LARVAL HABITAT SUITABILITY AND OVIPOSITION PREFERENCE IN THREE RELATED BUTTERFLIES[1]

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Abstract. A simple hypothesis about habitat choice by ovipositing butterflies is that females prefer to lay their eggs on plants in habitats where juvenile growth and survival are best. This hypothesis was evaluated by studying 3 *Aristolochia*-feeding swallowtail butterflies (Papilionidae: Troidini).

Results show that the eggs and larvae of all 3 butterfly species survive significantly better in shady habitats than in sunny habitats. Pupal survival is similar in the 2 habitats for at least 1 species. Larval growth rates were similar in the 2 habitats for all 3 species. Thus, for all 3 species shady habitats appear to be more suitable for juvenile development and survival than sunny habitats. Only *Parides montezuma* lays most of its eggs in shady habitats, however; *Battus philenor* and *B. polydamus* females lay most of their eggs in sunny habitats. The original hypothesis is therefore not upheld by this study. Three alternative explanations for the discrepancy between the relative suitability of habitats for the juvenile stages and habitat choice by ovipositing females are suggested.

Key words: Aristolochia; Battus; *Insecta; larval ecology; larval growth rate; larval survivorship; Lepidoptera; Mexico; oviposition behavior;* Parides; *swallowtails.*

INTRODUCTION

The larvae of many plant-feeding holometabolous insects are relatively immobile and are not able to move great distances in search of an appropriate food plant. They must often feed on the plant on which they hatch. The choice of the proper food plant for larval growth and development is thus often made by ovipositing females. Females that lay eggs on plants on which larval mortality rates are high or on which growth is poor will probably leave fewer descendants than females that oviposit on more suitable host plants. Because food plant choice appears to be at least partly genetically determined in many insect species (Hovanitz and Chang 1963, 1965, Huettel and Bush 1971), it is reasonable to expect differences in the suitability of food plants to influence the evolution of oviposition behavior.

One aspect of oviposition behavior that determines the food plants on which an insect will lay eggs is habitat choice. Many ovipositing butterflies do not use all of the habitats in which their host plants grow (Peterson 1954, Lorkovic 1958, Shapiro and Carde 1970, Singer 1971, Ehrlich et al. 1975, Wiklund 1977). Very little is known about the ultimate causes of habitat preference in butterflies, however. Several authors have speculated that ovipositing females will avoid plants on which larval growth and development is poor and will search preferentially for plants on which growth and development is good (Wiklund 1974; Chew 1975, 1977; Feeny 1975; Gilbert and Singer 1975; Gilbert 1977; Rausher 1978). The same argument suggests

that females will avoid habitats in which larval growth and development is poor and will concentrate on habitats in which larvae survive and grow well (Singer 1972, Gilbert and Singer 1975, Wiklund 1977).

Preliminary observations on the *Aristolochia*-feeding butterflies *Battus philenor, B. polydamus,* and *Parides montezuma* in northeastern Mexico suggest that, for each species, ovipositing females tend to search for larval food plants in only 1 of 2 habitats where those plants grow. Both *Battus* species seemed to search primarily in sunny, open habitats, whereas *Parides* seemed to search mostly in shady habitats. In this study I examine the habitat preferences of these butterflies and the suitability of the 2 habitats for larval growth and survival. In particular, I have attempted to answer 3 specific questions: (1) Do the species differ in their choice of habitat in which to search for larval food plants and oviposit? (2) Does juvenile survivorship or larval growth differ in the 2 habitats? (3) Do ovipositing females preferentially search for larval food plants and lay most of their eggs in the habitat that is more suitable for larval growth and survival?

METHODS

Experimental organisms.—The butterflies *Battus philenor, B. polydamus,* and *Parides montezuma* are common at low elevations along both coasts of Mexico. All 3 are conspicuous elements of the wet-season fauna in the lowlands of the Gomez Farias region of Tamaulipas in northeastern Mexico (latitude 29°20'N, longitude 107°42'W), where I conducted this study. The larvae feed only on species of the family Aristolochiaceae, as do most other species in the papilionid tribe Troidini (Scriber 1973). In the Gomez Farias area, the 2 host plants are *Aristolochia orbicularis* and *A. micrantha.* Both are procumbent perennial herbs

TABLE 1. Site characteristics for survival censuses of naturally laid eggs and larvae

Study Site	Patch	Food Plants[1]	Sampling Period[2]	Butterfly Species	Sample Size[3]
El Encino	Sun #1	orb.	1	B. philenor	161
				B. polydamus	144
			3	B. philenor	45
				B. polydamus	216
	Sun #2	mic.	1	B. philenor	100
			3	B. philenor	91
	Shade #1	orb., mic.	1	B. polydamus	70
				P. montezuma	47
			3	P. montezuma	48
Pico de Oro	Sun #3	orb.	2	B. philenor	38
				B. polydamus	68
	Shade #2	orb.	2	B. polydamus	24
				P. montezuma	19

[1] orb. = *Aristolochia orbicularia*; mic. = *Aristolochia micrantha*.
[2] 1 = 27 Jun–17 Jul 1975; 2 = 17–31 Jul 1975; 3 = 2–28 Aug 1975.
[3] Number of eggs from which survivorship curves were determined.

that invade disturbed habitats such as forest clearings, forest edges, and abandoned sugar cane fields.

