# BIOLOGY OF *SPEYERIA ZERENE HIPPOLYTA* (NYMPHALIDAE) IN A MARINE-MODIFIED ENVIRONMENT

DAVID V. MCCORKLE

Biology Department, Western Oregon State College,
Monmouth, Oregon 97361

AND

PAUL C. HAMMOND

2435 E. Applegate, Philomath, Oregon 97370

**ABSTRACT.** This paper examines life history and adaptations of *Speyeria zerene hippolyta* (Edwards) along the Oregon and Washington coasts where cold wind, rain, and fog persist during much of the year. The butterfly uses an open grassland habitat on salt-spray meadows and higher headlands adjacent to the ocean, where the larvae feed on the common *Viola adunca* J. E. Smith. Four unusual adaptations to this environment are seen in *S. zerene hippolyta* that are absent from the closely related *S. z. bremnerii* (Edwards) of the inland Willamette Valley: small body size and extensive dark basal suffusion which enhance body heating from solar radiation; normal flight activity under cool, cloudy or foggy conditions; prolonged larval development which coordinates adult emergence with the most favorable weather conditions in late summer and fall; and much individual variation in larval development rate and adult emergence which compensates for variable and unpredictable weather from year to year.

**Additional key words:** *Speyeria zerene bremnerii, Viola adunca,* adaptation, grassland, coastal habitat.

*Speyeria zerene* (Boisduval) is a complex polytypic species with 14 recognized subspecies (Grey & Moeck 1962). The subspecies occupy a wide diversity of habitats ranging from coastal rainforests in the Pacific Northwest to arid sagebrush plains in the Great Basin. *Speyeria z. hippolyta* (Edwards), informally known as the "Hippolyta Silverspot" or "Oregon Silverspot", is restricted to a cool, wet, marine-modified environment adjacent to the Pacific Ocean in western Washington and Oregon. This subspecies is of special concern because of its decline toward extinction and its official classification as a threatened species (Hammond & McCorkle 1983).

The closely related *S. z. bremnerii* (Edwards) occupies inland areas of the Pacific Northwest from Vancouver Island S through the Puget Sound trough and Willamette Valley of western Oregon. The primary difference in adult phenotype between these subspecies is the small wing of *S. z. hippolyta* although extinct Oregon populations of *S. z. bremnerii* also differed in having reduced basal suffusion on the dorsal wing surfaces (Fig. 3). In addition, *S. z. hippolyta* differs in several aspects of life history and developmental physiology which appear to be specific adaptations to the coastal environment. An investigation of

these characteristics is the subject of the present paper. It should be noted that both Moeck (1957) and Howe (1975) confused this coastal subspecies with a population of dwarfed *S. z. conchyliatus* (Comstock) endemic to the volcanic ash and pumice fields along the E slope of the Oregon Cascade Range.

## MATERIALS AND METHODS

Field and museum studies were conducted from 1960 to 1986 together with laboratory rearing of larvae. Most public and many private collections in Washington and Oregon were examined. In 1963 and 1964, one of us (McCorkle) developed a technique for rearing *Speyeria* larvae using a modification of a procedure (Magnus 1958) for the European fritillary *Argynnis paphia* L. A variant of the former technique was described by Mattoon et al. (1971), and was used in the present study, except that larvae were kept over winter in hollow wooden blocks and reared in small jars instead of nylon sleeves.

Capture-recapture studies were done at the Rock Creek study site in Lane Co., Oregon, during 1980 using the 1-2-4-7 marking system described by Ehrlich and Davidson (1961). Sex, wing length, general condition, time, place, and type of activity at time of capture and recapture were recorded.

Voucher specimens are deposited in the Systematic Entomology Laboratory at Oregon State University, Corvallis.

