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SELECTION OF OVIPOSITION SITES BY THE BALTIMORE CHECKERSPOT, *EUPHYDRYAS PHAETON* (NYMPHALIDAE)

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ABSTRACT. Selection of oviposition sites by the Baltimore checkerspot (*Euphydryas phaeton*) was examined in a natural population. Females chose leaves larger than average. Egg clusters were clumped, with 1% of the available leaves and 3% of the available stalks used. The behavior resulting in this non-random pattern is discussed.

Butterflies choose host plants which promote larval survival and avoid those which do not (Wiklund, 1974, 1975; Chew, 1975, 1977; Rausher, 1980). Ovipositing females may discriminate among conspecific host plants either by avoiding eggs on plants or by depositing their eggs with those of other females (e.g. Ehrlich & Gilbert, 1973; Gilbert, 1975; Benson et al., 1975; Rothschild & Schoonhoven, 1977; Rausher, 1979). Most butterflies deposit their eggs singly (Stamp, 1980), but the Baltimore checkerspots (*Euphydryas phaeton* Drury: Nymphalidae) lay clusters of eggs and tend to deposit egg clusters with clusters already present. The advantages for a female in discriminating among conspecific host plants and depositing eggs with other egg clusters have been linked to avoidance of parasitoids and predators and to aspects of the host plants such as the size of the host plant, the part of the plant used by larvae, and the distribution of the host plant (Benson, 1978; Stamp, 1980).

My objective was to examine selection of oviposition sites by *E. phaeton* by determining searching behavior, characteristics of the oviposition sites, characteristics of the host plants available for oviposition, and distribution of egg clusters.

METHODS

E. phaeton was studied at the Conservation and Research Center of the National Zoological Park at Front Royal, Warren Co., Virginia from 1977 through 1979. This butterfly is univoltine and deposits large clusters ($\bar{x}$ = 274 eggs per cluster; Stamp, 1982c) in June. The early instars make communal webs on their larval host plants and then diapause in webs in August. The caterpillars overwinter on the ground in the plant litter (Bowers, 1978). The larval host plant, turtlehead (*Chelone glabra* L.: Scrophulariaceae), is a clonal perennial growing in dense patches (up to 2.3 m in diameter) in wet meadows. Although

a few isolated plants consist of one stalk, most plants contain numerous stalks.

Plants were searched for egg clusters, and those stalks with clusters were tagged. Host plant and leaf-searching behavior were recorded by following females searching for oviposition sites. By making quick sketches of plants, stalks and leaves and numbering them in order of visitation, I kept track of females searching plants, stalks and leaves they had previously encountered during the observations.

In 1979, 107 female *E. phaeton* were marked using Testor's enamel paint on the wings, thorax and abdomen with no detrimental effects. One area (12 × 55 m) was surveyed for host-searching and ovipositing females from 1000 to 1700 hours on 9 through 23 June. Each survey required about 45 min. Upon finishing a survey, another survey was begun immediately. The position of egg clusters was marked with a spot of permanent black ink on the upper surface of the leaf and the stalk tagged with designation of which female laid the cluster, date, height of the cluster from the ground, and leaf upon which the cluster was deposited. To determine the proportions of ovipositions actually observed, all leaves were examined twice a week for additional egg clusters, and those stalks with clusters were tagged. To determine if any egg clusters were missed, the area was searched every week through the second week of July for untagged stalks with red egg clusters (deposited prior to 24 June) and webs of *E. phaeton* larvae. Based on 267 egg clusters (of which 99% were located prior to hatching), I observed 87% of the ovipositions in this area over the 14-day period using the survey method described above.

To determine the size of stalks available to *E. phaeton,* 15 plants were sampled. A rod was placed through each plant until 20 stalks were partitioned. Those stalks were measured for height and for length of leaf nearest to the midpoint of the stalk. The total number of stalks and the number of stalks in the outer 15 cm of each plant group were counted. The width and perimeter of the plant groups were measured. In one area turtlehead was mapped using a reel tape stretched across a grid (of 3 × 3 m units) and moved at 30 cm intervals along the grid. The perimeter of the plant groups and mean width of the plant groups were calculated using a map meter (which determined distance).

RESULTS

Oviposition Behavior

Females searching for oviposition sites flew from stalk to stalk about 0.6 m above the ground along edges of host plant groups, in contrast to non-searching females which generally flew above the vegetation

TABLE 1. Searching behavior exhibited by female *E. phaeton* (n = 21).