Two of the butterflies, *Battus philenor* and *Parides montezuma,* lay eggs on both host plant species. Neither butterfly shows any significant preference for one host plant over the other. In contrast, *B. polydamus* oviposits only on *A. orbicularis. B. philenor* and *B. polydamus* lay small clusters of 1–9 eggs per plant; *P. montezuma* always lays eggs singly, not in clusters. The adults of all 3 species become abundant in late May or early June at the onset of the rainy season. Several generations are produced through the next 6 mo. At the beginning of the dry season, usually in November or December, the butterflies cease to be abundant and presumably enter diapause.

Habitats and study sites.—The dominant vegetation types in the lowlands in the Gomez Farias region are primary and secondary deciduous forests and cultivated fields. Scattered among this vegetation are patches of habitat in which *Aristolochia* grows. Although an intergradation doubtless exists, 2 fairly distinct habitat types can be recognized: sunny habitats and shady habitats. Shady habitats, principally forest edges, natural forest disturbances, and roads and trails through forests, are disturbed areas that are shaded throughout the day by a closed canopy and have characteristic mid-day light intensities of approximately 4305.6 lx at ground level. Sunny habitats, principally open second-growth areas with few trees, are exposed to sunlight at ground level throughout the day and have characteristic mid-day light intensities of approximately 62 431.2 lx.

Sunny and shady habitats were sampled in each of 2 study sites. The primary site, El Encino, was located adjacent to the Rio Sabenas, approximately 5 km west of the town of El Encino, Tamaulipas, Mexico. This site consisted of disturbed riverine forest, primary and secondary deciduous forests, cultivated fields, and abandoned fields in various stages of secondary succession. Within the El Encino site, 3 habitat patches were sampled to study egg and larval survivorship. Sun #1 was a sugar cane field that had been abandoned for several years and was well into secondary succession. This habitat contained many *Aristolochia orbicularis* plants but few *A. micrantha.* Sun #2 was an uncultivated, open field that had been cleared of secondary forest about 1 yr before this study. Secondary succession was in its initial stages. Many *A. micrantha* plants grew in this habitat; *A. orbicularis* was absent in the 1st census period (see below), but had become common by the time of the 2nd census period. Shade #1 was a section of abandoned, unpaved road through secondary forest. The road was seldom used by vehicles, and vegetation, including both host plant species, had grown up on the surface. The surrounding forest formed a closed canopy over the road and blocked most of the sunlight throughout the day.

A second study site, Pico de Oro, was located on the ranch Pico de Oro, ≈16 km south of the town of El Encino on the Inter-American Highway. The vegetation was similar to that at the El Encino site. I measured egg and larval survivorship in 2 habitat patches at Pico de Oro. Sun #3 was an open 2nd-growth area that had been abandoned to secondary succession several years before I began the study. It had never been planted in sugar. Shrubs up to 2 m tall were widely scattered throughout the field, but there were no trees present and the herbaceous vegetation was exposed to sunlight throughout the day. Of the 2 host plants, only *A. orbicularis* was present. Shade #2 was a well-travelled section of unpaved road through secondary forest. The forest formed a closed canopy over the road and shaded both the road and the vegetation on either side of it throughout the day. *Aristolochia orbicularis* grew among the vegetation at the side of the road. The characteristics of the various study sites are given in Table 1.

Juvenile survivorship.—I measured the survivorship of naturally laid eggs and the larvae hatching from them in the 2 habitat patches at Pico de Oro between 17 June and 31 July 1975. At El Encino I measured egg and larval survivorship in each habitat patch during 2 periods, 25 June–17 July and 2–28 August 1975. In each patch all plants within an area of ≈ 10 m^2 were marked with surveyor's flags at the beginning of the sample period. The marked plants were censused daily and the appearance of new egg clusters was recorded. Each egg was checked daily until disappearance, death, or hatching; each hatched larva was checked until disappearance. Larvae remain on 1 plant until all foliage is eaten, at which point they disperse to neighboring plants. Dispersal normally occurs only during the last 2 instars. Because I sampled all plants within a defined area, I was able to detect larvae that had left 1 plant and moved onto another within the sampling area. The chances that I would count as dead a larva that had moved from 1 plant to another were thereby minimized, although there were doubtless some cases in which larvae wandered out of the sampling area and found new host plants. The sudden appearance of a large larva on a plant where there had been none the previous day was usually associated with the disappearance of a similarly-sized larva from another plant the previous day. In such cases, the 2 larvae were assumed to be the same individual.