## BIOLOGY OF STAGES

### Oviposition

*Speyeria zerene hippolyta* is usually a grassland butterfly that lives on open salt-spray meadows and grassy headlands adjacent to the Pacific Ocean, where the larvae feed on the common blue violet, *Viola adunca* J. E. Smith. Based on more than 100 observations, females oviposit singly among vegetation near host plants. Females are apparently stimulated to oviposit by some volatile compound emanating from violets. We found that females oviposit only in the presence of violets, but that direct physical contact with the host is not necessary. We observed oviposition up to 20 cm downwind of even dried violet leaves.

During oviposition behavior, the butterflies flew near the ground, working their way upwind. When violets were near, they paused to climb in meadow vegetation, probing with curved abdomen until a suitable site was contacted, and an egg deposited. We even observed females crawling into knee-deep layers of grass that overgrew violets by late summer. Oviposition observations and location of larvae indicate that females favor sunny sites, and usually avoid N slopes of steep meadow rises.

Eggs are cream colored when first laid, but if fertile, darken to pinkish tan by the second day. Eggs began to hatch 16 days after oviposition with ambient room temperature varying from 21 to 24°C (N = ca. 1000). A large quantity of lipid is stored in *Speyeria* eggs which appears to serve as a food reserve during larval diapause. This lipid, in the form of a light oil, is readily observed in yolk by dissecting eggs.

## Larva

Newly hatched larvae (N = ca. 1000) usually wander short distances. As in other *Speyeria*, first instar *S. z. hippolyta* soon enter a diapause that lasts over winter. After selecting a suitable site, they spin a thin silk mat on which they rest until spring. Larvae exhibit considerable resistance to desiccation during diapause. In the laboratory, they survived a month or more without moisture, but this stress may diminish survival by spring. Thus, in years with delayed fall rains, the earliest hatched larvae may be at a disadvantage. When moisture is available, laboratory larvae touched their mouths to a wet surface, and some nearly doubled in size within a short time.

The following description of the last (6th) instar is based on larvae from about 10 family lines. The spiny larva (Fig. 1) is dark brown with a pair of pale lines running down the back, each of which has a row of black patches running parallel to it on the outside. These black patches are located on both sides of each body segment adjacent to the pale dorsal lines. Lateral parts of the body are finely and irregularly mottled with pale yellow. The head is mostly black, but the occipital area is yellow. Spine bases, especially those of the lateral rows, are straw colored similarly to the lines on the back. This color pattern resembles that of the inland *S. zerene bremnerii* (Hardy 1958), and blends with dried leaves where larvae take refuge when not feeding.

The first instar possesses unbranched setae or hairs. Later instars bear branched spines in the pattern illustrated by Scott and Mattoon (1982) for *S. nokomis* (Edwards). We reared all 13 species of *Speyeria*, and this setal pattern is consistent throughout the genus. However, it should be noted that a lateral spine is present on the 10th abdominal segment that was omitted from the Scott-Mattoon setal map. Superficially, this spine appears to be on the 9th segment. Spine branches or spinules are attached to the primary shaft in such a way that they can swing in toward the shaft apex when the larva withdraws from an entanglement. When pushed outward, the spinules lock into the outstretched position. In larger larvae, these sharp spines may provide protection from predators such as mice and, perhaps, shrews (unpubl. obs.).