Searching behavior	Mean per female based on total observations	Standard error
Minutes observed	11.4	±1.4
Plant groups visited	1.6	±0.2
Stalks visited	8.1	±0.9
Leaves touched	7.5	±1.0
Leaves examined	2.1	±0.3
Turns on top surface of leaves	4.9	±0.8
Times abdomen placed under leaves	9.2	±1.7
Times returned to top surface of leaves	8.1	±1.6

without landing on turtlehead. Usually a female settled at a host plant after landing on one or two plants and stalks and began oviposition after examining an average of two leaves (Table 1). Frequently, a female returned to a host plant, stalk or leaf which she had already visited during this searching period; 28% of the leaves and 32% of the stalks visited had been examined a few to 35 min earlier. However, oviposition on these re-examined leaves was similar to that on newly-examined leaves (8 ovipositions on 47 leaves and 10 ovipositions on 120 leaves, respectively; χ^2-test, $P > 0.10$). Oviposition on re-examined stalks was also similar to that on newly-examined stalks (9 ovipositions on 49 stalks and 9 ovipositions on 103 stalks, respectively; χ^2-test, $P > 0.10$). Thus, females appeared to be sampling available oviposition sites rather than just responding to each potential site, positively or negatively. In addition, females examined and oviposited on damaged leaves, partially eaten by sixth instar larvae of *E. phaeton*.

A female examined a leaf in detail by repeatedly walking over its upper surface, tapping it with her antennae, occasionally making 180 or 360° turns on the leaf and examining the under surface of the leaf with her ovipositor while hanging onto the edge of the leaf with the midlegs (Table 1). Often a female examined the under surface of a leaf by hanging first from one side of the leaf and moving along the edge. Then she returned to the top surface, walked to the other side of the leaf, and examined the under surface of the leaf from that side (Table 1).

Each of the 21 females followed oviposited within 22 min. The majority of these females were initially flying quickly from patch to patch of turtlehead and basking intermittently, rather than having started to search among the host plants. Since some other marked females were observed to search for up to three hours before ovipositing, 22 min is a conservative (short) estimate of average search time.

TABLE 2. Affect of inclement weather on oviposition. Sixteen and 15 females deposited single clusters and 23 and 22 females deposited eggs with others, before and after poor weather, respectively.

Ovipositions	Single clusters	Other clusters present	Total
Day before:			
Observed	16	15	31
Expected	16.1	14.9	
Day after:			
Observed	26	24	50
Expected	25.9	24.1	
	42	39	81

Most females oviposited in early afternoon, although some were observed ovipositing from 1100 to 1700 hours. Recently-emerged females (with bright, unworn wings) and older females deposited clusters in the morning and afternoon at a similar rate (for recently-emerged females, 27 deposited eggs in the morning and 44 in the afternoon; for older females, 16 laid eggs in the morning and 62 in the afternoon; χ^2-tests, $P > 0.10$). Poor flight conditions (e.g., cool, windy, rainy) inhibited egg depositions (χ^2-tests, $P < 0.001$; Table 2). However, neither the numbers of egg clusters deposited nor the number of females depositing eggs was significantly different between the day before and the day after inclement weather (χ^2-tests, $P > 0.10$).

Deposition of an egg cluster took an hour and a half ($n = 24$, $\bar{x} = 88$ min $\pm$ 37 S.D.). The number of egg clusters laid over a 13-day period (by females marked on the first to eighth day of that period) ranged from 0 to 6 ($n = 98$ females, $\bar{x} = 1.3$ clusters $\pm$ 14 S.D.). However, the count of egg clusters per female was conservative, because 13% of the ovipositions in this area were not observed, and some females may have oviposited in adjacent areas (about 20 m away). Thus, based on a mean of 274 eggs per cluster, a female may lay up to 1650 eggs during her lifetime of two to three weeks. Of the 153 observed ovipositions by marked females, 13% involved females making two or more depositions in a single day.