Because ovipositing females do not use the full range of habitat types available, I supplemented the measurement of survivorship of naturally laid eggs with larval stocking experiments. These experiments were designed to compare larval survivorship for each butterfly species in sunny and in shady habitats. Eggs of each species were obtained from females that had been collected in the field. Females were placed in plastic boxes with larval food plants. When the boxes were placed under an incandescent lamp, the females laid eggs on the food plants that had been provided. The eggs were removed from the food plants and placed in the plastic petri dishes until hatching. On the morning that the eggs hatched, the new 1st-instar larvae were placed out on randomly selected *A. orbicularis* plants in habitats Sun #1 and Shade #1 at El Encino. For *B. philenor* and *B. polydamus,* 3 larvae were placed out on each plant in each treatment; for *P. montezuma* 1 larva was placed out on each plant. No plant was used for >1 butterfly species. The plants were censused daily for larval disappearance.

Pupation normally occurs on a twig or branch of a shrub or herb, where the larva spins a silk sling that secures the pupa to the surface of the twig. A larva that is ready to pupate wanders off the host plant in search of a suitable pupation site, but usually remains in the same habitat in which it fed. To determine the relative survivorship of pupae in sunny and shady habitats, I placed out 20 *B. philenor* pupae in Shade #1 and Sun #1 habitat patches at El Encino on partially concealed twigs and branches of shrubs. I allowed larvae to pupate on aluminum screening, which I then attached securely to a twig with nylon thread. The locations of the pupae were marked with surveyors' flagging, and the pupae were censused daily. Whenever possible, death in the field was attributed to a specific mortality factor such as ant predation or parasitism. Parasitism by an unidentified chalcidoid wasp could be detected in the field by the presence of a small, round, exit hole in a hollow pupal case. Complete disappearances of pupae were recorded as a separate category. After 12 days I removed the pupae that were still alive and determined the proportion parasitized by holding the pupae in closed plastic containers until either wasp or butterfly emerged. The normal duration of the pupal stage is approximately 14 days.

Larval growth rates.—The effect of habitat on larval growth rates was examined for each butterfly species. Using a millimeter ruler I measured the length of larvae in the larval stocking experiments for the first 5 days after the larvae were placed out. Growth during this period is approximately linear with time. I subtracted the original larval length from each measurement to obtain the increase in length. I then performed a linear regression of increase in length on the number of days a larva had been growing. In the regression model used, the fitted regression line passes through the origin, since at time zero the increase in larval growth is zero. The use of this model is justified by the fact that in none of the tests did the y-intercept of the regressions differ significantly from zero (Snedecor and Cochran 1967). The slopes of the regressions are equal to the growth rate of the larvae. For each species, the regression slope (growth rate) of larvae growing in the shady habitat was compared with that of larvae growing in the sunny habitat using standard stitistical methodology for linear models (Searle 1977).

Use of habitats by females.—I compared habitat use by ovipositing females of the 3 butterfly species in 2 ways. The 1st method involved comparing the number of egg clusters (for *Battus philenor* or *B. polydamus*) or eggs (for *Parides montezuma*) laid by each species on the plants in each of the 5 habitat patches. The plants that were censused for egg and larval survivorship were examined daily during the censuses for the appearance of new egg clusters. Ovipositing *Battus* females normally lay a tight cluster of eggs on a plant and then resume flight without laying other eggs on the same plant. Each egg cluster thus represents a unique discovery of a host plant by a butterfly and a "decision" to oviposit. Eggs of the 3 species are easily distinguishable by color, size, and surface texture. A *G*-test (Sokal and Rohlf 1969) was used to test whether similar proportions of egg clusters were laid in the 2 habitats by all 3 butterfly species. In these tests the data for the 2 habitat patches Sun #1 and Sun #2 at El Encino were combined.

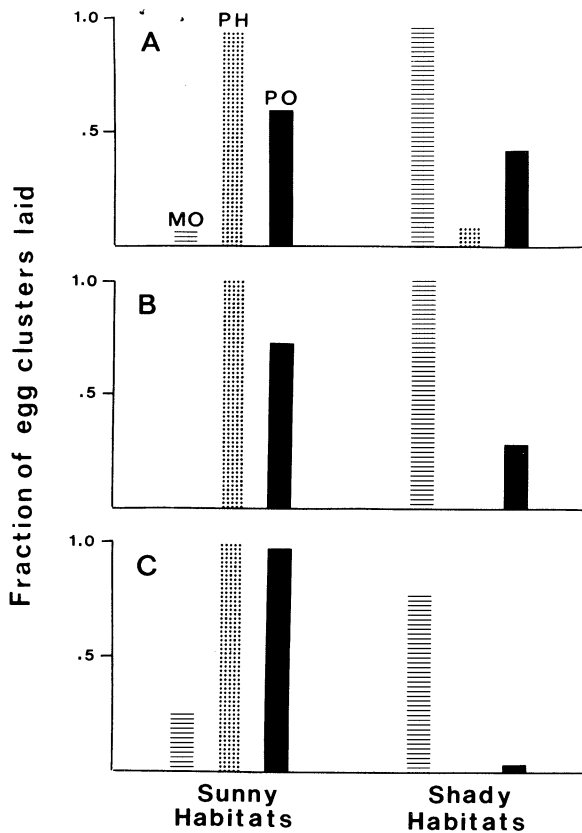I also compared the use of habitats by the 3 species

