

EARLY STAGE OF HOST RANGE EXPANSION BY A SPECIALIST HERBIVORE, *EUPHYDRYAS PHAETON* (NYMPHALIDAE)¹

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Abstract. We examined whether larval and adult behavior, physiology, and chemical defense were altered as a result of host range expansion by the Baltimore checkerspot (*Euphydryas phaeton*, Nymphalidae) from the native host plant, turtlehead (*Chelone glabra*, Scrophulariaceae), to the introduced weed, plantain (*Plantago lanceolata*, Plantaginaceae). We found that newly hatched larvae from eggs collected from a population using plantain were heavier than those from a population using turtlehead. Nonetheless, both the pre-diapause and postdiapause larvae derived from the turtlehead population and fed turtlehead in a laboratory experiment gained more mass than those from the plantain population fed plantain. Collections of diapausing larvae from field sites corroborated that pattern. Regardless of the population source (i.e., those using either turtlehead or plantain), postdiapause larvae reared on turtlehead exhibited higher relative growth rate (RGR), efficiency of conversion of ingested food (ECI), and efficiency of conversion of digested food (ECD) than those fed plantain, even though approximate digestibility (AD) and leaf nitrogen concentrations were lower for turtlehead. Regardless of their population of origin, choice tests showed that newly hatched larvae preferred turtlehead. Likewise, adult females reared from larvae collected from both populations oviposited exclusively on turtlehead. Both *C. glabra* and *P. lanceolata* contain iridoid glycosides. The iridoid glycoside profile of butterflies reared on these two plants differed, reflecting the differences of the host plants. The shift of some populations of *E. phaeton* onto plantain is most likely a function of several ecological factors rather than genetic differentiation between populations using turtlehead and plantain.

Key words: checkerspot butterflies; *Chelone glabra*; insect herbivory; iridoid glycosides; larval host plant preference; oviposition; *Plantago lanceolata*; plantain; plant chemistry; plant–insect interaction; turtlehead; unpalatability.

INTRODUCTION

Many herbivorous insect species are composed of populations that differ in the host plant species used (Hsiao 1978, Fox and Morrow 1981, Scriber 1983, Singer 1983, Tabashnik 1983, Futuyma and Peterson 1985). Such a pattern raises the evolutionary question: how are new host plant species incorporated into the diet of a herbivorous insect? Such changes are of interest because of the insight they may provide on the evolution and diversification of insect–plant relationships (Ehrlich and Raven 1964), as well as speciation in phytophagous insects (Bush 1969, Diehl and Bush

1984, Katakura et al. 1989). Although the processes by which novel crop species are incorporated into insect diets have been well studied because of their economic importance (Myers 1976, Hsiao 1978, Shapiro and Masuda 1980, Tabashnik 1983), such processes have been rarely studied in natural plant and insect populations, where the dynamics are likely to be quite different.

For a novel host plant to be incorporated into the diet of an insect herbivore, the insect must recognize the novel plant as food and be able to survive on it. Thus, there are several components to this process, including: (1) female ability to find the host plant, (2) female acceptance of the host plant as a place to oviposit, (3) larval acceptance of the host plant, (4) larval ability to find and recognize the host plant, and (5) sufficient larval growth and survival on the host plant (Rauscher 1982, 1983, Thomas et al. 1987, Thompson

¹ Manuscript received 10 August 1990; revised 20 April 1991; accepted 27 April 1991; final version received 31 May 1991.

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1988). In turn, there are many consequences of such host plant shifts for the insects: (1) use of the new host plant may increase food availability, (2) food quality may change in a positive or negative way, which may affect larval growth, survival, and fitness, (3) there may be different physiological costs for using the new host plant, and (4) there may be changes in susceptibility to predators and parasitoids (Price et al. 1980, Scriber and Slansky 1981, Tabashnik 1983, Bernays 1988, Weis and Berenbaum 1989).

The recent host range expansion by the Baltimore checkerspot, *Euphydryas phaeton* Drury (Nymphalidae), from its native host, turtlehead, *Chelone glabra* L. (Scrophulariaceae), to an introduced weed, plantain, *Plantago lanceolata* L. (Plantaginaceae), provides an unusual opportunity to examine the early stages of such a host range expansion. Extremely large populations of *E. phaeton* are using *P. lanceolata* exclusively, and these plantain-using populations appear to be of relatively recent origin (Stamp 1979; M. Mello, *personal communication*). Because *E. phaeton* is a well-studied butterfly and popular with collectors, it is likely that populations of *E. phaeton* using host plants to the exclusion of turtlehead would have been reported had they occurred to any extent. Although there are records of postdiapause *E. phaeton* larvae occasionally using *P. lanceolata* (Bruce 1883, Bowers 1980), until recently there had been no reports of the entire life cycle, including female oviposition, being exclusively on *P. lanceolata*. Thus, at the species level, there has been a host range expansion, but at the population level there has been a shift to using exclusively *P. lanceolata* (see Hare 1990 for a discussion of host range expansion and host shift).

This system is an excellent one with which to ask several questions about the early stages of such a host range expansion. Specifically, our objective was to determine what changes, if any, had occurred in the plantain-feeding populations compared to the turtlehead-feeding populations. To do this, we compared several attributes of insects from both these populations: (1) oviposition preference of females; (2) preference and performance of both prediapause and postdiapause larvae; (3) pupal masses; and (4) adult chemical defense.