Females frequently chose stalks and leaves which already had egg clusters (Fig. 1). At the peak of the oviposition period for an area with plantain (*Plantago lanceolata* L., an alternate host plant; Stamp, 1979) and by the end of the oviposition period in areas with turtlehead, over 23% of the stalks with egg clusters had two or more clusters. However, of those turtlehead stalks with clusters just after the first week of oviposition ($n = 46$), 47% had two or more clusters. Additional clusters were deposited a few days apart (2.4 days $\pm$ 0.3 S.E., range 0 to

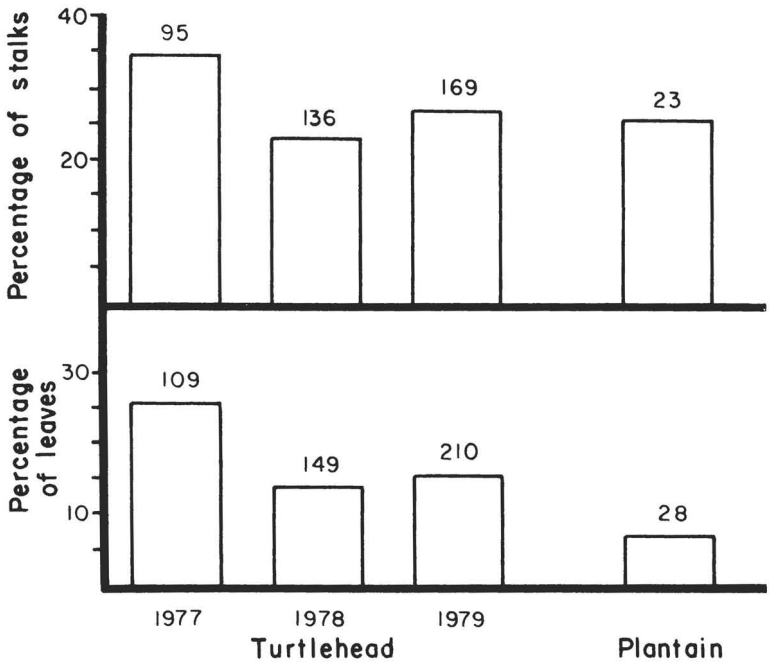

FIG. 1. For those stalks and leaves with egg clusters, the percentages of stalks and leaves with two or more egg clusters are shown. Numbers above the bars indicate total stalks and leaves with egg clusters. Plantain data are from Stamp (1979).

16 days, n = 82). Of stalks with two or more clusters (n = 42), the mean number of depositions was 3.0 (±0.3 S.E.), with up to a total of 10 clusters per stalk.

Females laid their clusters with those of other females. Of 153 observed ovipositions of marked females, 46 females laid eggs with clusters deposited by other marked females. Only one female laid two clusters on the same stalk. For these 153 females (which used 125 stalks), the binomial probability of two clusters deposited by a female in one place is less than 0.001. Twice I observed a female examining a leaf on which another female was ovipositing. The searching female examined the under surface of the leaf from both sides, crawled across and jostled the ovipositing female, and within a few minutes oviposited next to the other female with their wings touching.

Once oviposition began, females exhibited some degree of site tenacity. I observed 10 ovipositing females which were interrupted by males or my movements and then flew 1.5 m or more from their clusters. Within 2 min, three resumed oviposition on the leaves with their

TABLE 3. Comparison of oviposition sites among years. One standard error is indicated and sample sizes are in parentheses. The first four variables were tested each with one-way ANOVA; χ^2-test was used for egg clusters in the outer portion of plant groups.

	1977	1978	1979	Statistical significance
Height of stalk in cm	74.9 ± 1.0 (165)	60.7 ± 1.1 (168)	60.9 ± 1.3 (166)	$P < 0.01$
Height of egg cluster from ground in cm	49.8 ± 0.9 (165)	43.2 ± 0.8 (168)	50.8 ± 0.3 (166)	$P < 0.01$
Width of plant group in cm	54.4 ± 3.0 (114)	50.9 ± 2.5 (129)	66.9 ± 1.9 (122)	$P < 0.01$
Leaf length in cm	12.2 ± 0.2 (165)	11.4 ± 0.2 (168)	10.7 ± 0.2 (168)	$P < 0.01$
Percentage of egg clusters in outer 15 cm of width of plant group	99.3 (165)	91.7 (168)	90.0 (240)	$P < 0.01$

partially laid clusters. Within 5 min three others resumed oviposition on leaves within 15 cm of the first oviposition sites. The rest of the females left the plant groups and did not return that day.

Oviposition Sites

Considerable among-year variation occurred in the characteristics of oviposition sites: height of stalks chosen by females, height of egg clusters from the ground, width of plant groups, and length of leaves with clusters (Table 3). This may reflect variation among years in the growth of the host plant, probably a consequence of the amount of spring precipitation (Stamp, unpubl. data). Most of the egg clusters occurred in the outer 15 cm of the plant groups. Females chose larger

TABLE 4. Dispersion of egg clusters on host plant stalks, based on an estimate of 6554 available stalks.

