 → 4 → 1 → 2. At the end of each 2-day period (=1 trial) all the plants were removed, the eggs on each plant were counted, and the females were given new plants in the appropriate configuration. Each female was tested this way for 6 days (=3 trials) unless she died sooner.

Design B (3 replicates for wild females, and all tests of lab-reared females): Females were placed individually in screen cages (28 cm × 22 cm × 22 cm) with 1 pot of alfalfa and 1 pot of vetch. Two configurations of plants were used (Fig. 1b). The initial configuration was chosen at random. After each day (=1 trial) all the plants were removed, the eggs on each plant were counted, and the females were given new plants in the other configuration (i.e., 1 → 2 → 1 → 2). Each female was tested this way for at least 5 trials unless she died sooner.

All behavioral assays were conducted at a photoperiod of 16 h light: 8 h dark, 32° C day: 22° C night. Females were fed a solution of honey:water (1 ml:3 ml) twice daily.

This index of preference was used:

$$\frac{\# \text{ of eggs laid on alfalfa}}{\# \text{ of eggs laid on alfalfa} + \text{vetch}} \times 100\%.$$

Values >50% show a tendency to prefer alfalfa, values <50% show a tendency to prefer vetch, and values close to 50% show weak preference or no preference.

This index was used to measure two parameters: 1) female's preference: based on the sum of all trials for a given female, 2) trial preference: based on each trial for each female. Females which laid less than 80 eggs total were excluded from the data analysis. Females included in the data analysis laid an average of more than 200 eggs each.

In general, the distributions of percentages may be different from a normal distribution (Sokal and Rohlf 1969). Therefore, in each case when a statistical test was used which requires a normal distribution, the sample was checked for normality by a Kolmogorov-Smirnov test (Sokal and Rohlf 1969), and in all such cases the distribution was not significantly different from normal ($P > 0.2$ for each test).

Effects of Larval Conditioning

The oviposition preferences of females reared in the laboratory on vetch were compared to the preferences of females reared on alfalfa. Unfortunately, due to technical problems of rearing larvae on alfalfa in the laboratory, the sample size for alfalfa-reared females was small ($n=3$). However, in the area where wild *C. eurytheme* females were sampled, alfalfa is the only abundant legume, and it is likely that most (if not all) of the wild females sampled fed on alfalfa as larvae. Therefore, in order to increase the sample size, we assumed that wild females fed on alfalfa as larvae, and we compared the preferences of wild females to vetch-reared females.

Effects of Conditioning on Naive, Lab-Reared Females

Before being tested for preference, 6 newly emerged females were exposed to alfalfa and 5 were exposed to vetch. Four females from 2 broods (2 from each brood) were split so that 1 female from each brood was exposed to alfalfa while the other was exposed to vetch. Females were reared on vetch as larvae, and mated with lab-reared males within 24 h of emergence. Mating pairs were placed in screen cages with either alfalfa or vetch. The next day males were removed, and females were placed in the cages used for preference testing (see above), with 2 pots of the same plant as before (either alfalfa or vetch). After 24 h the females were removed, the eggs on each plant were counted, and females were tested for preference using Behavioral Assay Design B. The preferences of females which were exposed to alfalfa were compared with the preferences of females which were exposed to vetch in order to evaluate the effects of conditioning on naive adults.

Effects of Conditioning on Experienced, Wild Females

First, wild females were tested for preference using either Behavioral Assay A ($n=6$ females) or B ($n=4$ females). After their preference was established, 9 of these females were isolated in screen cages with the "non-preferred" plant. (If they laid >50% of their eggs on alfalfa, they were placed on vetch, if <50% on alfalfa, they were placed on alfalfa.) One female which showed a weak preference for vetch was isolated on vetch. After one day in "isolation" with one plant species, females were removed, eggs laid on each plant were counted, and females were tested for preference again using the same Behavioral Assay that they were tested with initially. This procedure made it possible to compare females' preferences before and after isolation on vetch or alfalfa. One of the 10 females laid only 5 eggs in the post-isolation preference test, and was excluded from the data analysis. All the other females laid more than 40 eggs in the post-isolation preference test.

Heritability

We used two approaches to estimate the heritability of oviposition preference in *C. eurytheme*: (1) full-sib analysis and (2) parent-offspring analysis.

