

PRE- AND POST-ALIGHTING HOST DISCRIMINATION BY *EUPHYDRYAS EDITHA* BUTTERFLIES: THE BEHAVIOURAL MECHANISMS CAUSING CLUMPED DISTRIBUTIONS OF EGG CLUSTERS

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Abstract. Egg clusters of the checkerspot butterfly, *Euphydryas editha*, are contagiously distributed among host plants (*Pedicularis semibarbata*) at one mid-elevation montaine site in California. Large, isolated plants receive more egg clusters than is expected from their proportional representation in the population. This study attempts to determine the behavioural causes of that contagious distribution.

Non-random alighting by ovipositing females appears to be the primary cause of the observed contagious distribution. Females alight more often than would be expected by chance on large, isolated plants. Females also appear to exhibit a weak post-alighting bias in favour of large, isolated plants, though this bias is not statistically significant. However, manipulative experiments reveal that post-alighting acceptance is not random; certain plants are accepted repeatedly while others are rejected repeatedly. The results also indicate that searching females distinguish among different classes of plants within a host species.

Many studies have reported that eggs of herbivorous insects are not randomly distributed among individuals of a given host species. Often eggs are overdispersed, a pattern that arises from the tendency of ovipositing females to avoid plants on which eggs are already present (Prokopy 1972; Mitchell 1975; Rothschild & Schoonhoven 1977; Rausher 1979). Less commonly, eggs may exhibit an aggregated distribution, with some plants receiving more eggs or egg clusters than expected under a random distribution and some receiving fewer (Stamp 1980; Benson et al. 1976).

While the causes of such clumping have seldom been investigated, at least three mechanisms can be proposed that could produce aggregation: (1) Some plants are more available than others to searching females (or in Feeny's (1976) terminology, some plants are more apparent than others). In an extreme case, only a small fraction of the plants in a population may be readily available to females. These plants would then be oviposited on repeatedly, while the remaining plants would escape discovery and oviposition. The resulting distribution of eggs would be highly aggregated. (2) Ovipositing females lay eggs preferentially on certain classes of host plant and discriminate against others. If, for example, females discriminate against small plants, large plants will receive more eggs and small plants fewer eggs than would be expected if all plants were equally preferred. (3)

Egg disappearance rates are higher on some plants than on others (e.g. Tilman 1978). If, for example, eggs are readily eaten by predators, they will survive for extended periods only on plants on which predators are rare or absent. An analysis of egg distributions will thus reveal an aggregated pattern even though all plants are equally susceptible to discovery and oviposition by females.

In this study we first demonstrate that egg clusters of the checkerspot butterfly, *Euphydryas editha* (Boisd.), exhibit an aggregated distribution in the population studied. We then examine, by means of behavioural observations and experiments, whether the first two mechanisms described above contribute to the observed distribution of egg clusters. Specifically, we examine two hypotheses: (1) the susceptibility of a plant to being alighted upon by a searching female butterfly is greater for some plants than for others of the same host species, and (2) the probability that a plant will receive eggs, once a female alights on it, is greater for some plants than for others. In testing these hypotheses, we also evaluate whether the more susceptible plants are those on which a greater-than-expected number of egg clusters are found in nature.

Because differential susceptibility among plants to alighting may be due either to differential availability (apparency) of plants to searching females or to preferential approach to

and alighting on certain plants, a failure to reject hypothesis 1 does not provide convincing evidence for the operation of mechanism 1. Nevertheless, mechanism 1 can be ruled out by falsification of hypothesis 1. Moreover, additional evidence can be used to suggest whether differential availability or preferential response is the more likely explanation for differential alighting, should hypothesis 1 fail to be rejected.

Subjects and Methods

Study Organism and Study Site

The checkerspot butterfly, *E. editha*, is widely distributed throughout California and several other western states (White & Singer 1974), although it is normally found in highly localized populations exhibiting limited dispersal (Ehrlich 1961; Gilbert & Singer 1973). The population we studied, Generals Highway, is located at an altitude of 2360 m on the western slope of the Sierra Nevadas, approximately 3 km southwest of Buck Rock lookout tower (population GH of White & Singer (1974)). Although most populations of *E. editha* are highly monophagous, with females normally ovipositing on only one of several available potential host species in the family Scrophulariaceae and in the genus *Plantago* (Plantaginaceae), the butterflies at Generals Highway are markedly polyphagous. In the population as a whole, females were observed ovipositing commonly on two varieties of *Collinsia torreyi*, as well as on *Pedicularis semibarbata*, a *Castilleja* species, and a *Mimulus* species (all Scrophulariaceae).

