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**HOST PLANTS AND HABITATS OF THE BALTIMORE
CHECKERSPOT BUTTERFLY, *EUPHYDRYAS PHAETON*
(LEPIDOPTERA: NYMPHALIDAE),
IN THE GREAT LAKES REGION**

Brian G. Scholtens¹

ABSTRACT

The habitats and host plants of *Euphydryas phaeton* in the Great Lakes region are examined using data from several different populations spread over much of the region. The range of habitats and host plants used by this species is wider than commonly believed. While many populations are found in seasonal or permanent wetlands, others are located in dry, old fields or woodland areas. The host plants used vary with habitat, but they include all major primary hosts and many secondary hosts previously reported plus several new records. The biology of *E. phaeton* is shown to be similar to western *Euphydryas* butterflies in which variation in habitat and host plant use is well documented.

Euphydryas phaeton (Drury) is a wide ranging, univoltine species that flies from early to mid-summer (Opler and Krizek 1984). While *E. phaeton* is the only member of its genus in eastern North America, four species are recognized in western North America and eight in the Northern Hemisphere of the Old World (Bauer 1975, Ferris 1989, Gunder 1929, Higgins 1950, 1978; Miller and Brown 1981). The Baltimore checkerspot has long been known as a wetland species specializing on turtlehead, *Chelone* spp., as its larval host plant (Klots 1951). Klots mentioned only *Chelone* as a host plant for this species. More recently two sets of geographically separate populations (subspecies *phaeton* (Drury) and *ozarkae* Masters) have been recognized, each specialized on a particular host plant (*Chelone* and *Aureolaria*, respectively) and in a different habitat (wetlands and oak woodlands, respectively) (Bauer 1975, Opler and Krizek 1984, Scott 1986). Although *E. phaeton* is a well known species and extensive work has been done documenting its interaction with iridoid glycoside-containing plants (Bowers 1983b, 1988; Bowers and Puttick 1986), predators and parasitoids (Bowers 1980, 1983a; Stamp 1984), and various aspects of its natural history (Bowers 1978), relatively few populations have been examined for host plant and habitat relationships.

Such a limited survey of populations can lead to a biased, often inaccurate view of a species' biology, and misconceptions about "standard" life history information of *E. phaeton* are common. By examining data gathered from several populations in the Great Lakes region, where *E. phaeton* is widespread, and comparing this information with data on other *E. phaeton* populations and several intensive studies western species, I will show that a significantly broadened view of the habitat and host plant choices of *E. phaeton* is warranted.

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MATERIALS AND METHODS

To characterize the habitats and host plants used by *E. phaeton*, I studied several populations of this species during the summers of 1987, 1988 and 1989. These populations were spread over much of the Great Lakes region, including populations in northern Michigan, southern Michigan, and central Ohio. A population in the Ozarks of Missouri was also examined for comparison. These localities included all major habitat types previously reported, three different primary host genera, *Chelone*, *Aureolaria* and *Plantago*, and a wide variety of secondary hosts. Secondary or alternate hosts are defined here as species used as food plants by larvae but not chosen by females for oviposition.

The main study population, located three miles east of Cheboygan on Alpena State Road (referred to below as ASR), in Cheboygan Co., MI, was intensively studied during all three years. Two other populations in Cheboygan Co. were also examined, one 6 miles west of Cheboygan, during the summers of 1988 and 1989, and one 12 miles west of Cheboygan, during the summer of 1989. In southern Michigan, a population in Washtenaw Co., at Park Lyndon North on Embury Rd., was examined during the spring and fall of 1988 and the spring of 1989, and a population in Allegan Co., at the Allegan State Game Area, was studied during June of 1989. A population in Ross Co., OH, at a Nature Conservancy preserve called Betsch Fen, was studied during June of 1988 and 1989, and one population was examined in Meramec State Park, in the Ozarks of Missouri, during late May and early June of 1989.

When possible, several types of observations on host plants and habitats were made at each site. Oviposition was observed or egg masses located to determine what species were used as primary host plants. In most cases exhaustive searches were done of several potential host plant species in an attempt to locate egg masses. In the spring, late instar larvae were located to document which secondary host plants were used by each population. Each locality was characterized by noting the habitat type, the general physiognomy, the dominant species present, and as much as possible, all potential host species, both primary and secondary.

The information recorded for these populations was used to describe the variation observed in the use of primary and secondary host plants by these populations as it relates to the habitat in which the population occurs. Populations were compared and contrasted with a 'standard population' very much like that described by Klots (1951), and exemplified by the main study population at ASR.