MATERIALS AND METHODS

The system

Euphydryas phaeton (the Baltimore checkerspot) is a univoltine species, with a fourth-instar larval diapause. Adult flight and oviposition occur in July in Massachusetts and New York, and the gregarious prediapause larvae produce a web on the host plant in which they live and feed. In mid to late August, the third-instar larvae cease feeding and, after molting, enter diapause. They overwinter in leaves at the base of the host plant (Bowers 1979, Stamp 1982c) and emerge in the spring to resume feeding and complete

development. The larvae are warningly colored orange with black stripes and spines and are unpalatable to birds (Bowers 1980). Adults are also aposematic, black with red and yellow spots, and are unpalatable to vertebrate predators (Bowers 1980, Bowers and Farley 1990). Larvae and adults of *E. phaeton* contain iridoid glycosides, which they sequester from their host plants (Bowers and Puttick 1986, Belofsky et al. 1989), and which appear to be responsible for their unpalatability (Bowers 1980, Bowers and Puttick 1986).

Chelone glabra (turtlehead) is a long-lived, clonal, herbaceous perennial found throughout the northeastern United States in wet meadows and along streams (Pennell 1935). Its range extends from Newfoundland in the north, south to Georgia, and west to the plains (Pennell 1935). *Chelone glabra* contains the iridoid glycoside, catalpol, and sometimes aucubin may be present as well (M. D. Bowers and E. Fixman, *unpublished data*; M. D. Bowers et al., *unpublished data*).

Plantago lanceolata (plantain) is a short-lived perennial that was introduced into eastern North America from Europe \approx 150–200 yr ago (Cavers et al. 1980) and is now extremely widespread and abundant throughout the United States. It may be common in disturbed areas, abandoned agricultural fields, and roadsides, habitats very different from that of turtlehead. The range of plantain overlaps that of turtlehead, although this plantain prefers drier habitats (Cavers et al. 1980). *Plantago lanceolata* contains two iridoid glycosides, primarily aucubin, with, usually, smaller amounts of catalpol (Duff et al. 1965, Fajer et al. 1989).

Oviposition and prediapause larval feeding of *E. phaeton* are usually confined to turtlehead (Howe 1975, Bowers 1980, Scott 1986). Postdiapause larvae may exhaust the available turtlehead and switch to other host plants (Bowers 1980, Stamp 1982a), including *Penstemon hirsutis* (Scrophulariaceae) (Muller 1969), *Fraxinus americana* (Oleaceae) (Clark 1927, Bower 1972), *Lonicera ciliata* (Caprifoliaceae) (Fernald 1884, Howe 1975), and *Plantago lanceolata* (Plantaginaceae) (Bruce 1883, Stamp 1979). Although *P. lanceolata* may not occur in the same habitats as turtlehead, hungry postdiapause larvae that have run out of food may wander substantial distances and encounter and feed on plantain (Bruce 1883, Bowers 1980). In the past decade, there have been increasing numbers of reports of *E. phaeton* populations that use only plantain (Stamp 1979; M. Mello, *personal communication*). In these populations, adult oviposition and prediapause larval feeding as well as postdiapause larval feeding are on plantain. These reports are from upstate New York, southeastern Massachusetts, and Rhode Island.

Larval growth, survival, and nutritional indices

Prediapause larval growth and survival.—On 19 July 1987, five egg clusters of *E. phaeton* deposited on *P. lanceolata* were collected at Nimmensburg, New York, a site where a large population of *E. phaeton* used

plantain, maintained by a fortuitous mowing schedule. On 20 July 1987, five egg clusters deposited on turtlehead were collected at West Monroe, New York, a site where *E. phaeton* have been using turtlehead for many years (D. Miller, *personal communication*). At each site, the five egg clusters were likely to have been deposited by five different females (Stamp 1982b). To determine the growth of larvae on their own population's host plant species and on that of the other's, larvae from the collected egg masses of each population were combined and then randomly assigned to one of the two treatments. Half of the larvae from each population were reared on turtlehead and half on plantain. Larvae were reared in groups of 20 because they are less likely to survive when reared in smaller groups (M. D. Bowers and N. E. Stamp, *personal observation*). There were 12 replicates per population–host plant combination. Newly hatched larvae were weighed as a group and placed in clear plastic 0.5-L containers. Each container contained an aquapic with leaves, paper toweling to absorb excess moisture, and a lid with pin-sized holes for air circulation. The larvae were reared in an environmental chamber with a 25:20°C, 14:10 h light : dark temperature and light cycle for 20 d. Larvae were counted and weighed every 5 d. By the 20th d, larvae were entering diapause.

As a consequence of group rearing, it was necessary to use a test period of 20 d for all the treatments rather than using the number of days to the fourth instar as the test period. That is, within each group, some larvae took 20 d to reach the fourth instar but others did not. To avoid disturbing these web-making larvae too much and thus interfere with their feeding, the webbing within which they fed was opened only on weighing days. Consequently, the number of larvae reaching the fourth instar before day 20 was not determined. But, observations indicated that almost all of the turtlehead-derived, turtlehead-reared larvae reached the fourth instar by day 16, whereas many of the turtlehead-derived, plantain-reared larvae molted to the fourth instar on days 19 and 20.