The spatial distributions of these five host species at Generals Highway are only partially overlapping. We confined our observations and experiments to an approximately 5-ha area in which *P. semibarbata* grew abundantly. This area was in turn divided into two subsections, the 'Upper Area' and 'Lower Area'. The Upper Area consisted of a flat expanse of pine woodland with a dense ground cover of grasses and forbs. Separated from the Upper Area by a gentle slope and a distance of about 50 m was the Lower Area, itself a gently sloping area of pine woods, where the ground cover was sparse and plants were separated by large patches of sand and pine needles. *Pedicularis semibarbata* was the only host species growing in the Lower Area. In the Upper Area, *Collinsia torreyi* also grew. At the time of our study in June and July of 1979, however, the *Collinsia* plants had set seed, wilted, and dried. During the entire study females were never observed to oviposit on these

dried *Collinsia* plants, though they readily did so on individuals of the same species that persisted in more moist areas approximately 200 m away.

Distribution of Egg Clusters

One plot, approximately 100 m × 50 m, was set up in each of the two subsections of the study area. Within each plot, all *P. semibarbata* plants were located and marked with numbered flags. The Upper Area plot contained 572 plants, while the Lower Area plot contained 269. A series of characteristics, defined in Table I, was measured or computed for each plant in each area between 23 June and 4 July 1979. All of these characteristics except Obstruction were judged sufficiently continuous that they could be analysed by parametric multivariate statistics. Obstruction, by contrast, had only 3 possible values. Consequently, all analyses involving this variable were performed separately using non-parametric techniques.

Euphydryas editha females at Generals Highway lay clusters of between 50 and 150 eggs. Between 1 and 4 July marked plants were thoroughly examined and the number of egg clusters present on each plant was determined. Each cluster found was assumed to be the result of an independent act of oviposition. The distribution of egg clusters was compared with the numbers expected on the basis of equal susceptibility (Poisson distribution). In addition, the continuous variables listed in Table I were compared for plants with and without egg clusters by Multivariate Analysis of Variance (MANOVA) and by Discriminant Function Analysis (Timm 1975).

Table I. Characteristics Measured or Estimated for Each Plant

Short Name	Characteristic
Ant nests	Number of ant nest entrances within 20 cm
Neighbours	Number of other <i>Pedicularis</i> plants within 1 m
Cover	Estimate of area of ground covered by plant; estimated as $\pi \times$ Major axis \times Minor axis
Obstruction	Estimate of proportion of plant obscured by surrounding vegetation. Three categories were used: 0-33%; 33-67%; 67-100%
Inflorescences	Number of inflorescences on plant
Leaves	Number of leaves on plant
Major axis	Longest horizontal dimension
Minor axis	Longest horizontal dimension perpendicular to Major axis

Analysis of Alighting Probabilities

To determine whether certain plants are alighted on differentially by females, we followed searching females in each of the two experimental plots. Females were chosen for observation by walking through the study area until a female was spotted. Each female was followed until she flew out of the study plot or until she began laying eggs. A female normally takes between 30 and 60 min to lay a full cluster and she usually does not resume searching for host plants for several hours afterwards; consequently, it was not possible to follow a female long enough to observe more than one oviposition. During the time a female was followed, all plants on which she alighted were recorded, as were all acts of oviposition.

Data were pooled for all females observed within each of the Upper and Lower Areas. To determine whether plants alighted on were a random sample of those available, the characteristics of the plants on which females alighted were compared with those of plants on which females did not alight by MANOVA and Discriminant Analysis.

Analysis of Post-Alighting Probabilities

The plants on which females alighted were divided into two sets; those on which females oviposited and those on which they did not. Characteristics of these two sets of plants were compared using MANOVA and discriminant analysis to determine whether plants accepted by females represent a non-random subset of those on which females alighted.