(1) Full-sib analysis: Of the laboratory-reared females, there were 9 families with 2 or more sisters tested per family (total=32 females). The variation among families vs. within families was compared by

one-way ANOVA. The proportion of the variance due to the among-family component, called the "intra-class correlation coefficient" (t), was calculated as in Sokal and Rohlf (1969) and used to estimate heritability: $2t \geq h^2$ (Falconer 1960). In this analysis, we assumed that females from the same brood were full sibs; i.e., they all had the same father. This assumption holds for F_2 and F_3 offspring of wild females, because their mothers were mated singly in the laboratory; but multiple mating is common in *Colias* (Stern and Smith 1960; Graham et al. 1980) and some of the wild females may have mated more than once. However, because there is sperm precedence in *Colias* (Watt and Boggs in prep.), the last male to mate with a female before she was caught should be the father of the remainder of her offspring. Thus, the assumption of one father per brood is also reasonable for the laboratory-reared F_1 -offspring of wild females.

(2) Parent-offspring analysis: For seven families, it was possible to compare the oviposition preference of the mother with the preference of her daughters. The mean offspring (daughter) value was regressed against the parent (mother) value, and the regression coefficient was used to estimate heritability as in Falconer (1960): Estimated heritability (h^2) equals twice the slope of the regression (b), $h^2 = 2b$. The parent-offspring correlation was used to estimate heritability as in Spiess (1977): Estimated heritability (h^2) equals twice the correlation coefficient (r), $h^2 = 2r$. These two methods are equivalent when the parents and offspring have equal variance (Spiess 1977).

Results

Females' Behavior in Cages

Females' choices were based solely on short-range cues, which differs from natural situations where long-range searching behavior is important (Stanton 1980). However, in other respects, oviposition behavior in the test cages was similar to the oviposition behavior of *Colias* females in nature (see Stern and Smith 1960; Stanton 1979, 1980): After landing on a plant, females in the test cages often tapped the foliage with their front legs, presumably "tasting" the plant with chemoreceptors in their tarsi (see Stanton 1979, 1980). Females laid their eggs singly, and they usually began flying after laying an egg.

Of the 15 females offered control plants (Design A), 14 laid significantly fewer eggs on control plants than on alfalfa and vetch (G-tests, $P \leq 0.001$ for each female). Among these 14 females the percentage of eggs laid on controls ranged from 0% to 6%, with a total of 2.2% (97/4330, $G = 5204$, $df = 1$, $P \leq 0.001$). The fifteenth female laid eggs everywhere: on the cage, on the sides of the pots, on controls, on alfalfa and on vetch. Accordingly, her results were not included in further analyses of preference. Her offspring were raised to try to determine if her lack of discrimination was due to a genetic defect, but none of the offspring survived to adults.

Distribution of Wild Females' Preferences

The strongest preferences were shown by one female that laid 97% (619/638) of her eggs on alfalfa and another that laid 96% (156/163) of her eggs on vetch (Fig. 2). There was no significant difference among the 5 replicates (ANOVA, $F_{4,33} = 0.94$, $P > 0.25$) or between results from Behavioral Assay Designs A and B (ANOVA, $F_{1,36} = 0.94$, $P > 0.25$). Therefore, the data from the 5 replicates were pooled. The distribution of all wild females' preferences was normal and essentially continuous (Fig. 2).

The variation among females was significantly greater than the within-female variation (among trials) (ANOVA, $F_{34,136} = 2.18$, $P < 0.005$). In other words, there were consistent differences in preference among individual females.

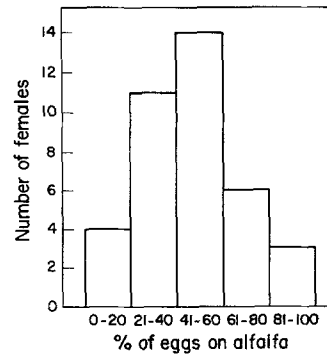


Fig. 2. The distribution of oviposition preferences of wild *C. eurytheme* females from alfalfa fields near Tracy, California. Based on 38 females which laid > 80 eggs each (mean number of eggs laid per female = 379). The distribution of preferences is not significantly different from normality: Kolmogorov-Smirnov test, $D = 0.064$, $P > 0.2$.