Number of clusters per stalk	Number of stalks observed	Percentage of egg clusters
0	6385	—
1	123	47.5
2	28	21.6
3	9	10.4
4	4	6.2
5	0	0
6	2	4.6
7	1	2.7
8	1	3.1
9	0	0
10	1	3.9

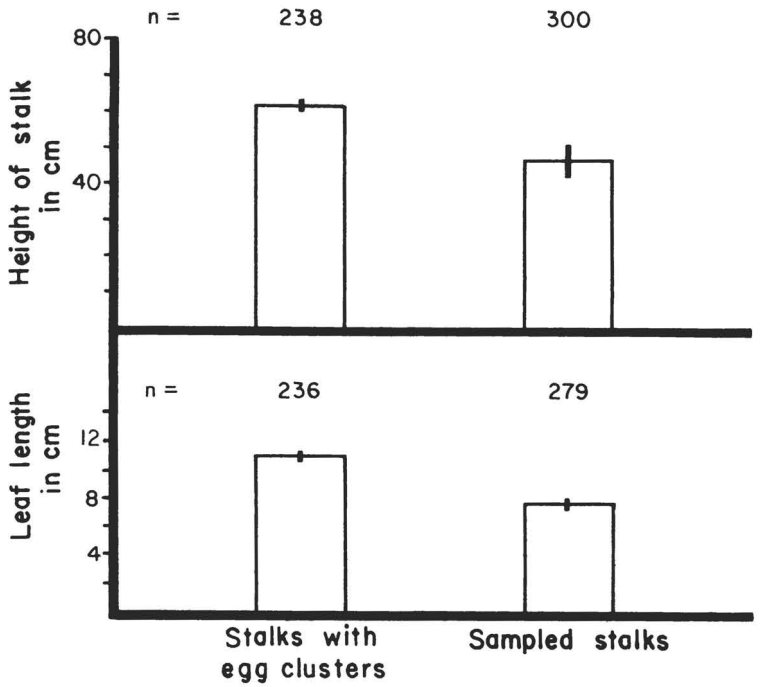

FIG. 2. Comparison of oviposition sites and stalks available for oviposition in 1979, with ± one standard error. Numbers above bars are sample sizes.

stalks and larger leaves than the mean available (two-sample t tests, $P < 0.01$ for both variables; Fig. 2). Stalks with multiple clusters were compared to stalks with solitary clusters deposited late in the flight period to evaluate the hypothesis that multiple clusters occurred on larger leaves and stalks. However, the height of stalks and length of leaves with eggs were similar for stalks with solitary and multiple clusters ($\bar{x}$ = 59.6 cm ± 2.6 S.E. and $\bar{x}$ = 62.3 cm ± 4.6 S.E. for stalks, and $\bar{x}$ = 11.0 cm ± 0.4 S.E. and $\bar{x}$ = 11.2 cm ± 0.6 S.E. for leaves, respectively; n = 22 solitary and 25 multiple clusters, two-sample t tests, $P > 0.50$ for both variables). *E. phaeton* used 53 to 59% of the plant groups available to them. Also, plant groups were classified by size: perimeter less than 100 cm, between 100 and 500 cm, and greater than 500 cm. These butterflies were not selecting plant groups by size (4 of 17, 34 of 58 and 7 of 7 of the plant groups had egg clusters for the respective plant group sizes, χ^2-test, $P > 0.05$). In 1977 and 1979, egg clusters were randomly distributed among the quarters of plant groups (χ^2-tests, $P > 0.05$). However, in 1978 the southwest quarter

TABLE 5. Dispersion of egg clusters on leaves, based on an estimate of 26,216 available leaves.

Number of clusters per leaf	Number of leaves observed	Percentage of egg clusters
0	26,006	—
1	177	68.3
2	25	19.3
3	3	3.5
4	2	3.1
5	3	5.8

of plant groups had significantly more egg clusters ($P < 0.01$). This was probably a consequence of the availability of edges of host plant groups, with some edges not discovered by butterflies due to the height of adjacent vegetation.