Because the number of plants on which females oviposited was small, the power of our analysis to detect differences between accepted and rejected plants was low. Consequently, we performed an additional experiment to determine whether females were exercising post-alighting preferences. The null hypothesis of the experiment was that females that have alighted do not discriminate among conspecific host plants; rather, females accept the first plant on which they alight after motivation to oviposit rises above a threshold (e.g. Singer 1971; Jones et al. 1975).

Individual females were followed and observed alighting on a sequence of host plants. When an alighted female accepted a plant (we could detect this by observing the curling of the female's abdomen and the extrusion of her ovipositor), we removed her from the plant (ultimate plant) before she had time to lay eggs and placed her in a

net cage for about 5 min. This resting time presumably negated any carry-over effect from the butterfly's acceptance of the plant (Singer 1971). We then tested the female by replacing her on both the last plant she had rejected (penultimate plant) and the plant she had accepted (ultimate plant) and noting her response to each plant. Curling the abdomen constituted acceptance; failure to curl the abdomen within 3 min or flying off the plant constituted rejection. Order of placement on the two types of plant was random. The female was placed in the cage for approximately 3 min between tests on the two plants.

Acceptance of the ultimate plant by a female before its capture indicates that its motivation to oviposit has risen to the level at which at least some *P. semibarbata* plants are accepted. Under the null hypothesis tested by this experiment, therefore, penultimate and ultimate plants should be accepted with equal probability during testing. If, however, females actively discriminate against some plants, ultimate plants should be accepted more often than penultimate plants. In other words, the responses of females to plants during testing should be similar to their natural reaction. Plants preferred naturally should also be preferred during testing.

The statistical significance of differences in reaction to ultimate and penultimate plants was tested as follows. Assume the probability that a female accepts a plant, regardless of whether it accepted or rejected it before, is p . The probability of rejection is $(1 - p)$. The probability of seeing the same response in the test as in the field (i.e. rejection of penultimate plant followed by acceptance of ultimate plant) is $(1 - p)p$, and $1 - (1 - p)p$ is the probability of seeing a different response. p is not known. Nevertheless, we can apply a conservative test by assuming $p = \frac{1}{2}$. If $p = \frac{1}{2}$, then the probability of rejection followed by acceptance is $\frac{1}{2} \times \frac{1}{2}$ or $\frac{1}{4}$. If p is not equal to $\frac{1}{2}$, then the probability of seeing that response is less than $\frac{1}{4}$. Consequently, if a statistically significant result is obtained assuming $p = \frac{1}{2}$, we know that the result would have reached statistical significance for any value of p , including the true value. Our null hypothesis is that the number of test responses in which there is rejection of the penultimate plant and acceptance of the ultimate plant is $p(1 - p)N$, where N is the number of tests. Our alternative hypothesis is that females make the same type of discrimination in the test as they do in the field, i.e. females discriminate in a consistent manner.

This alternative hypothesis implies $x > (\frac{1}{4})N$ and hence the test is one-tailed, using the right tail of a binomial distribution.

With $p = \frac{1}{4}$, the probability of seeing x or more test responses to be identical to the response seen in the field is

$$\sum_{K=x}^N \binom{N}{K} \left(\frac{1}{4}\right)^K \left(\frac{3}{4}\right)^{N-K}$$

Results

Correlations Among Plant Characteristics

The plant characteristics measured are not all statistically independent. The correlation matrices given in Table II show that Major axis, Minor axis, Cover, Inflorescences, and Leaves are all highly correlated with each other. This result is not surprising, since each of these variables is an indicator of plant size. Each of these variables is in turn negatively correlated with Neighbours, the number of other *P. semi-barbata* plants growing within 1 m of the measured plant, though the magnitude of these negative correlations is normally less than half the magnitude of the correlations between pairs of the size-related variables. The variable Ant nests exhibits only weak and inconsistent correlations with the other variables.

Because several of the plant characteristics measured show strong intercorrelations, all subsequent analyses employ multivariate

methods. The significance of differences for individual plant characteristics was evaluated using simultaneous confidence intervals for differences between means as described by Timm (1975).