Field diapause masses.—Because larval mass during diapause is correlated with probability of survival over the winter (Lincoln et al. 1982), we compared the masses of diapausing larvae from turtlehead- and plantain-feeding populations. Diapausing larval aggregations were collected from two turtlehead-feeding populations in New York. On 7 September 1987, 10 aggregations were collected from a site at Ithaca, New York, and on 12 September 1987, 9 aggregations from the West Monroe population were collected. Larvae from each of these aggregations were counted and weighed. On 10 October 1987, 16 diapausing aggregations were collected from a plantain-feeding population in North Dartmouth, Massachusetts. Larvae from each of these aggregations were counted, with up to 20 individuals from each aggregation weighed. Because growth rates of individual larvae in an aggregation are not indepen-

dent, we compared the mean larval mass from each aggregation.

Postdiapause growth and survival.—To compare the response of postdiapause *E. phaeton* larvae from the two populations to the two host plants, turtlehead and plantain, larvae from a turtlehead-feeding population in Ithaca, New York, were collected on 12 May 1988. Larvae from a plantain-feeding population in South Dartmouth, Massachusetts, had been kept in the laboratory over the winter. The postdiapause larvae from the turtlehead population had fed for a day or two in the field, but the larvae from the plantain population were unfed at the beginning of the experiment. Larvae were reared in groups of five for 10 d in petri dishes with damp paper toweling taped to the lid to maintain humidity, in an environmental chamber with a 25:20°C, 14:10 h day : night cycle. They were fed ad libitum. After 10 d the larvae had reached the penultimate instar. Within each population–diet treatment, larvae were combined and a set of 20 larvae removed to be used for determination of nutritional indices in the last instar, and for pupal masses. The other larvae were reallocated into groups of five larvae and reared to pupation to obtain pupal masses. The gender of emerging adults was determined.

Nutritional indices.—Standard nutritional indices (approximate digestibility, AD; efficiency of conversion of ingested plant material, ECI; efficiency of conversion of digested plant material, ECD; relative growth rate, RGR; relative consumption rate, RCR; Waldbauer 1968) were determined over the entire last instar, using larvae from the postdiapause feeding experiment. We used a 2 × 2 factorial design, with population of origin (turtlehead-feeding or plantain-feeding) and host plant diet (turtlehead or plantain) as the main effects. All indices were calculated on a dry mass basis. Therefore, two separate sets of larvae (10 from each population) were weighed, frozen, dried, and reweighed to calculate a wet mass to dry mass conversion factor to estimate initial dry mass. Leaves to be fed to larvae were split in half down the midvein; half was fed to the larvae and half was used to calculate wet mass to dry mass conversion factors for food given to larvae. Since turtlehead has opposite leaves, opposite leaves occasionally were used instead of splitting each leaf in half (Waldbauer 1968). Sample sizes ranged from 12 to 15 larvae for each population–diet combination. Tests were conducted in an environmental chamber under a 25:20°C, 14:10 h day : night cycle. The indices were arcsine transformed for statistical analysis.

Larval preference tests

To compare larval food plant preference between the two populations, we used newly hatched, unfed larvae from females from the postdiapause larval feeding experiment. We used 5 groups of 10 larvae from each of 4 females from a turtlehead-feeding population and from each of 10 females from a plantain-feeding pop-

ulation. Each female had been mated with a male from the same population. For the preference tests, a disc (5 mm in diameter) was cut from each plant to be tested, and paired discs (turtlehead vs. plantain) were placed next to each other, with edges touching in the middle of a petri dish (6 cm in diameter) with moistened filter paper on the bottom (Bowers 1985). A group of 10 larvae was placed at the juncture of the discs and allowed to feed for 24 h in an environmental chamber under a 25:20°C, 14:10 h day: night cycle. Then the larvae were removed, and the discs taped to a piece of paper. The amount eaten of each disc was estimated to the nearest 10% by two independent observers, and the mean of those estimates used for analysis.

Oviposition tests

Oviposition tests were conducted in outdoor screen cages (1 m high by 0.5 m wide by 1 m long, with 1 mm² mesh). One turtlehead and one plantain plant were planted in each cage, 0.5 m apart. These plants differed in size due to their different morphology, as females would encounter naturally. The turtlehead plants had been growing in place for several years, and the plantain plants were planted 1 wk–10 d prior to the first trial and had recovered from any transplanting shock. There was a total of 12 pairs of plants, so pairs were used more than once. Leaves on which eggs were laid were removed from the plant to prevent females from using egg masses as oviposition cues. The tests were conducted from 21 June to 25 July 1988, using females from the postdiapause experiment that had been reared throughout development on either plantain or turtlehead.

Females were mated with males that had been reared on the same host plant. On the first sunny day following mating, females were placed in the oviposition cages in the morning, and left there through the early afternoon. Females that did not lay eggs on the 1st d were tested again on the next sunny day. If they did not lay eggs by that time, they were not used again. *E. phaeton* females lay large batches of eggs on both host plant species (≈ 275 eggs per cluster; Stamp 1979, 1982b); thus each female made a single oviposition choice during this test. A total of 9 females from the turtlehead-feeding population and 26 females from the plantain-feeding population were tested successfully.

Iridoid glycoside content of insects

To determine the effect of a shift to feeding on *P. lanceolata* for adult chemical defense, we quantified the iridoid glycoside content of butterflies reared on plantain or turtlehead. Butterflies reared for their entire development on either *P. lanceolata* ($n = 15$) or *C. glabra* ($n = 15$) were frozen upon emergence, dried to a constant mass at 50°C, and extracted for analysis using the methods described in Gardner and Stermitz (1988). We quantified iridoid glycoside content of in-

sects using gas chromatography (Gardner and Stermitz 1988, Belofsky et al. 1989).