I estimated the number of turtlehead stalks and leaves available to *E. phaeton* for oviposition in one area, based on stalks in the outer 15 cm of the plant groups and large leaves on the upper half of stalks. Although these stalks and leaves are referred to as available, no assumption is made here that they are necessarily suitable to ovipositing females. A mean of one stalk per 3.8 cm ± 0.2 S.E. of perimeter was calculated. This mean was multiplied by the total perimeter of the mapped plant groups to estimate the number of available oviposition sites. The estimate was 6554 stalks available to *E. phaeton* for oviposition in this area. The estimate of number of leaves available for oviposition was calculated based on four large leaves on the upper half of the stalk for each stalk in the outer 15 cm of the plant groups rather than for all leaves (mean of 18) per stalk. I multiplied four leaves per stalk by 6554 stalks to obtain an estimate of the number of leaves per stalk which were available for oviposition. This estimate was 26,216 leaves.

Only 2.6% of the estimated available stalks and 0.8% of the estimated available leaves were used by *E. phaeton* for oviposition (Tables 4 and 5). These values may be lower if more of the stalks and leaves were available as oviposition sites. Females did occasionally use stalks near the center of the plant groups as well as leaves on the lower half of stalks. The index of dispersion was used to determine if egg clusters were distributed randomly on stalks and leaves (Southwood, 1978). The number of clusters per stalk and per leaf indicated clumped distributions significant at the 0.001 level.

Some stalks may provide more stimulus for oviposition than others and, consequently, *E. phaeton* may respond to these stalks rather than to the egg clusters on them. At four-day intervals from 13 through 25

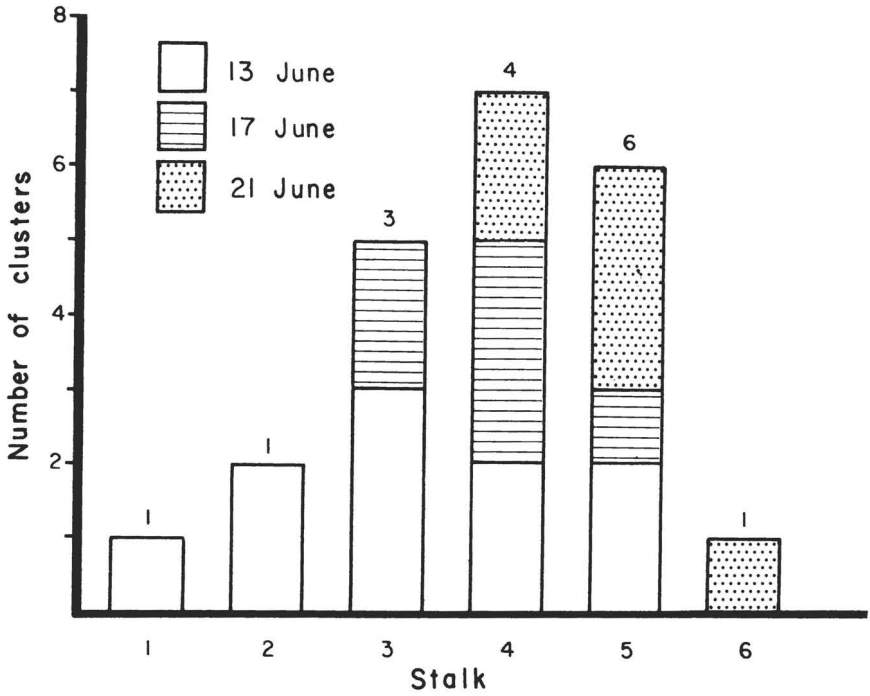

FIG. 3. Repeated use of particular stalks for egg deposition in a moderate-sized plant group. Leaves with egg clusters were removed from these stalks on each date. Total number of leaves with clusters are indicated above bars. No clusters were found on 25 June, at the end of the flight period.

June, the stalks in one plant group were checked for clusters and leaves with clusters were removed. The plant group was 74 cm in diameter with more than 30 stalks in the outer 15 cm of the plant group. Over a period of 12 days, six stalks had clusters (Fig. 3) and the mean number of clusters on those stalks was 3.7 (±2.7 S.D.). Thus, females were repeatedly using particular stalks even though I was removing leaves and the potential stimulus of those stalks either due to those leaves or the egg clusters was reduced.

DISCUSSION

Overall, *E. phaeton* females carefully assessed the suitability of host plant groups and stalks by detailed examination of the leaves upon which they oviposited. *E. editha* are also known to spend considerable time in search of oviposition sites and in depositing egg clusters (Labine, 1968). *E. phaeton* do not appear to be discriminating among plants to avoid parasitoids, predators or competitive larvae.