Distribution of Egg Clusters among Plants

Egg clusters of *E. editha* exhibit a highly aggregated distribution in each of the two study areas. In the Upper Area, a total of 354 clusters were found on 557 plants (mean = 0.636 clusters per plant). Many more plants had either 0 or more than 3 clusters than would be expected under a Poisson distribution (Table III, $P < 0.0001$). In the Lower Area, 114 egg clusters were found on 245 plants (mean = 0.47 clusters per plant). Again, more plants than expected had either 0 or 2 or more clusters, while fewer plants than expected had just one cluster (Table III, $P < 0.0001$).

A comparison by MANOVA of the characteristics measured for plants with and without egg clusters revealed that plants with egg clusters were not a random sample of the plants in the habitat (Upper Area: Hotelling's $T = 236.03$, $df = (7,539)$, $P < 0.001$; Lower Area: $T = 98.19$, $df = (7,243)$, $P < 0.001$). Moreover, discriminant analysis provided a good separation between plants with and plants without eggs. The difference in mean discriminant scores for the two groups of plants was 1.49 times the standard

Table II. Pairwise Correlations between Measured Plant Characteristics†

Upper Area. $N = 572$ plants

	Minor axis	Cover	Leaves	Inflorescences	Neighbours	Ant nests
Major axis	0.91***	0.92***	0.78***	0.80***	- 0.33***	- 0.18***
Minor axis		0.96***	0.82***	0.82***	- 0.35***	- 0.17***
Cover			0.85***	0.86***	- 0.33***	- 0.16***
Leaves				0.90***	- 0.29***	- 0.13***
Inflorescences					- 0.32***	- 0.14***
Neighbours						0.18***

Lower Area. $N = 269$ plants

	Minor axis	Cover	Leaves	Inflorescences	Neighbours	Ants nests
Major axis	0.91***	0.79***	0.84***	0.73***	- 0.23***	0.04
Minor axis		0.83***	0.84***	0.76***	- 0.24***	0.14
Cover			0.75***	0.98***	- 0.13*	- 0.11
Leaves				0.75***	- 0.25***	0.04
Inflorescences					- 0.11	- 0.01
Neighbours						- 0.11

* $P < 0.05$; *** $P < 0.001$.

†Values are Pearson product-moment correlation coefficients.

deviation of the within-group scores for plants in the Upper Area and 1.45 times the analogous standard deviation for plants in the Lower Area.

Discriminant analysis also provides estimates of the differences between the two groups of plants for each of the variables in the analysis (Table IV). In the Upper Area, plants with egg clusters are significantly larger (variables Major axis, Minor axis, Cover, Leaves, Inflorescences) and more isolated (Neighbours) than those without egg clusters. The two types of plants did not, however, differ in proximity to Ant nest entrances. In the Lower Area, a similar pattern is evident (Table IV). There, differences between means were positive and significant for the size-related variables Major axis and Minor axis, negative and significant for Neighbours, and not significant for the remaining variables. Egg clusters are thus found more often on large, isolated plants and less often on small, non-isolated plants, than is expected under the null hypothesis of random distribution of egg clusters with respect to measured plant characteristics.

In the Upper Area, the presence or absence of egg clusters and the proportion of a plant's foliage that is overlaid by other vegetation (Obstruction) were analysed by a *G*-test (Sokal & Rohlf 1969). The two variables were not independent ($G = 27.65$, $df = 2$, $P < 0.001$).

Table III. Frequency Distribution of Number of Egg Clusters Per Plant†

Upper Area			
No. egg clusters	No. plants expected	No. plants observed	Contribution to χ^2
0	295	408	43.28
1	187	74	68.28
2	59.6	30	14.68
3	12.6	20	4.32
> 3	2.8	20	175.23
Overall $\chi^2 = 305.79$, $P < 0.0001$			
Lower Area			
No. egg clusters	No. plants expected	No. plants observed	Contribution to χ^2
0	153.8	182	5.15
1	71.6	38	15.76
> 1	19.6	25	1.50
Overall $\chi^2 = 22.41$, $P < 0.0001$			

†Expected column gives expected number of plants with indicated number of egg clusters based on Poisson distribution. Observed column gives actual number of plants observed.

Plants with egg clusters were less likely to have 67% to 100% of their foliage overlaid by other vegetation than were plants without eggs.