FIG. 1. Fraction of egg clusters laid in sunny and shady habitats. Shaded bars: *Parides montezuma* (MO); Stippled bars: *Battus philenor* (PH); Black bars: *Battus polydamus* (PO). (A) El Encino, 25 June–17 July (N = 35, 92, 53). (B) Pico de Oro, 17–31 July (N = 10, 21, 10). (C) El Encino, 2–28 August (N = 59, 46, 55).

FIG. 2. Fraction of females seen searching in sunny and shady habitats. Bars and abbreviations as in Fig. 1.

by comparing the proportional distributions of sightings of ovipositing females between the 2 habitat types. The search behavior of ovipositing *Battus* and *Parides* butterflies is very characteristic. Females fly slowly above the herbaceous vegetation and periodically approach and land on plants (Rausher 1978). Sighted butterflies were captured with a net to verify that they were females and then released. A standard path was marked at the El Encino study site. This path consisted of 3 major segments: (1) a roughly circular segment of abandoned roadway through a 2nd-growth deciduous forest with a closed canopy; (2) a continuation of the roadway, no longer in the forest, past 2 abandoned open fields; and (3) a trail leading from segment 2 and cutting through more 2nd growth deciduous forest. Segments 1 and 3 were deeply shaded throughout the day. Any butterflies seen searching for oviposition sites in these segments were considered to be searching in a shady habitat. Segment 2 and the adjoining abandoned fields were exposed to sunlight most of the day. Any female butterflies seen searching in these areas were considered to be searching in a
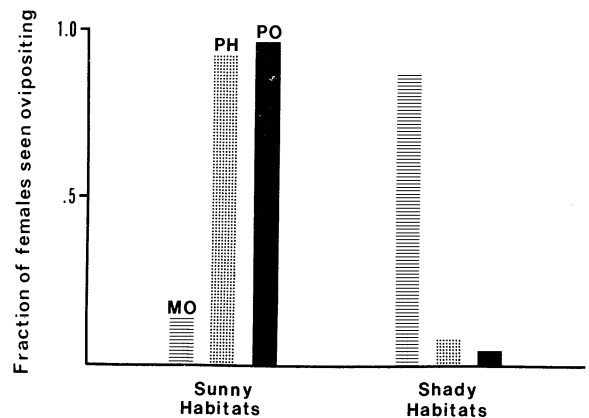
sunny habitat. A standard walk was conducted by walking along the 3 path segments at a constant speed and noting the species and locations of any butterflies searching for food plants. I walked the segments of the path in the following order: segment 1, first abandoned field, segment 2 (1 way), second abandoned field, segment 2 (return), segment 3 (both directions). I repeated this sequence until 2 h had elapsed. When walking through the abandoned fields, I spent about 5 min moving in a circular path. The standard walks were made only on sunny days between 1000 and 1200 h. A total of 37.5 h was spent conducting this survey between 27 June and 10 September 1975. A G-test was used to test whether proportions of females of the 3 butterfly species sighted in the 2 types of habitat were similar.

RESULTS

Habitat use by ovipositing females.—Egg-laying *Battus philenor* and *B. polydamus* females tend to lay most of their eggs in sunny habitats, whereas *Parides montezuma* females lay most of theirs in shady habitats. This difference is evident from the distribution of egg clusters among the censused habitat patches (Fig. 1). Virtually all *B. philenor* egg clusters were laid on plants in Sun #1 and Sun#2 areas at El Encino and in Sun #3 area at Pico de Oro. A slightly higher fraction of eggs was laid by *B. polydamus* females in shady habitats, but this species still laid most of its eggs in the sunny areas. In contrast, *P. montezuma* laid 76–100% of its eggs in the shady habitats.