Egg parasitoids and predators are of more immediate concern than larval enemies, because the eggs are exposed on the leaves three weeks before hatching. However, *E. phaeton* oviposited frequently on leaves and stalks that they examined previously a few seconds to many minutes earlier. This suggests that females were responding to other qualities of the stalks and leaves than the presence of egg parasitoids and predators. The sequence of egg clusters deposited on a leaf did not affect the level of parasitism or number of parasitized eggs per cluster (Stamp, 1981b). Furthermore, loss of eggs to predators was small, with no clear difference between single and multiple clusters on leaves (Stamp, 1981b). Thus, depositing eggs with those of other females did not lower the risk to eggs, as it might by surrounding eggs with others, predator satiation, or causing parasitoids to run out of their own eggs.

E. phaeton chose larger leaves on larger stalks than those generally available and only used a small portion of the available host plant. Furthermore, females oviposited repeatedly on particular stalks, suggesting a paucity of attractive stalks. Perhaps these butterflies were selecting by chemical cues particular stalks of plant groups which promote higher survival of offspring and consequently, yielded a clumped distribution of egg clusters. The fact that more stalks received multiple depositions early in the flight period than later suggests that females later in the flight period may have had to choose between particularly attractive stalks (frequently with several egg clusters) and less attractive stalks. The clonal, perennial turtlehead may benefit by producing a few attractive stalks if that reduces the number of potential flowering stalks which are destroyed by this herbivore. This would be similar to poplar (*Populus angustifolia*) providing a limited amount of optimal resources and thereby, restricting successful colonization by a gall-making aphid (Whitham, 1978).

Frequently *E. phaeton* deposited their eggs with those of other females. Depositing eggs with other clusters has been observed in other populations of *E. phaeton* (Bowers, 1979) and in populations of *E. gillettii* (Williams, 1981) and *E. aurinia* (Keith Porter, pers. comm.). The proposition that *E. phaeton* may deposit eggs with those of others with the result that larvae benefit from large group size (from two or more egg clusters) was examined in detail (Stamp, 1981a, b, 1982a, c). These studies indicated that belonging to a large group over the entire larval period was not essential and was perhaps even detrimental. The group size with highest survivorship to diapause did not exceed the average number of eggs per cluster (Stamp, 1981a).

However, the value of belonging to a large group may fluctuate on a daily and even hourly basis as a consequence of larval and parasitoid

activity (Stamp, 1982a, b, unpubl. data). For example, newly-hatched larvae moved from the oviposition site to the top of the host plant stalk, built a communal web, and then began feeding. Without their webs and the body spines characteristic of the other instars, first instar larvae were particularly vulnerable to parasitoids and predators. One value of belonging to a large group was that such a group quickly reached the top of the stalk. Newly-hatched larvae from all but the first egg cluster deposited on a stalk had a silk trail to follow and a communal web to occupy immediately.

Furthermore, these caterpillars may benefit from membership in large groups due to particular defensive mechanisms (e.g. webs, head-jerking, unpalatability, aposematic coloration). For example, *E. phaeton* reared on turtlehead were unpalatable to blue jays (*Cyanocitta cristata*; Bowers, 1980) and, thus, the effect of the aposematic coloration of these larvae may have been enhanced by large group size. Also, by head-jerking, second and third instar larvae warded off parasitoids effectively (Stamp, 1982a). If caterpillars in contact with each other on the outside of a web were disturbed by a parasitoid, they simultaneously head-jerked for several minutes. However, if these larvae were not touching each other and were disturbed, only a few caterpillars head-jerked and for a shorter period. In the latter case the parasitoid continued to search and make contact with caterpillars.

Since observed survival was highest for moderate-sized groups (that is, equivalent to a single egg cluster), why then were many (30%) of the clusters in groups? Variation in group size of *E. phaeton* may be the result of two opposing and variable selective pressures. Group size of eggs and the ensuing larval aggregations of these checkerspots varied tremendously, with one to 10 egg clusters occurring per stalk and, thus, about 250 to 2500 newly-hatched caterpillars per web (Stamp, 1981a.). By depositing moderate-sized clusters with those of other females, *E. phaeton* may benefit from spreading their eggs, and the offspring may benefit during critical larval periods from membership in large groups. Thus, clumping of egg clusters may enhance reproductive success under some circumstances. However, spreading eggs may also maximize the probability that some of a female's eggs will survive.

In conclusion, *E. phaeton* females were carefully choosing oviposition sites and frequently depositing their eggs with those of other females. These behaviors suggest a scarcity of particularly attractive or high quality stalks. These oviposition behaviors may also indicate the value of group membership for larvae during critical periods, such as the first instar.

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