Pattern of Alighting by Females

Females observed in the Upper Area alighted on a total of 73 plants. Those plants were compared as a group with the remaining 499 plants in the area to determine whether plants alighted on constituted a random sample of plants in the habitat. A MANOVA comparison of plant characteristics for the two sets of plants demonstrated that plants alighted upon were significantly different from those not alighted upon (Hotelling's $T = 47.22$, $df = (7,570)$, $P < 0.001$). The separation between mean discriminant scores of the two types of plants was 0.98 times the within-group standard deviation. The size-related variables Major axis, Minor axis, Leaves and Inflorescences all contributed significantly to the overall difference between plants on which females alighted and plants on which they did not alight (Table IV). Females thus alighted preferentially on larger plants.

Females observed in the Lower Area revealed a similar pattern of alighting, though differences between plants alighted upon and those not alighted upon are not statistically significant (Hotelling's $T = 7.42$, $df = (7,267)$, $P > 0.10$). Among the comparisons of individual plant characteristics, differences between means are positive for size-related characteristics and negative for Neighbours (Table IV).

Although the Lower Area differences in this analysis were not statistically significant, a combined probability test (Sokal & Rohlf 1969) indicates that when the results from the two areas are considered as independent tests of the null hypothesis of no differences between plants alighted upon and plants not alighted upon, that hypothesis can be unequivocally rejected ($\chi^2 = 15.20$, $P < 0.005$). Females therefore alight on a non-random set of plants. Moreover, in both areas the pattern of differences between means for individual plant characters was similar to the pattern found in the previous analysis of egg cluster distribution (Table IV). Females tended to alight upon large, isolated plants more often and upon small, non-isolated plants less often, than is expected by random alighting.

We also compared the probability that a plant with egg clusters present during the early July census was alighted on by a female during our observations with the same probability for plants that did not have egg clusters at the time of the

Table IV. Results of Discriminant Analysis Applied to Plants in Upper and Lower Areas†

Upper Area			
Variable	Plants with eggs; Plants without eggs	Plants alighted on; Plants not alighted on	Plants accepted; Plants rejected
Major axis	8.34**	3.85*	1.81
Minor axis	8.97**	4.27	4.15
Cover	369.3**	103.8	111.0
Leaves	11.39**	6.38*	3.08
Inflorescences	2.24**	1.09*	0.53
Neighbours	- 2.83**	- 1.77	- 0.90
Ant nests	- 0.14	0.02	- 0.13

Lower Area			
Variable	Plants with eggs; Plants without eggs	Plants alighted on; Plants not alighted on	Plants accepted; Plants rejected
Major axis	6.57**	1.76	4.25
Minor axis	6.79**	2.65	5.46
Cover	153.10	143.07	519.20
Leaves	8.63	2.28	7.36
Inflorescences	1.60	1.26	5.49
Neighbours	- 6.93	- 0.25	- 1.22
Ant nests	0.21	- 0.25	0.15

* $P < 0.05$; ** $P < 0.01$.

†Values are differences between mean values for groups of plants indicated at head of each column. Significance of differences between means tested by simultaneous confidence interval procedure (Timm 1975).

census. In the Upper Area, 32% of the plants with eggs at the end of the study were alighted upon, whereas only 6% of those without eggs were alighted upon (Table V; $G = 53.43$, $P < 0.001$). Similarly, in the Lower Area, 47% of the plants with eggs were alighted on but only 25% of those without eggs were alighted on (Table V; $G = 10.46$, $P < 0.005$). Thus, plants on which egg clusters are found more often than would be expected by chance are those upon which females alight more often than expected by chance.

In the Upper Area, the probability that a plant would be alighted upon by a searching female was independent of the proportion of that plant's foliage that was overlaid by other vegetation ($G = 2.52$, $df = 2$, $P > 0.10$).