Nitrogen analyses of plants

Plant samples that had been used to calculate the conversion factors for the nutritional indices experiment were analyzed for nitrogen content. Leaf nitrogen concentrations of 15 samples each of turtlehead and plantain were determined using a micro-Kjeldahl method (Bremner 1965), with a Kjeltec automatic nitrogen analysis system.

RESULTS

Larval growth, survival, and nutritional indices

Prediapause larval growth and survival.—For a reason we cannot determine, at hatching, larvae from the plantain-feeding population weighed significantly more than those from the turtlehead-feeding population (turtlehead, $\bar{X} = 0.07$ mg/larva; plantain, $\bar{X} = 0.10$ mg/larva; $F = 113.75$, $df = 1,43$, $P < .001$). Larvae derived from the plantain-feeding population remained larger than those from the turtlehead-feeding population when they were eating the same food (day 20, two-way ANOVA, population, $F = 8.45$, $df = 1,39$, $P < .01$; Fig. 1, P-C vs. C-C and P-P vs. C-P). However, larvae from both the turtlehead- and plantain-feeding populations had a higher growth rate on turtlehead than on plantain (day 20, two-way ANOVA, host plant, $F = 31.24$, $df = 1,39$, $P < .001$; Fig. 1, P-C vs. P-P and C-C vs. C-P). There was not a significant population \times host plant interaction (day 20, two-way ANOVA, $F = 1.19$, $df = 1,39$, $P < .25$).

Larvae derived from the plantain population exhibited higher survivorship than did those from the turtlehead population (day 20, two-way ANOVA, population, $F = 4.95$, $df = 1,43$, $P < .05$; Fig. 2). This difference may simply reflect that newly hatched larvae from the plantain population were heavier than those from the turtlehead population. There was no direct effect of host plant on survivorship of larvae (day 20, two-way ANOVA, host plant, $F = 0.73$, $df = 1,43$, $P = .40$); however, there was a significant population \times host plant interaction (day 20, two-way ANOVA, $F = 6.45$, $df = 1,43$, $P < .02$). The larvae from the turtlehead population that were fed plantain had the poorest survivorship (Fig. 2).

Biomass of field-collected diapausing larvae.—There was no significant difference in the mean biomass per larva of field-collected diapausing aggregations from the two turtlehead populations (turtlehead number 1: $\bar{X} \pm 1 \text{ SE} = 7.9 \pm 0.4$ mg; turtlehead number 2: 7.6 ± 0.5 mg; $t = 0.80$, $df = 17$, $P > .10$). Thus these samples were combined, and compared to the mean biomass per larva of field-collected diapausing aggregations from the plantain population. The diapausing larvae from the turtlehead populations were significantly heavier

than those from the plantain population (6.8 ± 0.2 mg) ($t = 2.24$, $df = 33$, $P < .05$).

Postdiapause larval growth and survival.—After 10 d, postdiapause larvae from the turtlehead population had gained significantly more biomass than those from the plantain population (two-way ANOVA, $F = 45.475$, $df = 1,36$, $P < .001$; Fig. 3). Larvae reared on turtlehead, regardless of the population from which they were obtained, had gained significantly more biomass than those reared on plantain (two-way ANOVA, $F = 13.882$, $df = 1,36$, $P < .001$; Fig. 3). There was no significant population \times diet interaction. Survivorship of larvae during this experiment was high, i.e., 94–100%.

Pupal masses of both males and females were significantly heavier when reared on turtlehead than on plantain, regardless of whether larvae were reared alone or in groups (Fig. 4, Table 1). There was no effect of population origin, nor was there an interaction of population and diet (Table 1). Pupae from larvae reared alone were always heavier than those from larvae reared in groups, for males and females from all four population \times diet combinations (Fig. 4, $P < .05$ in every case).

Nutritional indices.—Plantain was significantly more digestible than turtlehead (AD, Table 2). Larvae from the plantain population, regardless of diet in the post-

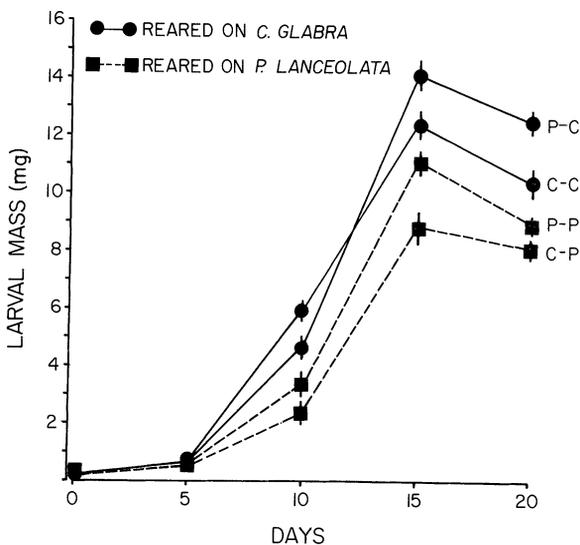


FIG. 1. Growth of prediapause *Euphydryas phaeton* larvae on their own and the other population's host plant until they molted to the diapausing fourth instar. C-C = larvae collected from *Chelone glabra*-using population and reared on *C. glabra*; C-P = larvae taken from *C. glabra*-using population and reared on *Plantago lanceolata*; P-P = larvae taken from *P. lanceolata*-using population and reared on *P. lanceolata*; P-C = larvae taken from *P. lanceolata* population and reared on *C. glabra*. Twelve groups of 20 larvae were used for each population \times host plant combination except P-P, which only had 11 groups. At the end of 20 d, the number of groups in each treatment was: P-C, $n = 11$; C-C, $n = 11$; P-P, $n = 12$; and C-P, $n = 9$. Data are means \pm 1 SE.