In addition to spines, *Speyeria* larvae possess what may also serve as a defense against predators in the form of a fleshy, eversible osmeterium.
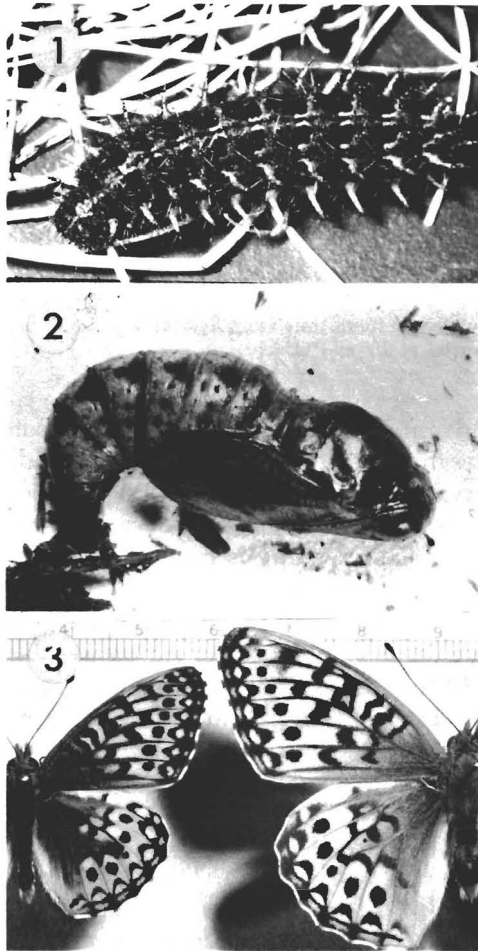
FIGS. 1–3.    S. zerene. 1, Mature 6th instar of S. z. hippolyta; 2, Pupa of S. z. hippolyta; 3, Reared males of S. z. hippolyta (left) and Willamette Valley S. z. bremnerii (right).

Whenever this structure is extruded, a disagreeable musky smell becomes apparent. This odor is faint in the small S. zerene hippolyta, but is much stronger in larger-bodied species such as S. coronis (Behr) and S. edwardsii (Reakirt). Unlike the long dorsal osmeteria of papilionid larvae, Speyeria osmeteria are short, wedge-shaped organs located ventrally just behind the head and before the first pair of thoracic legs. In addition, the musky smell of Speyeria osmeteria is distinctly different from the more pungent, aromatic smell of papilionid osmeteria.

As with most Speyeria, older larvae of S. z. hippolyta retreat to shelter sites sometimes several centimeters from host violets. These sites may
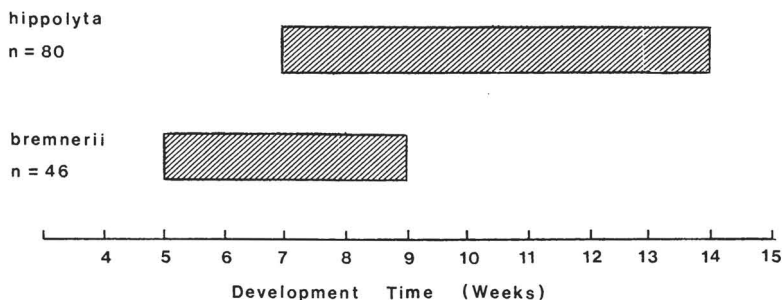
hippolyta
n = 80

bremnerii
n = 46

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       4    5    6    7    8    9   10   11   12   13   14   15
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Development   Time   (Weeks)

FIG. 4.   Laboratory development time from first instar to adult in S. *zerene hippolyta* and S. *z. bremnerii* reared at 22° ± 1°C.

provide thermal advantages as well as cover from predators (McCorkle 1980). Some species may be mostly nocturnal (Dornfeld 1980:75). However, one field larva of S. *z. hippolyta* found during daytime in the present study was feeding, and laboratory larvae of many *Speyeria* feed both night and day. Their feeding is typically rapid so that they are exposed from cover only briefly. In the constantly heated laboratory, larvae probably grow faster than in nature. Their growth rate in the field may be delayed especially by cooler spring weather. Nevertheless, in the laboratory, they still required from one to three months to grow through six instars (Fig. 4, Table 1), and they spent about two weeks in the pupal stage.

Larval feeding signs were evident on violets in the Rock Creek meadow on 15 April 1980, indicating that at least some larvae were well into feeding activity. On 8 May 1986, one early 4th instar was observed. On 5 July, we found one nearly mature 6th instar (not parasitized) and several violets with fresh feeding signs, indicating that at least some larvae were still active. On the same date, however, the first adult male was taken, although normally the males do not begin to eclose until after 10 July with peak emergence in early August. Thus, the minimum natural larval feeding span is from mid-April to mid-June, some two months. It may be that a few larvae continue to feed well into August, producing the fresh adults present in early September.