RESULTS

The "Standard" Population

The main study population (ASR) occurs in an old, wet field habitat. The vegetation here is dominated by perennial graminoids and forbes. Typical of this association are the genera *Scirpus*, *Carex*, *Agrostis*, *Poa*, *Solidago*, *Aster* and *Eupatorium*. As the habitat progresses through succession *Salix*, *Prunus*, *Cornus* and *Spiraea* become dominant.

The area in Cheboygan County is in constant flux between the earlier and later successional stages because the main habitat occurs on a power line cut, which is periodically brushed to clear the invading shrubby plants. Over the three year period of the study, the part of the habitat not immediately under the power line became noticeably more shrubby, and perhaps less suitable as habitat for *E. phaeton*.

Seasonality with respect to moisture is an additional important aspect of the old field habitat. In general, these are areas of poor drainage. During periods of increased moisture, primarily spring and fall, the areas are at least soggy, and often have shallow standing water. In the summer, during periods of reduced rainfall, the

habitat gradually dries, often becoming entirely dry by mid-summer. This seasonality is important in determining the composition of the community, and seems favorable to the growth of the host, *Chelone*.

Because of this seasonal variability plants can be strongly affected by unusually wet or dry years. During the three year duration of my study, two years (1988–89) were unusually dry for long periods, and this had an adverse effect on the condition of the plants in the area. During 1988, drought started early in the summer, with only about 5.7 cm of rain falling from May through mid July compared with an average of about 17.8 cm. Although not quantified, plants looked badly wilted and some species flowered little or not at all, with many flowers burning off in the bud. During 1989, drought conditions existed through the month of July, when less than 0.63 cm of rain fell compared with an average of about 5.7 cm. This dry spell seemed to have less effect on plants than that of the previous year. They appeared less wilted and most species did not appear to have significantly reduced flowering compared to 1987.

Chelone was probably adversely affected, though not severely, as I did not find evidence of dried stems, or, later in the year, dried flower buds. In 1988, the effect may have been simply to reduce the percentage of flowering stems. An estimated less than 10% of the stems flowered that year, while more flowering stems were observed during 1987 and 1989, when up to 35% flowered in areas without caterpillars (Scholtens unpub. data).

The host plant, *Chelone*, is perennial and, in the Great Lakes region, grows as isolated individuals or small clumps of stems. Individual stems start growing early in the spring, and, as long as they are not eaten by checkerspot larvae, they grow as unbranched stems (very tall stems may branch later in development). The buds on flowering stems in northern Michigan are formed from the end of July to the beginning of August, with flowering continuing through mid to late September. If the apex of the stem is damaged by larvae during development, either one or two branches form from an upper pair of leaves. These branched stems may flower if the branching occurs early in the season, but usually they remain vegetative.

In the populations I studied, adults of *E. phaeton* are most active from 1100 to 1700 hr. Males either set up a loose territory or patrol throughout the habitat to locate mates. Both are previously well documented mating strategies in butterflies (Scott 1974). Females, after mating, spend most the late morning and afternoon searching for potential oviposition sites and ovipositing. Nectaring by both sexes is a much more common and extended behavior than previously reported (Opler and Krizek 1984), with males and females visiting several species of nectar plants (Table 1). The species used as nectar plants are dictated mainly by their presence or absence in the habitat of a particular population.

In the southern part of the Baltimore checkerspot's range the flight period is from late May to early June, in central Ohio to southern Michigan from mid-to late June, and in northern Michigan from mid-July to early August. Egg masses of 100 to 700 eggs (mean about 200–250) are laid on the underside of a host leaf (Stamp 1982, Scholtens unpub. data). Synchronous hatching of the egg mass occurs in about three weeks. Before diapause in third or fourth instar the larvae web together the leaves and stems of the plant upon which they are feeding. Larvae usually overwinter in small groups in the leaf litter (Bowers 1978), but may occasionally remain in the "pre-hibernation" web throughout the winter (pers. obs.). As feeding proceeds in the spring, the small groups of larvae gradually break up into individuals that complete development and pupate in isolation.

Because host stems are very small in the spring, when larvae resume feeding they quickly defoliate any one stem, often eating the entire stem to the ground. Additional primary host plants can often be located nearby, due to the clumped distribution of host stems. However, stems of the primary host, *Chelone*, may become increasingly more difficult to find as the spring progresses, especially if many larvae survived from the previous year.