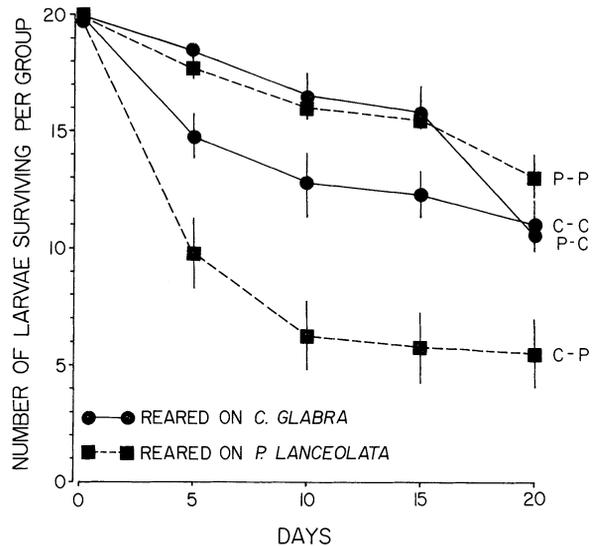


FIG. 2. Survival of prediapause *Euphydryas phaeton* larvae from their own and the other population's host plant until they molted to the diapausing fourth instar. C-C = larvae from *Chelone glabra*-using population and reared on *C. glabra*; P-P = larvae from *C. glabra*-using population and reared on *Plantago lanceolata*; P-P = larvae from *P. lanceolata*-using population and reared on *P. lanceolata*; P-C = larvae from *P. lanceolata* population and reared on *C. glabra*. Twelve groups of 20 larvae were used for each population \times host plant combination except P-P, which only had 11 groups. At the end of 20 d, the number of groups in each treatment was: P-C, $n = 11$; C-C, $n = 11$; P-P, $n = 12$; and C-P, $n = 9$. Data are means \pm 1 SE.

diapause instars, had higher relative consumption rates than those from the turtlehead population (RCR, Table 2). But the relative growth rates of larvae reared on turtlehead, regardless of population origin, were significantly higher than those for larvae reared on plantain (Table 2). Larvae from the turtlehead population

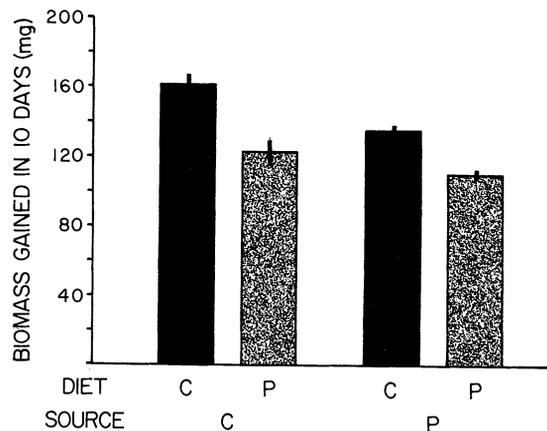


FIG. 3. Biomass gained in 10 d by postdiapause *Euphydryas phaeton* larvae reared on their own and on the other population's host plant. C = *Chelone glabra* and P = *Plantago lanceolata*. Data show means and 1 SE.