Similar patterns of habitat use by the 3 butterflies are revealed by the observations of searching females along the standard path at El Encino (Fig. 2). More than 90% of *B. philenor* sightings were in sunny habitats. Most of these females were seen searching in the abandoned fields adjacent to segment 2 of the standard path. The same pattern of sightings is exhibited by *B. polydamus*. Female *P. montezuma* use the habitats
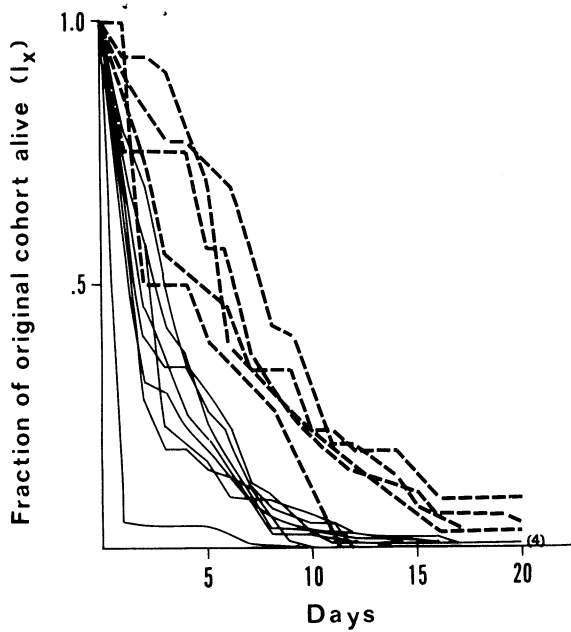
FIG. 3. Egg and larval survivorship curves for all combinations of butterfly species and habitat patches listed in Table 1. Solid lines represent curves for sunny habitats, broken lines represent curves for shady habitats. Day zero is day egg cluster was first discovered. The "(4)" in the figure means that 4 curves for sunny habitats converge to approximately the same value and are represented by 1 line segment between days 17 and 20.

TABLE 3. Comparison of mean daily survival probabilities for 3-day intervals for naturally laid eggs

Period (days)	Sunny[a] Habitats	Shady[b] Habitats	P[c]
0–3	.650	.885	<.001
3–6	.788	.887	<.05
6–9	.582	.819	<.05
9–12	.629	.715	n.s.
12–15	.734	.831	n.s.
15–18	.846	.789	n.s.
18–21	1.000	.938	n.s.

[a] Mean of values for each of the 8 species—time period combinations listed in Table 1 under "Sun" habitat.
[b] Mean of values for each of the 5 species—time period combinations listed in Table 1 under "Shade" habitat.
[c] Mann-Whitney U-test. n.s. = not significant.

differently. Less than 15% of these females seen searching for food plants were in sunny habitats.

A pairwise statistical comparison of the use of sunny and shady habitats for oviposition by the 3 species reveals that *B. philenor* and *B. polydamus* use the habitats similarly, while both differ markedly from the way in which *P. montezuma* uses them (Table 2). The 1 exception to this rule appears to be period 1 at El Encino, when *B. polydamus* had a significantly greater tendency to use shady patches than did *B. philenor*.

TABLE 2. Pairwise comparisons of habitat use by ovipositing females. Values are probabilities that the 2 species differ in patch use by chance (G-test)

Species Compared	Distribution of Egg Clusters in Patches[a]			Habitat Use by Ovipositing Females
	El Encino Period 1	El Encino Period 3	Pico de Oro Period 2	
B. philenor *B. polydamus*	<.001	n.s.	n.s.	n.s.
B. philenor *P. montezuma*	<.001	<.001	<.001	<.001
B. polydamus *P. montezuma*	<.001	<.001	<.001	<.001

[a] Period 1 = 25 Jun–17 Jul 1975; Period 2 = 17–31 Jul 1975; Period 3 = 2–28 Aug 1975.

Even at this time, however, a majority of the *B. polydamus* egg clusters were found in sunny habitats. These results suggest that differences in the ways in which the 3 species distribute egg clusters among habitat types are largely determined by differences in the relative amount of time allocated to searching in the 2 habitats.

Egg and larval survivorship.—When the natural survivorship curves of all habitat patches are examined, it is evident that egg and larval survival are greater in shady habitats than in sunny habitats (Fig. 3). Survivorship to day 20, which corresponds approximately to the 3rd day of the 5th (ultimate) instar, was significantly greater for eggs and larvae in the shady habitats than for those in sunny habitats ($P < .05$, Mann-Whitney U-test). Survivorship values after day 20 tend to be of lower reliability because larvae begin to leave the host plant to pupate and cannot be found again.

The mortality factors responsible for lower survival in sunny habitats operated during the egg stage (days 1–6) and during the early instars (days 7–15). Mean daily survival probabilities for successive 3-day periods were calculated as

$$p_x = \sqrt[3]{\frac{l_{x+3}}{l_x}}$$

where p_x is the mean daily survival probability for the period from day x to day $x + 3$ and l_x is the fraction of individuals surviving from day 0 to day x. In this case x takes the values $x = 0,3,6, \ldots ,18$. Mean daily egg survival (days 0–6) and 1st instar larval survival (days 7–9) are significantly lower for the sunny habitats (Table 3). Second and 3rd instar larvae also did not survive as well in the sunny habitats, although differences are not significant. The larger 4th and 5th instar larvae (approximately days 15–20) appear to survive slightly better in the sunny habitats, but the differences are not significant and do not make up for the greater mortality of eggs and smaller larvae.