Table 1. — List of nectar plants of *Euphydryas phaeton* (includes all field sites).

Family	Genus and Species
Rosaceae	<i>Rosa palustris</i> <i>Spiraea alba</i> <i>Potentilla fruticosa</i>
Apiaceae	<i>Daucus carota</i>
Cornaceae	<i>Cornus stolonifera</i>
Apocynaceae	<i>Apocynum cannabinum</i>
Asclepiadaceae	<i>Asclepias incarnata</i> <i>Asclepias syriaca</i>
Asteraceae	<i>Achillea millefolium</i> <i>Eupatorium maculatum</i> <i>Eupatorium perfoliatum</i> <i>Solidago canadensis</i> <i>Solidago graminifolia</i> <i>Rudbeckia serotina</i>

When primary host stems are difficult to locate, caterpillars are forced to utilize secondary hosts. The secondary hosts used vary with the habitat in which the population is located (Opler and Krizek 1984, Scott 1986). At my study site in Cheboygan Co., MI, the secondary host used is *Fraxinus pennsylvanica*. In some years, nearly all late instar larvae are feeding on this alternate host. All known primary and secondary hosts are united by a secondary chemistry which includes iridoid glycosides (Bowers 1983b). These chemicals are apparently one important contact cue used by females and larvae to identify host plants (Bowers 1983b, 1988). At least in some cases, these chemicals are stored in various tissues (Bowers and Puttick 1986), making the butterfly unpalatable to avian predators (Bowers 1980). Secondary hosts will be discussed below in relation to the habitat in which they occur.

Permanent Wetland

The first variation on the usual habitat is that of a permanent wetland. This habitat type grades, in many forms, into the typical old, wet meadow habitat. I have seen intermediate examples such as willow/bog birch wetlands in Schoolcraft Co., MI and permanently soggy depressions in Washtenaw Co., MI. In both of these instances, the composition of species at the site indicates a successional habitat that would eventually become unsuitable for *E. phaeton* populations, if disturbance were not maintained in the form of periodic flooding, fire or removal of woody vegetation by humans.

The other end of this scale is typified by a true fen, such as Betsch Fen in Ross Co., OH. Here, the wetland is fed by an upwelling of groundwater that maintains the dominance of graminoids, mostly *Carex* spp., characteristic of permanent wetlands. In the wettest spots, *Acorus* and *Typha* dominate. There are fewer weedy associates than in the wet, old field habitat, although genera such as *Aster*, *Solidago* and *Eupatorium* are still prominent.

The main characteristic that distinguishes this habitat from the wet field is decreased seasonality with respect to moisture. In true fens there is rarely a period during which the ground is not at least very soggy, and usually there is standing water in depressions. I have seen similar habitats with checkerspot populations in Clark Co., OH and northern Washtenaw Co., MI. These permanent wetlands may

well be what was once the most common habitat for *E. phaeton* in the northern and eastern states. Few such areas remain, and human disturbance has created many areas in the wet, old field category that checkerspots now occupy. Even at Betsch Fen, not all of the habitat is actual fen. Some areas resemble more the wet, old field habitats and are characterized by a similar species composition.

Chelone glabra is the oviposition plant used by *E. phaeton* in these habitats. Although the species is not usually abundant, individual stems thrive in these areas, often reaching greater heights than in old fields. In Cheboygan Co., MI the average height of a *Chelone* stem during the checkerspot's oviposition period is about 35 cm with an extreme of 100 cm, while in the fen in Ohio the average height is about 60 cm with an extreme of 130 cm. Because the number of stems is still limited, *Chelone* is sometimes defoliated in the spring. This was observed during the spring of 1989 in one part of Betsch Fen. Alternate hosts containing iridoid glycosides are used by the larvae to complete development. At Betsch Fen these alternate hosts are *Pedicularis lanceolata* and an introduced wetland species, *Valerianella locusta*, both newly reported as larval hosts of *E. phaeton*. At the site in northern Washtenaw Co., MI, *Valeriana sp.* is the only confirmed alternate host, but other species also may be used.

Old Field

A small number of *E. phaeton* populations occur in typical dry, old field habitats. These also grade into the wet meadow type, but are always dry for a prolonged period during the summer months. Examples of this association are known from New York (Stamp 1979) and Cheboygan Co., in northern Michigan (pers. obs.).