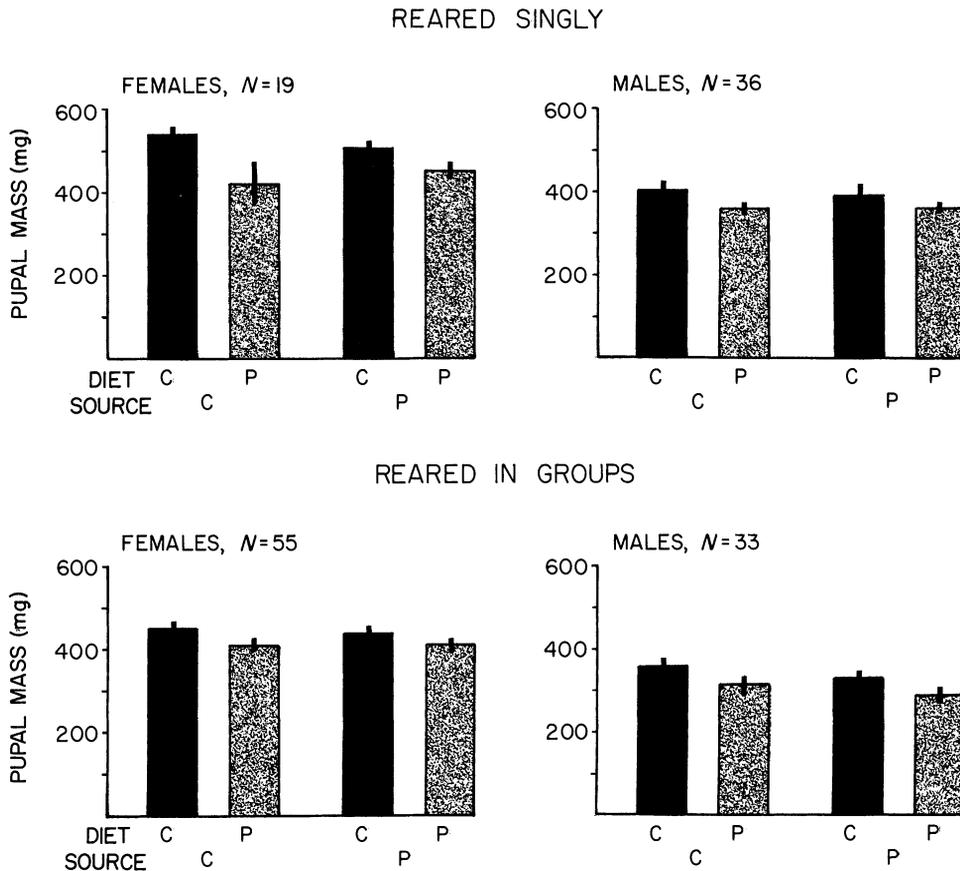


FIG. 4. Pupal masses of male and female *Euphydryas phaeton* reared singly or in groups of five, on their own and on the other population's host plant. C = *Chelone glabra* and P = *P. lanceolata*. Data show means and 1 SE.

were significantly better at converting ingested food into larval biomass than those from the plantain population, and turtlehead was more efficiently converted to larval biomass than plantain (ECI, Table 2). Once digested, turtlehead was more efficiently converted into biomass, and larvae from the turtlehead population were more efficient at doing so (ECD, Table 2).

Larval preference tests

Regardless of whether the parents had come from a turtlehead or plantain population, newly hatched lar-

vae significantly preferred to feed on turtlehead (Fig. 5). In 70% of the trials using larvae from females from the turtlehead-feeding population and in 78% of the trials using offspring from females from the plantain-feeding population, only turtlehead discs had damage we could detect.

Oviposition tests

All the adult females tested, regardless of their population origin, oviposited their egg masses on turtlehead, and none deposited egg masses on plantain. Al-

TABLE 1. Results of two-way ANOVAs on pupal masses of *Euphydryas phaeton* reared singly or in groups. Data are in Fig. 4. Larvae derived from *Chelone glabra* or *Plantago lanceolata* populations were reared on their own and on the other population's host plant. Data for individuals reared singly were analyzed separately from those reared in groups.

Treatment group	Effect		
	Population (P)	Host plant (H)	H × P
	Significance level*		
Males reared singly	>.40 NS	<.001	>.45 NS
Males reared in groups	>.05 NS	<.01	>.70 NS
Females reared singly	>.90 NS	<.01	>.20 NS
Females reared in groups	>.35 NS	<.01	>.70 NS

* NS = not significant.

TABLE 2. Nutritional indices for *E. phaeton* larvae derived from *Chelone glabra* and *Plantago lanceolata* populations reared during the last instar on their own and on the other population's host plant. Data are means \pm 1 SE.

A) Index values for the four diet treatments.				
Source population	<i>Chelone glabra</i>		<i>Plantago lanceolata</i>	
Rearing host plant	<i>C. glabra</i> (<i>N</i> = 15)	<i>P. lanceolata</i> (<i>N</i> = 14)	<i>C. glabra</i> (<i>N</i> = 12)	<i>P. lanceolata</i> (<i>N</i> = 15)
Nutritional index*				
RGR	0.139 \pm 0.006	0.121 \pm 0.006	0.159 \pm 0.002	0.144 \pm 0.005
RCR	0.766 \pm 0.042	0.746 \pm 0.043	1.026 \pm 0.019	0.970 \pm 0.041
AD	27.89 \pm 0.706	35.51 \pm 1.282	27.73 \pm 0.680	35.23 \pm 1.371
ECI	18.13 \pm 0.563	16.27 \pm 0.406	15.58 \pm 0.290	14.97 \pm 0.398
ECD	65.67 \pm 2.690	45.60 \pm 2.821	56.71 \pm 2.194	42.98 \pm 1.475

B) Results of two-way ANOVAs on digestive indices.			
Nutritional index*	Effect		
	Population (P)	Host plant (H)	H \times P
Significance level†			
RGR	<.001	<.002	>.80 NS
RCR	<.001	>.25 NS	>.70 NS
AD	>.80 NS	<.001	>.95 NS
ECI	<.001	<.01	>.15 NS
ECD	<.02	<.001	>.15 NS

* RGR = relative growth rate; RCR = relative consumption rate; AD = approximate digestibility; ECI = efficiency of conversion of ingested plant material; ECD = efficiency of conversion of digested plant material.

† NS = not significant.

though we did not count the eggs in individual masses, the egg masses appeared to be of normal size. Butterflies from these two host plants do not, therefore, differ in their ranking of these two host plants for their first oviposition.

Iridoid glycoside contents of butterflies

Total iridoid glycoside contents of butterflies reared on turtlehead or plantain were not significantly different, which reflected the variation in iridoid glycoside contents among individuals (Table 3). However, butterflies reared on turtlehead contained little if any aucubin and substantial amounts of catalpol, whereas those reared on plantain contained aucubin and smaller amounts of catalpol (Table 3). One butterfly reared on plantain contained no detectable iridoid glycosides.

Nitrogen analyses of plants

The mean leaf nitrogen concentration of turtlehead was 2.83 \pm 0.06% of dry mass ($\bar{X} \pm$ 1 SE, *N* = 15),

whereas that of plantain was 3.12 \pm 0.05% (*N* = 15), which was significantly higher (one-way ANOVA on arcsine-transformed values, *F* = 9.64, *df* = 1,28, *P* < .005).