Post-Alighting Response by Females

Observed females alighted on 73 plants in the Upper Area and on 80 plants in the Lower Area. Because many plants in each area were alighted on by more than one observed female we observed a total of 119 alighting events in the Upper Area and 221 alighting events in the Lower Area. Of these events, 12 were followed by oviposition in the Upper Area and 16 in the Lower Area. To compare the characteristics of accepted and rejected plants, we divided alight-

ings into two groups: those that were followed by oviposition and those that were not. We then compared plant characteristics for the two groups. One consequence of this method of analysis was that the characteristics of some plants, those accepted by some females and re-

Table V. Comparison of the Probability that Plants With and Without Eggs at End of Study were Alighted on by Observed Females

Upper Area		
	Egg clusters present	Egg clusters absent
Plant alighted on	47	26
Plant not alighted on	102	382
$G = 54.43$, $P < 0.0001$		

Lower Area		
	Egg clusters present	Egg clusters absent
Plant alighted on	30	46
Plant not alighted on	33	136
$G = 10.46$, $P < 0.005$		

jected by others, appear in each of the two groups, sometimes more than once.

In both Upper and Lower Areas, characteristics of accepted plants did not differ significantly overall from those of rejected plants that had been alighted on (Upper Area: Hotelling's $T = 7.22$, $df = (7,117)$, $P > 0.10$); Lower Area: $T = 5.73$, $df = (7,219)$, $P > 0.10$). A combined probability test is also not significant ($\chi^2 = 2.58$, $P > 0.10$). Nevertheless, in each area the differences between group means for the individual plant characteristics exhibit a pattern similar to that found in the two previous analyses (Table IV). The plants which females accepted were larger (i.e. differences between group means for Major axis, Minor axis, Cover, Leaves, and Inflorescences were positive) and more isolated (negative difference between group means for Neighbours) than plants on which females alighted but did not oviposit.

While these results suggested that females do not discriminate among conspecific host plants after alighting, the small sample sizes (12 and 16 acceptances in Upper and Lower Areas respectively) mean that the power of our analyses to detect small differences is low. We therefore attempted to determine experimentally whether females exhibit post-alighting discrimination among *P. semibarbata* plants.

As described above, females were followed and observed alighting on sequences of host plants. After a female had accepted a plant she was experimentally replaced on the penultimate and ultimate plants. In the 27 trials, we found the same response in the test as in the field situation 16 times (the expected value under the null hypothesis was $\frac{1}{4} \times 27 = 6.75$). The one-tailed (right) binomial probability of this event is approximately 0.0002. There is thus a marked tendency for the butterflies to repeat the natural response to host plants when placed on them in the test. This result indicates that the butterflies are actively discriminating between plants after alighting and that they are not simply ovipositing on any *Pedicularis* plant when motivation to oviposit crosses some single threshold.

Discussion

The distribution of eggs among host plants within any population of herbivorous insects is the result of at least two contributing patterns: the pattern of approach to, and alighting on, host plants by searching females and the pattern of post-alighting ovipositional responses by those females. In this investigation we have examined

each of these patterns and are able to interpret how they influence the overall distributional pattern of *E. editha* egg clusters.

The contagious distribution of egg masses within the Generals Highway population appears to be caused primarily by differential alighting by females on certain *P. semibarbata* host plants in the habitat. Egg masses are found disproportionately often on large, isolated plants, the same type of plants on which searching females alight at greater-than-expected frequency (Table IV). A knowledge of post-alighting preferences is thus unnecessary for explaining the clumping of eggs, although post-alighting preferences may strengthen this clumping.

In the introduction we suggested that differential alighting may arise from either or both of two causes. On the one hand, large plants may be more 'apparent' to searching *Euphydryas* females than are small plants (see Feeny 1976; Rhoades 1979). Larger plants would therefore be perceived and alighted on more frequently than would be expected from their proportional representation in the population. On the other hand, females may have evolved or learned preferences for approaching and alighting on large (or isolated) plants (Jones 1977; Jones & Ives 1979; Cromartie 1975), even though large and small plants are perceived in proportion to their abundance in the habitat.

These two explanations are not necessarily mutually exclusive. The apparency of an individual plant to a searching female will probably depend not only on various characteristics of that plant, such as its size and the degree to which it is obstructed by other vegetation, but also on the sensory capabilities and searching methods of that female (Feeny 1976; Rhoades 1979; Jones 1977; Cromartie 1975; Rausher 1978). Since these latter traits are evolved characteristics of searching insects, any behaviour that biases the ability of an individual to perceive, and that hence increases the apparency of some types of plants over others, can be viewed as a type of evolved preference. The distinction between differential apparency and differential preference as causes of differential alighting on plants of various sizes therefore has meaning only in terms of the proximate behaviours that elicit alighting on a host plant. Distinguishing between these two types of proximate behaviours would be exceedingly difficult experimentally, since it would necessitate knowing what a searching insect does and does not perceive. Consequently, while it would be of

interest to know whether the observed alighting bias toward large, isolated plants in *E. editha* is caused by differential perception or by differential response to the perception of different types of *P. semibarbata* plants, we can at this point state only that biased alighting appears to be a primary factor contributing to the clumped distribution of egg clusters.