In northern Michigan, this habitat harbors a higher percentage of weedy species than the wet, old field habitat. It is characterized by various grasses, and forb species including *Trifolium*, *Daucus*, *Rudbeckia*, *Chrysanthemum*, *Solidago* and *Aster*. As succession continues, this habitat is invaded by woody plants such as *Salix*, *Cornus* and *Populus*.

The primary or oviposition host in this habitat is the European introduction, *Plantago lanceolata*. *P. lanceolata* was first reported as a primary host for *E. phaeton* by Stamp (1979) although it has been known as a secondary host since at least the 1940's (Burns pers. comm.). The existence of a population in northern Michigan indicates that this host plant association may either be more general than originally thought, or may be becoming more general. Because *P. lanceolata* is so abundant, if *E. phaeton* populations become established in these habitats, the butterfly may become much more common.

Because of the habitat differences, the available choices of alternate hosts for late instar larvae are limited compared to wetter areas. It may not be unusual that, in these dry, old fields, there is no alternate host. That appears to be the case in the Cheboygan Co. population. Larvae have not been located on any host other than *P. lanceolata*, and no potential alternate hosts are known to be present. This situation may contribute to instability in these populations and help explain why *E. phaeton* has not invaded these areas to a greater degree. At some of the New York localities, *Chelone*, in addition to *P. lanceolata*, is present as a primary host (Bowers pers. comm.), and each must serve occasionally as an alternate host for the other. At one other population in Cheboygan Co., MI where *P. lanceolata* is suspected as the primary host, both *Plantago major* and *Castilleja coccinea*, neither previously reported, are used as secondary hosts.

Although this habitat is consistently drier than the typical wet field, seasonality of moisture still influences checkerspot populations. *P. lanceolata* grows luxuriantly in the moist spring and early summer, providing a good food plant supply for late instar larvae and, usually, for ovipositing females. As the summer continues, and the habitat dries, *P. lanceolata* grows less and becomes tougher. It is at this point in

the season when early instars grow to diapause size. If a drought occurs, the food plant supply may be very reduced, both at the level of the individual plant and the population. When this happens young larvae are forced to move from plant to plant more frequently, and a smaller percentage probably survives to produce adults in the next season. In 1988, following a year with adequate moisture, *E. phaeton* was extremely abundant at the *P. lanceolata* site in Cheboygan Co. Both of the next two summers had periods of prolonged drought. This, in addition to other factors including parasitoids and disease, contributed to a crash of the population, so that only a few adults were seen in 1989 and none in 1990.

The invasion of these drier, old field habitats by *E. phaeton* may actually be limited by such dry spells. *E. phaeton* flourishes in these habitats during wetter years and crashes or becomes locally extinct during very dry years. This same phenomenon is known to occur regularly in western *Euphydryas* populations (Dobkin et al. 1987, Ehrlich et al. 1980, Murphy and White 1984, White 1974). *E. phaeton* populations in the usual habitats are buffered from such fluctuations in precipitation because of their wetter baseline condition.

Woodland Habitats

Populations in the southwestern part of the species' range feed mainly on scrophulariaceous plants that are hemiparasitic on oaks. The confirmed primary hosts are *Aureolaria* (Masters 1968) and *Seymeria* (Sullivan pers. comm.). These hosts grow both in the woods and along woodland edges. Therefore, these habitats are very different than those typically used by the species. Because of these ecological distinctions and some small differences in maculation and size, these populations have been recognized as the subspecies *E. phaeton ozarkae* Masters (Opler and Krizek 1984).

Due to the habitat relationships of these populations, the usual options for secondary hosts are not available. Often, the larvae may not need plants other than the primary host to complete development, but it is probable that earlier reports of *Lonicera* as the primary host plant for these populations (Bauer 1975) resulted from this genus being used as an alternate host in late instars.

It is difficult to predict how seasonality of moisture might affect these populations. Because the plants used as hosts are hemiparasitic, it might be predicted that drought would affect the relationship very little, but the very dry character of the habitat would suggest otherwise. This second aspect could be a major contributing factor to the noted fluctuations in the size of these populations (Heitzman and Heitzman 1987), similar to the dry, old field populations mentioned above.

Populations in habitats similar to those occupied by subspecies *ozarkae* occur scattered over the rest of the range of the species. These have, up to this point, received only a passing recognition. Originally reported from Connecticut by Shapiro (1974), and also known from New York (Scott 1986) and Michigan (pers. obs.), *Aureolaria*-feeding populations may be much more common than originally believed. If the uniqueness of the host plant and habitat is a major reason for maintaining the subspecies *ozarkae* (Masters 1968, Opler and Krizek 1984), evidence of similar populations occurring throughout the range may result in a revised view of the distinctness of this subspecies.