DISCUSSION

In contrast to some populations of *Euphydryas editha* that have incorporated *P. lanceolata* as one of a set of acceptable host plants (Singer 1982, 1983, Thomas et al. 1987, Singer et al. 1988, 1989), certain populations of *E. phaeton* in the northeastern United States have shifted to using *P. lanceolata* exclusively. Since *P. lanceolata* was introduced into the United States only 150–200 yr ago (Cavers et al. 1980), a maximum of 200 generations of this univoltine butterfly could have been exposed to this potential host plant. Although this period of time may be sufficient for the evolution of preference for, and enhanced performance on, a novel host plant (e.g., Tabashnik 1983 for *Colias* and alfalfa; Thomas et al. 1987 for *E. editha* on *P.*

TABLE 3. Iridoid glycoside content of *Euphydryas phaeton* butterflies reared on *Chelone glabra* or *Plantago lanceolata* throughout larval development. Statistics are reported for one-way ANOVAs on arcsine-transformed iridoid glycoside content (measured as percent of dry mass). *N* = 15 butterflies reared on each host plant. NS = not significant.

Measure	Reared on <i>C. glabra</i>			Reared on <i>P. lanceolata</i>			ANOVA results	
	Mean	SE	Range	Mean	SE	Range	<i>F</i>	<i>P</i>
Dry mass of butterflies (mg)	83.91	6.52	59.14–134.69	73.05	3.97	51.54–99.85
% dry mass aucubin	0.05	0.03	0–0.48	0.43	0.12	0–1.54	9.13	<.01
% dry mass catalpol	0.86	0.21	0.25–3.45	0.34	0.09	0–1.04	5.24	<.05
% dry mass total iridoids	0.91	0.21	0.26–3.58	0.77	0.21	0–2.14	0.22	>.05 NS

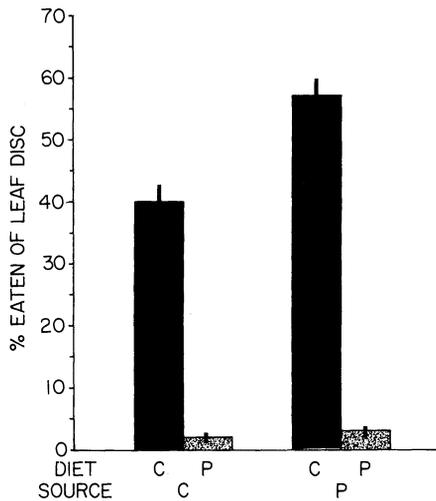


FIG. 5. Percent area eaten of *Chelone glabra* (C) or *Plantago lanceolata* (P) leaf discs by newly hatched *Euphydryas phaeton* larvae from C and P populations. Means (and 1 SE) are shown for five sets of 10 larvae from each individual female. $N = 4$ females from C and 10 females from P.

lanceolata), such evolution would depend on the population dynamics of the plant and the insect, as well as the selective regime to which both were exposed (Gould 1979, 1983, Shapiro and Masuda 1980, Strong et al. 1984, Rausher 1985, Waage and Bergelson 1985, Hare and Kennedy 1986, Horton et al. 1988, Thompson 1988).

In this system, adult recognition of a new host plant appeared to come first, before adult or larval physiological and behavioral adaptation to that host plant, a mechanism suggested previously for incorporation of new host plants into the dietary repertoire of a herbivorous insect (Dethier 1954, Thomas et al. 1987, Schultz 1988). We found that larval feeding preference and adult oviposition preference reflected larval performance. Females preferred to oviposit on and larvae preferred, and performed better on, the native host plant, turtlehead. Thus, although larvae and adult females can recognize the new host plant, plantain, and oviposit, feed, grow, and become adults on it, they do not perform as well on it as they do on turtlehead, the original host plant.

We used a limited set of populations from each host plant for our experiments, which could have affected the results of our experiments. For example, all populations of turtlehead feeders or plantain feeders may not respond in the same way to these two host plant species. In addition, differences in the response of these insects to turtlehead and plantain may reflect populational differences that have nothing to do with the host plant species used. We hope to address these issues in future studies.

The exclusive use of *P. lanceolata* by some populations of *E. phaeton* may have both negative and pos-

itive consequences. Our data suggest that there are several costs to populations feeding solely on this plantain species. For example, there was no indication of digestive specialization on plantain by plantain-feeding populations, except in larval survival (Fig. 2). Larvae from plantain-using populations survived better on plantain than on turtlehead, and likewise, larvae from turtlehead-using populations survived better on turtlehead (thus yielding a significant population \times host plant interaction). However, these differences in survivorship were not reflected in larval preference or other measures of performance. Despite more nitrogen available in plantain than turtlehead, plantain was less efficiently converted into caterpillar biomass than turtlehead; consequently caterpillars that ate plantain had lower growth rates and final pupal masses.

An unexpected result of the postdiapause growth experiment was that pupae of larvae reared alone were heavier than those reared in groups. Larvae of *Euphydryas phaeton* are gregarious, and in many insect species with gregarious larvae, aggregated larvae grow or survive better than solitary larvae (e.g., Ghent 1960, Ribeiro 1989, Stamp and Bowers 1990). However, food availability, food quality, and degree of crowding may determine whether aggregated or solitary larvae grow faster or larger (Haukioja 1980, Haukioja et al. 1988, Vulinec 1990, Bowers et al., *in press*). In our experiments with *E. phaeton*, larvae reared in groups may have been crowded and there may have been competition for the highest quality food, which larvae may prefer (e.g., Stamp and Bowers 1990), resulting in lower pupal masses of those larvae.