Although this pattern suggests that there are qualities of sunny habitats that render them less suitable

TABLE 4. Comparison of mean daily survival in sunny vs. shady habitats for naturally laid eggs of *Battus polydamus*. Data for all shady habitats are combined, as are data for all sunny habitats

| Period (days) | Habitats | | P^a |
	Sunny	Shady	
0–3	.692	.897	<.05
3–6	.791	.816	n.s.
6–9	.604	.882	<.05
9–12	.749	.553	n.s.
12–15	.771	.917	n.s.
15–18	.861	.857	n.s.
18–21	1.000	1.000	n.s.

[a] Arcsin test for equality of percentages.

for egg and larval survival than shady habitats, it does not conclusively demonstrate that juvenile survivorship is greater in shady habitats. The 2 sets of curves in Fig. 3 represent different butterfly species. The curves for sunny habitats include data for *B. philenor* and *B. polydamus*; the curves for shady habitats represent data for *B. polydamus* and *P. montezuma*. A better test for differences among habitat types involves controlling for differences among butterfly species.

Such a test may be done for naturally occurring eggs and larvae of *B. polydamus*. The data, taken from the curves in Fig. 3, reveal that survivorship is greater in shady habitats (Table 4). Once again, significant differences in survivorship occur during the egg and early instar stages, while differences for later instar larvae are not significant.

The larval stocking experiments were designed to eliminate the effects of species differences that might confound the results in Fig. 3. For all 3 butterflies, the pattern of larval survival in these experiments is the

TABLE 5. Comparison between shady and sunny habitats of mean daily survival probabilities of experimentally stocked larvae

| Period (day) | Habitats | | P^a |
	Sunny	Shady	
Parides montezuma			
0–3	.638	.790	<.05
3–6	.795	.929	=.05
6–9	.600	.864	n.s.
$(n)^b$	$(49)^b$	$(49)^b$	
Battus philenor			
0–3	.538	.692	<.01
3–6	.455	.520	n.s.
6–9	.600	.200	n.s.
$(n)^b$	$(99)^b$	$(81)^b$	
Battus polydamus			
0–3	.604	.783	=.065
3–6	.000	.470	<.001
$(n)^b$	$(51)^b$	$(21)^b$	

[a] Arcsin test for equality of percentages.
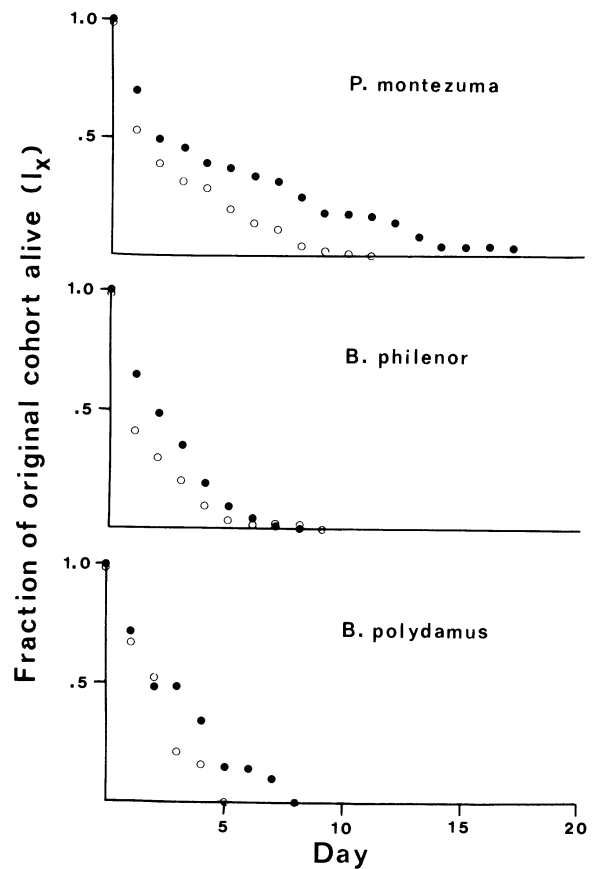[b] Sample size.

FIG. 4. Comparison of larval survivorship in shady (solid circles) and sunny (open circles) habitats in larval stocking experiments. (A) *Parides montezuma* $P < .11$, $N = 49, 49$: sun, shade respectively). (B) *Battus philenor* ($P < .02$, $N = 81, 99$). (C) *Battus polydamus* ($P \gg .10$, $N = 51, 21$). Day zero is day larvae were placed out on plants.

same. During the first 3–6 days, daily larval survivorship in the shady habitat is > in the sunny habitat (Table 5). Over the entire period of the experiment, survivorship in the shady habitat is significantly > in the sunny habitat for *B. philenor* ($P < .02$, Kolmogorov-Smirnov 2-sample test) and is almost significantly greater for *P. montezuma* ($P < .11$) (Fig. 4). Overall survivorship of *B. polydamus* appears to be greater in the shady habitat as well, but the difference is not significant.