I have examined two oak woodland populations in Michigan. These populations, in Allegan and Washtenaw counties, both use *Aureolaria flava* as their oviposition plant. In Allegan Co., the habitat is remnant oak opening prairies, while in Washtenaw Co. it is an oak woodland mixed with swamp forest. The associated plant communities (prairie vs. woodland or swamp) and terrain (flat vs. rolling hills) are the major differences between these two sites.

As in the Missouri populations, alternate hosts are poorly documented at these sites. In Allegan Co., no alternate hosts are known. Possibilities include *Lonicera*,

Table 2. — Primary and secondary host plants of *Euphydryas phaeton* populations examined in the present study.

Population	Primary host	Secondary host
Cheboygan Co., MI Alpena St. Rd.	<i>Chelone glabra</i>	<i>Fraxinus pennsylvanica</i>
Cheboygan Co., MI 6 mi. W of Cheboygan	<i>Plantago lanceolata</i>	none known
Cheboygan Co., MI 12 mi. W. of Cheboygan	<i>Plantago lanceolata?</i>	<i>Castilleja coccinea</i> <i>Plantago major</i>
Washtenaw Co., MI Embury Rd.	<i>Aureolaria flava</i>	<i>Pedicularis canadensis</i>
Washtenaw Co., MI 1 mi W of Embury Rd.	<i>Chelone glabra?</i>	<i>Valeriana</i> sp.
Allegan Co., MI Allegan St. Game Area	<i>Aureolaria flava</i>	none known
Ross Co., OH Betsch Fen	<i>Chelone glabra</i>	<i>Pedicularis lanceolata</i> <i>Valerianella locusta</i>
Franklin Co., MO Meramec St. Pk.	<i>Aureolaria grandiflora</i>	<i>Lonicera?</i>

found in the woods, or *Penstemon*, found in the prairie areas. Both genera have been previously reported as secondary hosts (*Penstemon* also as an occasional oviposition plant). In Washtenaw Co., one alternate host, *Pedicularis canadensis*, has been confirmed, and *Lonicera* is an additional possibility. All known primary and secondary hosts used by *E. phaeton* populations examined in this study are presented in Table 2.

DISCUSSION

Several *Euphydryas* species, especially the western United States representatives of the genus, have been and continue to be intensively studied (Ehrlich et al. 1975, Murphy and Weiss 1987). After examining several aspects of the biology of *E. phaeton*, it is appropriate to compare the range of host plants and habitats used by this species to its closest North American relatives. Such a comparison will allow a better evaluation of whether the variability observed in *E. phaeton* is unusual or typical of the genus.

Within any one species of the western *Euphydryas*, especially those with extensive ranges, the host plants can be quite variable. Different populations often use different primary hosts, and some populations use more than one (Bowers 1985, Singer 1971, White and Singer 1974, Williams 1990). There is a great deal of local population differentiation with regard to host usage and preference, both at the level of oviposition choice and larval host use (Bowers 1986, Holdren and Ehrlich 1982, Mackay 1985, Rausher 1982, Rausher et al. 1981, Singer 1983, Thomas et al. 1987)(Table 3). A similar pattern appears to be emerging in *E. phaeton* populations, with populations now known, scattered throughout the range, that feed on several different hosts, from four different plant families (Table 2). In some cases, two different primary hosts may be used by the same population (Bowers pers. comm.), and several alternate hosts may be used.

Table 3.—Host plants recorded for western *Euphydryas* species compiled from Bowers (1983b) and Williams (1990).

Species	Known host genera
<i>E. chalcedona</i> (including <i>E. colon</i>)	<i>Castilleja</i> <i>Diplacus</i> <i>Pedicularis</i> <i>Penstemon</i> <i>Scrophularia</i> <i>Symphoricarpus</i>
<i>E. anicia</i>	<i>Besseyia</i> <i>Castilleja</i> <i>Penstemon</i> <i>Symphoricarpus</i>
<i>E. editha</i>	<i>Castilleja</i> <i>Collinsia</i> <i>Orthocarpus</i> <i>Penstemon</i> <i>Plantago</i> <i>Lonicera</i>
<i>E. gillettii</i>	<i>Lonicera</i> <i>Valeriana</i> <i>Pedicularis</i> <i>Veronica</i>

At least one intensively studied western species, *E. editha* (Bdv.), shows a pattern of forced host switching during development like that seen in *E. phaeton* (Singer 1971, Weiss et al. 1987, White 1974). In both species, females have a preferred oviposition plant on which larvae begin development. After a period of time, the host species is either consumed or becomes unsuitable, and the larvae are forced to locate an alternate host plant. In *E. editha* this occurs before diapause due to the senescence of the primary host *Plantago erecta* (White 1974), and in *E. phaeton* it occurs after diapause due to the consumption of the primary host.