Another cost may be in increased search time for ovipositing females. All the females we tested from the plantain-using population preferred to oviposit on turtlehead. Females spend hours searching among turtlehead stalks, which indicates how choosy they are regarding oviposition sites and reflects that each oviposition probably commits a third to a fourth of their total egg production (Stamp 1982b). However, when they cannot find turtlehead, eventually they accept the less-preferred host plant, plantain (e.g., see Singer 1982). The lengthened search time may make females more vulnerable to predators (Miller and Strickler 1984, Bowers et al. 1985).

Furthermore, larval feeding on *P. lanceolata* is likely to make *E. phaeton* quite vulnerable to predators. *E. phaeton* larvae and butterflies fed on turtlehead are unpalatable and emetic to bluejays, whereas those fed on plantain are relatively palatable and nonemetic (Bowers 1980). Our chemical analyses indicated that some butterflies reared on *P. lanceolata* contained little or no detectable iridoid glycosides (Table 3), and so would be palatable. In addition, catalpol appears to be particularly important in determining the degree of unpalatability of an individual insect (Bowers 1988), and *P. lanceolata* is relatively low in catalpol, as are the butterflies that feed on that species (Table 3).

But there may also be some advantages for *E. phaeton* in feeding on plantain. The presence of plantain, an abundant and widespread weed (Cavers et al. 1980), could potentially contribute to both local and geographic range expansion. The native host plant, turtlehead, is not common in Massachusetts, and its wetland habitats are being lost through succession and destroyed by development throughout the northeastern United States. Plantain is also susceptible to the effects of succession, but populations that are periodically mowed persist. However, depending on the timing, mowing may also contribute to substantial larval mortality. So, despite the large butterfly numbers observed in plantain-feeding populations, *E. phaeton* populations on plantain may often be short lived. For example, we know of four sites where plantain-using *E. phaeton* populations have gone extinct.

Another advantage to a host shift from turtlehead to plantain may be in local escape from natural enemies. *Euphydryas phaeton* is parasitized by two specialist wasps, *Cotesia (Apanteles) euphydryidis* Muesebeck (Braconidae) and *Benjaminia euphydryadis* Viereck (Ichneumonidae) (Stamp 1982a, d), that have life cycles that are closely synchronized with that of *E. phaeton*. The ovipositing wasps are attracted to larval webs, where they attempt to lay eggs on unwary caterpillars (Stamp 1981, 1982a, d, 1984a). Because of the localized nature of the *E. phaeton* populations and the synchronization of parasitoid and host life cycles, the shift to using *P. lanceolata* may temporarily reduce *E. phaeton*'s parasitoid load. In addition, the low, rosette growth form of plantain, in contrast to the 25–100 cm stalks of turtlehead (Stamp 1984a), may make it more difficult for parasitoids to find the *E. phaeton* webs at plantain sites. None of the southeastern Massachusetts populations we have studied have been parasitized. However, of 35 late-instar larvae collected in July 1978, from a population in upstate New York using plantain exclusively, 94% were parasitized by *C. euphydryidis*, with a mean of 10 wasps per larva (Stamp 1984a; N. E. Stamp, unpublished data). Thus although use of plantain may provide a temporary escape from parasitoids, these wasps apparently can locate plantain-feeding *E. phaeton* populations.

Another advantage to a host shift from turtlehead to plantain may be in local escape from competitors. Larvae of the sawflies *Macrophya nigra* (Norton) and *Tenthredo grandis* (Norton) (Tenthredinidae) specialize on turtlehead (Stamp 1984b). At one site in New York, for four consecutive years, sawfly larvae decimated the turtlehead during the checkerspot pupation period and consequently most of the emerging females were forced to oviposit elsewhere (N. E. Stamp, personal observation).

Why then might this host range expansion from *C. glabra* to *P. lanceolata* have occurred? It is likely to be a function of several factors. First, *E. phaeton* larvae are probably preadapted to be able to feed on *P. lan-*

ceolata even though they do not perform well on it. *Chelone glabra* and *P. lanceolata* contain the same two iridoid glycosides, aucubin and catalpol (Duff et al. 1965; Fajer et al. 1989; M. D. Bowers and E. Fixman, unpublished data). These compounds serve as feeding stimulants for checkerspot larvae (Bowers 1983). The similarity in the secondary metabolites of these two plant species probably facilitated this host switch. Second, the high availability of the introduced plantain relative to the native turtlehead may be important. As a consequence of human disturbance, wetlands are destroyed, which reduces turtlehead populations, and abandoning of agricultural fields coupled with their periodic mowing promotes plantain colonization and persistence. Third, but perhaps less importantly, periods of favorable climatic conditions, such as cool but sunny spring weather, which has been shown to favor another *Euphydryas* species over its parasitoids (Porter 1982, 1983), coupled with the shift from wetland habitats where turtlehead occurs, to upland habitats where plantain is abundant, may provide a temporary escape from host-specific parasitoids.

ACKNOWLEDGMENTS

We thank Steve Courtney, Eric Fajer, John Jaenike, and Mike Singer for comments on the manuscript. We are grateful to Mark Mello for introducing us to the *E. phaeton* sites in southeastern Massachusetts, and to Allen Hankin for letting us collect caterpillars on his property. We also appreciate help in the field by Michael Cummings, Eric Fajer, and Michael Silver, and assistance with the laboratory experiments by Kenneth Boockvar. This work was supported by grants from the Whitehall Foundation and the NSF Research Experiences for Undergraduates program to M. D. Bowers.

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