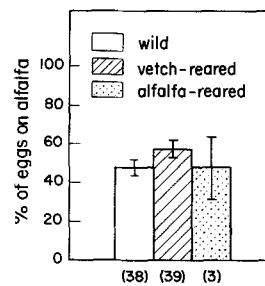


Fig. 3. Oviposition preference of wild and laboratory-reared *C. eurytheme* females. Wild females from alfalfa fields near Tracy, California. Sample sizes (number of females which laid > 80 eggs) are in parentheses. Bars show \pm S.E. Wild females and alfalfa-reared females did not show a stronger preference for alfalfa than vetch-reared females.

Effects of Larval Conditioning

The Hopkins Host Selection Principle (Hopkins 1917) predicts that females will prefer to lay eggs on the plant species which they fed on as larvae. This idea was not supported in experimental tests with *C. eurytheme*:

(1) Females reared on alfalfa in the laboratory did not prefer alfalfa more strongly than females reared on vetch (Fig. 3).

(2) Wild *C. eurytheme* females, which probably fed on alfalfa as larvae (see Materials and Methods), did not have a stronger preference for alfalfa than vetch-reared females (Fig. 3).

For three broods, it was possible to compare vetch-reared F_1 offspring to their wild mothers (which were presumed to have fed on alfalfa as larvae). In two of three broods, vetch-reared offspring preferred alfalfa more strongly than their wild mothers, and on average, vetch-reared offspring did not prefer vetch more strongly than their wild mothers (Fig. 4).

Effects of Adult Conditioning

The results show that females' experience with alfalfa and vetch as adults had little or no effect on their oviposition preference:

(1) There was no difference in oviposition preference between the lab-reared females which were exposed to alfalfa as naive adults and those which were exposed to vetch as naive adults (Fig. 5).

(2) Comparison of the preferences of nine wild, experienced *C. eurytheme* females' preferences before and after isolation on

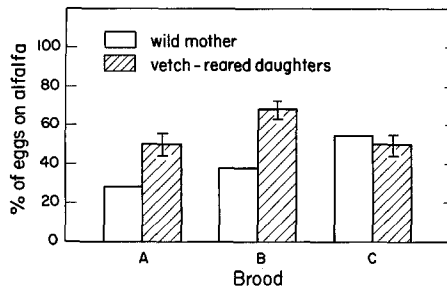


Fig. 4A–C. Oviposition preference of wild *C. eurytheme* females and their vetch-reared daughters. Wild females from alfalfa fields near Tracy, California. Sample sizes for daughters were 4, 3, and 4 for broods **A**, **B**, and **C** respectively. Bars show \pm S.E. for daughters. Mean % of eggs on alfalfa (\pm S.E.) for wild mothers = 40% (\pm 7.6%) for daughters = 55.7% (\pm 3.5%). Wild females did not prefer alfalfa more strongly than their vetch-reared daughters

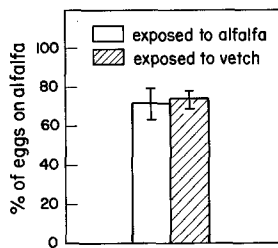


Fig. 5. Oviposition preference of lab-reared *C. eurytheme* females which were exposed to vetch or alfalfa as naive adults. Mean preference (\pm S.E.) of 4 females exposed to alfalfa vs. 4 females exposed to vetch. There was no difference in preference between females exposed to vetch and females exposed to alfalfa (t -test, $t=0.014$, $P > 0.75$)

Table 1. Estimation of the heritability of oviposition preference in *C. eurytheme* females by full-sib analysis

One-way ANOVA table

Source of variation	df	Sum of squares (SS)	Mean square (MS)	F
Among families	8	4052	506.5	2.94 *
Within families	23	3968	172.6	
Total	31	8021		

* $0.01 < P < 0.025$

Estimation of the among-family variance component (Sokal and Rohlf 1969): adjusted average sample size, $n_0 = 3.52$. The among-family variance component, $s_A^2 = \frac{MS_{\text{among}} - MS_{\text{within}}}{n_0} = 94.85$. The proportion of the variance due to the among-family component (t) equals the among-family variance component (s_A^2), divided by the total variance ($s^2 + s_A^2$) = 0.355. t estimates heritability (h^2): $h^2 \leq 2t$ (Falconer 1960), so $h^2 \leq 0.71$

vetch or alfalfa shows that five females' preferences shifted in favor of the plant they were isolated on, but four females' preferences shifted in the opposite direction. Overall, there was no net shift in preference in favor of the plant females were isolated on (Wilcoxon's signed-ranks test, $n=9$, $T=11$, $P > 0.1$), and the average change in preference was small (mean change in % of eggs on alfalfa = 8.6%).