Euphydryas phaeton and its western congeners occur in a wide range of habitats. *E. editha*, *anicia* (Doubleday), and *chalcedona* (Doubleday) inhabit dry areas ranging from open woodland to extensive grasslands (Bauer 1975, Scott 1986). *Euphydryas gillettii* (Barnes), *E. phaeton*'s closest North American relative, lives in wet or moist alpine meadows and open woodlands, often near streams (Holdren and Ehrlich 1981, Williams et al. 1983). *E. phaeton* populations span nearly this entire range of habitats. Populations in the Ozarks and other scattered populations occur in dry habitats, ranging from woodland and prairie openings in woodland, for the *Aureolaria*-feeders, to dry old fields, for the *Plantago*-feeders. The *Chelone*-feeding populations inhabit wet areas similar (with the notable exception of altitude) to those used by *gillettii*.

A strong effect of seasonality on population dynamics also seems to be common to *Euphydryas* species. In populations of *editha* where monitoring has continued for many years, the number of individuals fluctuates a great deal (Ehrlich et al. 1975). Declines, in some cases, have been linked to drought conditions (Ehrlich et al. 1980). Smaller populations often go extinct due to severe seasonality, and may or may not be reestablished by colonists from larger, more resistant populations during favorable years (Murphy and White 1984).

Similar dynamics probably occur in *E. phaeton*. This is indicated by the

observed large fluctuations in population size (Heitzman and Heitzman 1987, pers. obs.), and perhaps extinction and colonization of smaller, less favorable habitat areas. Although they have only been monitored for a short period compared to some *editha* populations, several northern Michigan populations of *E. phaeton* exhibit characteristics very similar to those demonstrated by Ehrlich and his colleagues. The *Plantago*-feeding population discussed above, after a favorable year (1987), had an extremely large population (in the hundreds of individuals) the following summer, but, after a year of severe drought (1988), experienced a crash to a maximum population of about 50 individuals. After another year with a prolonged drought (1989), the population appears to have gone extinct as did some of the smaller *editha* populations (Ehrlich et al. 1980, Murphy and White 1984).

Other areas appear to have been recently colonized. In two localities in Emmet Co., MI, individuals of *E. phaeton* have recently been collected where none had been seen previously. Neither of these cases is due to a lack of observation. Both have been visited regularly, over a number of years, by Dr. Edward Voss, a botany professor at the University of Michigan, but more importantly, an avid lepidopterist. He had seen no individuals of *E. phaeton* at either of these sites prior to their discovery in the last two years. The success or failure of these colonization events will be determined during future monitoring.

One last, intriguing similarity between the western species and the Baltimore checkerspot, is the expansion of their host ranges to include an introduced weed, *Plantago lanceolata*, both as a primary and secondary host. At one locality genetic variability exists among *E. editha* females in oviposition preference of *P. lanceolata* versus *Collinsia parviflora*, the original host plant, with some females preferring *Collinsia*, some *Plantago*, and others showing no preference (Thomas et al. 1987, Singer et al. 1988). Although a genetic basis has not been documented in *E. phaeton*, *P. lanceolata* is used by several populations (Stamp 1979, Bowers pers. comm., pers. obs.). In some instances, *P. lanceolata* is the only oviposition plant available, but in others *Chelone* is also present (Bowers pers. comm.), and a similar behavioral polymorphism for oviposition site selection may exist.

Overall, the host plant and habitat range of *E. phaeton* is comparable to that observed in western *Euphydryas*. The habitats used include permanent wetlands, seasonally wet meadows, dry old fields and woodlands. The host plants used by these populations include the primary hosts *Chelone*, *Aureolaria* and *Plantago*, and many alternate host species. In contrast to the impression of *E. phaeton* as a wetland species specializing on *Chelone*, this diversity of habitats and host plants calls for a substantially broadened view of the habitat and host plant ecology of the Baltimore checkerspot, a view supported by a comparison to the habitat and host plant ecology of the western *Euphydryas*.

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