The lower survivorship of eggs and early instar larvae in sunny habitats may be due to greater predation rates on these stages. Predatory ants and spiders on the vegetation appeared to be more numerous in sunny habitats. It is also possible that eggs and larvae in sunny patches are more exposed to heavy rains that wash them from the plant.

Pupal survivorship.—The differences in survivorship between *B. philenor* pupae placed out in the two habitats are not significant (Table 6). I calculated a mean daily predation rate as

TABLE 6. Comparison of pupal mortality in sunny and shady habitats

Source of mortality	Habitats		P^a
	Sunny	Shady	
Parasitoids	7	9	
Predators	10	6	
Disappearance	2	5	
Total Deaths	19	20	
Number Emerging	1	0	
Probability of Emerging	.05	.00	n.s.
Mean Daily Predation Probability	.039	.025	n.s.

[a] Arcsin test for equality of percentages.

$$d = 1 - \frac{\text{Number of pupae dying due to predation}}{\text{Number of days pupae exposed}}$$

For these calculations, complete disappearances of pupae were included in the category of deaths due to predation. The daily probability that pupae will be killed by predators does not differ significantly between sunny and shady habitats (Table 6). The probability that pupae will be parasitized is also similar in the 2 habitats.

The high pupal mortality rates observed in these experiments appear to be similar to those for larvae that pupate naturally. By following *B. philenor* larvae that had ceased feeding and were ready to pupate, I was able to locate 5 individuals that had selected their own pupation site. Of the 5, none successfully eclosed. Four were killed by ants and 1 by a parasitoid.

Larval growth rates.—Because of the greater insolation of sunny habitats, it might be expected that ambient temperatures for caterpillars growing in those habitats would be higher than for larvae growing in shady habitats, and that growth rates would therefore be greater. My results do not support this expectation. The growth rates of larvae growing in the sunny habitat do not differ significantly from those of larvae growing in the shady habitat for any of the butterfly species (Table 7).

One possible explanation for similar growth rates in the 2 habitats is that mean daily temperatures in the 2 habitats are similar. Although the greater insolation of sunny habitats probably means larvae experience higher temperatures during the day than they experience in shady habitats, the opposite may be true during the night. With no canopy to reflect radiation and create a thermal boundary layer, temperatures may fall further and more rapidly at night in sunny habitats than in shady habitats (e.g., see Kittredge 1948, Vaartaja 1954, Geiger 1965, Tuller and Chilton 1972). Lower night temperatures in sunny habitats may thus compensate for the higher day temperatures; such compensation would lead to the observed similarity of growth rates in the 2 habitats.

DISCUSSION

Although many species of butterflies have been observed to search for larval food plants and to oviposit in only some of the habitats that are available to them, the ultimate causes of such habitat preferences remain obscure. Singer (1972) and Ehrlich et al. (1975) have demonstrated that great differences in the survivorship of eggs laid on plants growing in serpentine and nonserpentine soils can account for the restriction of *Euphydryas editha* females to serpentine soils in many parts of California. Other authors have suggested that oviposition search behavior will evolve to ensure that females lay eggs in the habitats that are most suitable for the growth and development of the juvenile stages (Gilbert and Singer 1975, Wiklund 1977). The results of this study indicate, however, that the habitat in which a female lays most of her eggs is not always the one that is most suitable for the juvenile stages.

The choice of an oviposition site by a female butterfly can affect the success of her offspring in 2 major ways. It may affect the probability that her eggs will survive to reach the adult stage; it may also affect the size, and hence the fecundity, of her offspring. For all 3 swallowtails in this study, mortality of eggs and larvae was greater in sunny habitats than in shady habitats. Moreover, pupal survival was the same in both habitat types, at least for *B. philenor*. Although I did not examine pupal survivorship for the other 2 species, the results for *B. philenor* can probably be extended to them. Observations on a few (4 and 5 respectively)

TABLE 7. Larval growth rates of the 3 butterfly species in sunny and shady habitats. The growth rates are estimated from the slope of the regressions of increase in larval length on time growing

Species	Habitat	Growth rate (mm/day)	n^a	Explained[b] Variance	F	P
Battus philenor	shady	1.68 (±.07)	123	.81	1.37	>.25, n.s.
	sunny	1.73 (±.11)	101	.70		
Battus polydamus	shady	1.10 (±.05)	156	.73	3.03	>.05, n.s.
	sunny	1.18 (±.07)	80	.85		
Parides montezuma	shady	.86 (±.06)	74	.58	.03	>.50, n.s.
	sunny	.86 (±.06)	43	.63		

[a] Sample size.
[b] The fraction of the total variance that is explained by the regression.

natural pupations of *B. polydamus* and *P. montezuma* revealed that these species pupate in sites similar to those chosen by *B. philenor* and that, like *B. philenor*, both species suffer heavy mortality from predators and parasites. Thus, overall survivorship from egg to adult emergence is greater in shady habitats for *B. philenor* than in sunny habitats; the same is probably true for *B. polydamus* and *P. montezuma*.