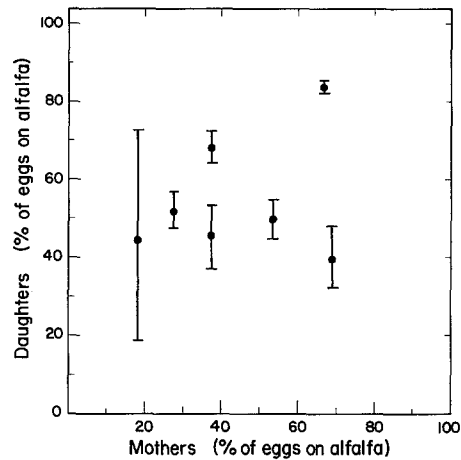


Fig. 6. Estimation of the heritability of oviposition preference in *C. eurytheme* by parent-offspring (mother-daughter) analysis. Bars show \pm S.E. for daughters ($n=2$ to 5 daughters per family). Heritability (h^2) was estimated by the slope of the regression (b): $h^2 = 2b$ (Falconer 1960), and by the correlation coefficient (r): $h^2 = 2r$ (Spiess 1977). $b = 0.21$ and $r = 0.27$, so heritability estimates are 0.42 and 0.54, respectively. Neither the slope nor the correlation coefficient were significantly different from zero ($P > 0.2$ for each)

Heritability

(1) Full sib analysis: The variation in oviposition preference among families was significantly greater than the variation within families, and the estimated heritability (h^2) was 0.71 (Table 1).

(2) Parent-offspring analysis: Estimates of heritability based on the relationship between mothers and their daughters were $h^2 = 0.42$ and $h^2 = 0.54$ for the regression and correlation methods, respectively (Fig. 6). However, neither the slope of the regression nor the correlation coefficient was significantly different from zero (Fig. 6).

The parent-offspring regression estimates only the additive genetic variance; but the full-sib estimate can be augmented by a common environment component and a dominance component, and is perhaps best viewed as an upper limit to the heritability (Falconer 1960). Therefore, it is not surprising that the heritability estimate based on the full-sib data is higher than the estimates based on the parent-offspring data.

The lack of statistical significance of the regression and correlation between mothers and daughters may be due in part to the small sample size. For example, if the "true" heritability were 0.5, the expected value for the correlation coefficient would be 0.25 ($r = \frac{1}{2} h^2$). The minimum number of mother-daughter pairs required for a correlation of 0.25 to be statistically significant ($P < 0.05$) is 63 (Sokal and Rohlf 1969). Analogously, if the "true" heritability were 0.4, the expected correlation coefficient would be 0.2, which would require a sample of more than 90 mother-daughter pairs to be statistically significant. Thus, when a single parent-offspring relationship is used to estimate heritability, small sample sizes are not likely to yield statistically significant results when heritability is 0.5 or lower. (Note: In this case, it is not possible to use the mid-parent-offspring relationship to estimate heritability because males can not be tested for oviposition preference.)

Discussion

The uniformly low fraction of eggs laid on the non-legume control plants shows that the *C. eurytheme* females were able to

discriminate accurately between legumes and non-legumes. However, in the choice between legume species, there was variation among females in preference – ranging from a strong preference for alfalfa to a strong preference for vetch. These results are similar to findings from chemical preference tests with *Colias meadii* (Stanton 1979) and *Colias philodice eriphyle* (Tabashnik 1981).

The results show that the oviposition choice of *C. eurytheme* females was not biased in favor of the host plant species they fed on as larvae. This finding is consistent with results of work on other *Colias* species (Stanton 1979; Tabashnik 1981) and other lepidoptera (e.g., Wiklund 1974). Further, there were no differences in preference between females exposed to alfalfa and vetch as naive adults, which suggests that *C. eurytheme* females' oviposition preferences are not "learned". The results also show that the preferences of experienced *C. eurytheme* females were not altered by isolation on alfalfa or vetch plant. By demonstrating that these potentially important environmental variables (i.e., larval and adult experience) do not affect oviposition preference, these results provide indirect support for the hypothesis that variation in oviposition preference in *C. eurytheme* is under genetic control.