The role of post-alighting preferences in leading to the observed spatial pattern of egg clusters is less clear. Our observations indicate that females have a tendency to lay eggs on large, isolated plants, a tendency that would reinforce the clumped distribution of egg clusters produced by biased alighting. However, this tendency is not statistically significant. Nevertheless, our experimental testing of females demonstrated that females do exhibit post-alighting preferences. Although these experiments permit no conclusions about how such preferences influence egg cluster distribution, they do permit us to draw some conclusions about the mechanism of intra-specific host discrimination in *E. editha*.

Singer (1971) has asserted that females in any given population of *E. editha* exhibit a definite preference ordering of the different species of host plants available in the habitat of that population. When motivation to oviposit, measured as time elapsed since last oviposition, is low, females accept only the most preferred host species. When motivation rises sufficiently, the second-most preferred host species becomes acceptable to females, and so on. One hypothesis that explains these observations is that there corresponds to each host species a motivation threshold. If a female's motivation state is above the threshold for a particular host and she lands on an individual of that species, she will oviposit. An alternative hypothesis is that for each species there are several motivation thresholds and females are therefore able to discriminate among several categories of conspecific plants as well as among host species.

Our results indicate that for *P. semibarbata* there is not one single motivation threshold that, when crossed, makes plants of that species acceptable. If this were true, we would predict that an *E. editha* female in the Generals Highway population would lay eggs on all *P. semibarbata* plants in the habitat after females had crossed the motivation threshold for that species. We did not find this to be the case, however. Observed females, after having accepted one *P. semibarbata* plant, would subsequently reject others, as demonstrated by our manipulative experi-

ments. The fact that in most cases the females during testing once again accepted the plants that they had accepted naturally demonstrates that non-acceptance of some plants is not an artifact of our testing procedure. The conclusion seems inescapable that for females at a given motivation level not all *P. semibarbata* plants are equally acceptable. Whether each host species has its own unique set of thresholds that does not overlap with the sets for other species is not known. An equally plausible hypothesis is that females discriminate among all potential host plants using a few characteristics that cross plant taxonomic lines. If this hypothesis is true, females would not be ranking host species per se and any ordering by species would be fortuitous.

Although *E. editha* females oviposit preferentially on large, isolated plants, we can at present only speculate about the adaptive significance of such behaviour. As in many other *E. editha* populations (White 1974; Ehrlich et al. 1975), pre-diapause larvae on *P. semibarbata* at Generals Highway often completely defoliate their host plants. They must therefore disperse to other plants to complete development. As in other butterfly species (Rausher 1979), it is likely that the probability that a dispersing larva will discover a new host plant is proportional to size at dispersal. Consequently, at low *E. editha* density, females that preferentially oviposit on large plants may maximize the expected survival of their offspring by maximizing larval size at dispersal. By contrast, when butterfly density is high, such behaviour will lead to a contagious distribution of egg clusters, as seen in this study. Many plants received five or more clusters while others received none. It seems probable that when butterfly density is high enough, there will be on the average so many egg clusters on large plants that the actual amount of foliage available per larva would be less than what is available on smaller plants. Under these circumstances, a preference for larger plants would no longer be favoured. The selection pressures that mould preference behaviour may thus be density-dependent.

Acknowledgments

We thank Rick Moore and Barbara Kelso for their cheerful and unstinting assistance in the field and Marcy Uyenoyama for statistical advice. Funding for field research was provided by NSF Grant DEB-78-11142 to M. C. Singer. Financial support to D. Mackay was provided by

a Charles Gilbert Heydon Travelling Fellowship from the University of Sydney. M. Rausher gratefully acknowledges the leave-of-absence granted by Duke University for the purpose of conducting this research.

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(Received 15 December 1980; revised 12 March 1981;
MS. number: A2583)