The effect of habitat on adult size could not be measured directly, since it was virtually impossible to collect large numbers of pupae in nature. I measured the effects of habitat on larval growth rates instead. Recent discoveries in the physiology of insect molting suggest that environmental factors affect pupal size in Lepidoptera primarily by affecting growth rates. Hormonal initiation of the events associated with pupation occurs only after larvae have reached a genetically programmed size. Some feeding occurs after the pupation sequence has been initiated, however, and results in some growth before the final gut clearance and the onset of searching for a pupation site (Nijhout and Williams 1974, Nijhout 1975). The weight attained above the threshold size at which the pupation sequence is initiated thus depends on the rate at which a larva grows between the initiation of the pupation sequence and the final clearing of the gut. Since growth rates are similar in the habitats for larvae of all 3 species in this study, it is probable that larvae in the 2 habitats reach the pupation threshold at approximately the same time, on the average. It is also probable that the average weight gain above the pupation threshold is similar. Thus, final pupal size and adult fecundity, which in Lepidoptera are usually correlated (Morris 1963, Englemann 1970, Lederhouse 1978), are probably similar in the 2 habitats.

Since the larvae of all 3 butterfly species survive better and grow as rapidly in shady habitats as in sunny habitats, shady habitats would appear to be the more suitable habitat for the juvenile stages of each. Only *P. montezuma* females lay most of their eggs in shady habitats, however. The females of *B. philenor* and *B. polydamus* lay most of their eggs in sunny habitats. The behavior of these 2 species appears to contradict the hypothesis that oviposition habitat preferences should reflect the relative suitability of different habitats for growth and survival of the juvenile stages. At least 3 alternative explanations may be proposed to account for the lack of correspondence between habitat suitability and habitat preference in the 2 *Battus* species.

1. *The relative suitability of habitats varies over time.*—The survivorship of the juvenile stages of Lepidoptera can vary greatly at 1 site over a period of several years (Morris 1963, Clark et al. 1967, Varley et al. 1973, Ehrlich et al. 1975). Moreover, the variations at 1 site may be independent of variations at another (Ehrlich et al. 1975). In such situations, habitat preferences will probably correspond to long-term averages in the relative suitability of the different habitats. My study may have been conducted in a year in which the relative suitabilities of sunny and shady habitats deviated greatly from the norm.

2. *The relative suitability of habitats varies over space.*—The 2 study sites in this investigation were separated by approximately 10–15 km. Over this distance shady sites appear to be about equally good and sunny sites about equally bad for larval growth and survival (Fig. 3). The number of habitats sampled was of necessity small, however, and the quality of different areas of the same habitat type may be much more variable than is indicated by this study. Furthermore, over distances >10–15 km the relationship between growth and survival in sunny and shady habitats may differ greatly from what I observed. Because *B. philenor* and *B. polydamus* are wide-ranging butterflies, their habitat preferences probably correspond to the average suitability of different habitats in a large region. They may not correspond to the relative suitability of 2 habitat types sampled from a small area in that region.

3. *The rate of food plant discovery is higher in habitats that are of lower suitability for the juvenile stages.*—The rate at which a female lays eggs may profoundly influence her reproductive success. Because adult butterflies of the species in this study are quite commonly captured by spiders, both those that capture prey in webs and those that sit on flower heads and seize butterflies that approach to drink nectar (*personal observation*), adult mortality rates may be quite high and expected longevity short. Under such circumstances, females with higher oviposition rates would probably lay more eggs before dying. The greater number of eggs laid by females with a preference for habitats in which oviposition rates are high might then more than compensate for lower juvenile survivorship. The structure and composition of vegetation in which host plants grow can profoundly affect the ease with which those host plants are discovered by phytophagous insects (Pimentel 1961, Smith 1969, 1976*a*, *b*, Tahvanainen and Root 1972, Atsatt and O'Dowd 1976), including *B. philenor*. The vegetative characteristics of shady and sunny habitats may differ sufficiently to result in *B. philenor* and *B. polydamus* females discovering more plants and laying more eggs in sunny habitats. A preference for sunny habitats may thus be favored in these 2 species despite the lower survivorship of the juvenile stages. Any other environmental factor that differs between habitat types and that affects searching ability, such as host plant abundance, thermal environment, or competition with other species for oviposition sites, may similarly influence habitat preference.

These considerations apply equally well to analyses of host plant preferences within a habitat. For a complete understanding of the evolution of habitat or host plant preferences one must examine not only the rel-

ative suitability of the habitats or host plants for larval growth and survival, but also temporal and spatial variation in suitability and the efficiency of female searching.

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