The results of experiments designed to test this hypothesis directly were not conclusive. Neither of the two approaches of estimating heritability were fully satisfactory. The full-sib analysis tends to overestimate heritability; and for the parent-offspring analysis, the sample size was small compared to what is likely to be needed to show statistically significant results. Consequently, the data from this study do not provide a reliable quantitative estimate of heritability. However, the trends in both the full-sib data and the parent-offspring data are consistent with the hypothesis that some of the variation in oviposition preference in *C. eurytheme* is due to genetic differences among females. This hypothesis is reinforced by the results which show that differences among females were expressed consistently, and environmental factors which might influence oviposition preference had little or no effect.

The distribution of preferences of wild *C. eurytheme* females was essentially continuous and normal. This result is consistent with the hypothesis that oviposition choice is controlled by many genetic loci (see Bush 1973; Mayr 1947, 1963). These loci may control different aspects of oviposition choice such as responses to visual, olfactory and chemotactile cues. Thus, the oviposition preference expressed by a female may be the result of a "summation" over a suite of characters.

If the variation in oviposition preference is genetically controlled, then it becomes important to ask the question: What selective forces may be acting to maintain the variation within a population? There may be temporal changes in host quality so that different plant species are the "best" hosts at different times (e.g., see Stanton 1980). Although alfalfa is the primary host of *C. eurytheme* in California, *eurytheme* uses vetch as an alternate seasonal host when alfalfa is not available (A.M. Shapiro, pers. comm.).

We can also ask, "What selective forces might be acting to eliminate the variation within a population?" If alfalfa and vetch are about equally good as larval host plants, then there may be no strong selection which favors preference for either of the two plants. *C. eurytheme* populations often reach outbreak levels in alfalfa fields, and cause millions of dollars of damage to alfalfa per year in California (C.D.F.A., 1978 and 1979). *C. eurytheme* has been maintained on vetch in the laboratory for more than fifty generations (W.B. Watt, unpublished results). So, both alfalfa and vetch are suitable host plants for *C. euryth-*

eme. This could explain why the variation in oviposition preference has not been eliminated. It may also explain why a substantial fraction of the females tested did not express a preference for either alfalfa or vetch: there may be little or no selective pressure to develop the ability to discriminate between these two hosts.

If alfalfa and vetch are both suitable hosts, why are there females with strong preferences? If oviposition preference is controlled by many loci which act in an independent and additive way, as hypothesized above, we would expect that by chance some females would have combinations of alleles which would result in strong preferences. These females would form the "tails" of a normal distribution. The fact that the distribution of preferences was normal, with a mean close to 50% (i.e., no preference) is consistent with this idea (Fig. 2).

These interpretations of the results are subject to an important qualification. It is not clear how the preferences seen in these experiments would be expressed in the field. Many factors which might affect oviposition choice were not examined, including the relative abundance, and spatial and temporal distribution of potential host plants (see Ives 1978; Rausher 1978; Stanton 1980). In addition, long-range searching behavior, which plays a significant role in oviposition choice in *Colias* females (Stanton 1980), was not examined in this study. Thus, the preferences expressed in these experiments must be viewed as "potential" preferences. Yet, it is important to note that although the flight paths and landing patterns of *Colias* females are selective, post-alighting discrimination is crucial in oviposition choice (Stanton 1980). *Colias* females often land on legume species which are not preferred oviposition targets, and less than half of all landings on legumes result in oviposition (Stanton 1979, 1980). Under these conditions, differences among females in post-alighting preferences would be likely to result in differences in "realized" oviposition preference. Further, Stanton (1979) found that the post-alighting preferences expressed by *C. meadii* females in laboratory tests were strongly correlated with the post-alighting preference hierarchy observed in the field. Therefore, the differences in oviposition preference among *C. eurytheme* females which were observed in this study could result in differences among females in the field.

Variation in oviposition preference among the females in a population could have important evolutionary consequences. This type of variation would make a population more flexible – if the primary host(s) were not available, some individuals would readily use alternate hosts; some individuals might even prefer alternate hosts. This type of variation could lead to shifts to new host plants (Tabashnik 1981) and might provide the starting point for further adaptive radiation, particularly when changes in host selection cause changes in the timing or location of mating (e.g., Bush 1969). There may be similar within-population variation in host selection characters in many oligophagous insects. Thus, intra-population variation in host selection characters such as oviposition preference may play a key role in host shifts and insect-plant coevolution.

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