## Pupa and Adult

The pupa (Fig. 2) is smooth, rounded, and mostly dark brown with variable paler areas on abdomen and wing covers, and a dark, transverse band on the anterior edge of each abdominal segment. As in most *Speyeria*, the pupal chamber consists of several leaves drawn together with silk, and the pupa is usually attached in a hanging position to the top of the chamber.
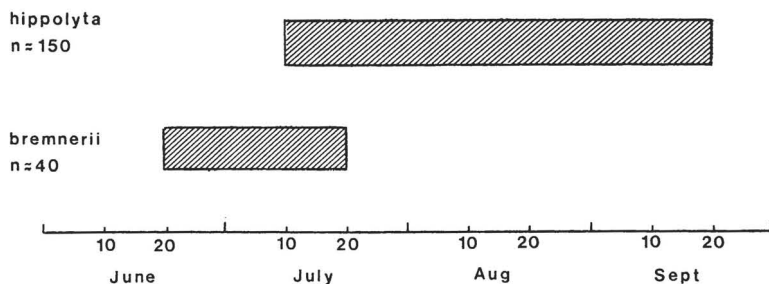
FIG. 5.    Time range in field presence of fresh adults of *S. zerene hippolyta* (central Oregon coast) and *S. z. bremnerii* (Willamette Valley).

As noted above, the first adult male was taken on 5 July, and a nearly mature larva was also found on that date. By early August, males were common (Fig. 5) (22 marked 1–3 August), and females had begun to appear (2 marked). Between 20 and 22 August, 22 new males and 7 new females were marked, including several fresh females and a few fresh males. On 4 September, 15 new males and 16 new females were marked. Of these, five females were fresh, three males were fairly fresh, and one very fresh. It is thus apparent that in this colony, males eclosed from mid-July until at least the end of August. The first females eclosed by the end of July, and eclosion continued through August to mid-September, with aging specimens surviving into October. Recapture results (McCorkle 1980) indicate that some adults live for at least three weeks, and disperse widely up to 2–3 km (1–2 miles). Butterflies fly inland and seek shelter along forest margins when strong winds are blowing off the ocean (McCorkle 1980).

## ADAPTATIONS TO COASTAL ENVIRONMENT

Both coloration and wing size appear to have a strong genetic determination, since *S. z. hippolyta* differs consistently from the larger and paler Willamette Valley *S. z. bremnerii* both in the field and in laboratory rearings (Figs. 3, 6). The difference between forewing lengths (Fig. 6) is highly significant ($P_t < 0.0001$). Data from Willamette Valley was obtained before the apparent extinction of these populations around 1977 (Hammond & McCorkle 1983).

There is evidence that small size and extensive dark basal suffusion as shown in *S. z. hippolyta* are adaptations to enhance solar heating, as would be needed in a marine-modified environment with persistent cold wind and frequent fog (McCorkle 1980). Butterflies, being heterothermic, usually depend on solar radiation to elevate body temperature sufficiently to allow flight necessary for foraging, mate seeking, escape from predators, and oviposition (Watt 1968, Douglas 1978,

TABLE 1.    Time required for larval and pupal development in *Speyeria zerene* populations reared at 21–23°C. Each entry represents progeny of one female, with number of individuals in parentheses.

| Subspecies | Locality | No. weeks | | | |
|---|---|---|---|---|---|
| | | Males | | Females | |
| *bremnerii* | Benton Co., Oregon | 6 | (2) | 7 | (3) |
| | | 5–6 | (5) | 6 | (5) |
| | Thurston Co., Washington | 6–7 | (3) | 8–9 | (3) |
| | | 6 | (2) | 7–8 | (3) |
| *hippolyta* | Pacific Co., Washington | 8–9 | (3) | 9–10 | (5) |
| | | 8–9 | (7) | 9 | (3) |
| | Clatsop Co., Oregon | 7–9 | (11) | 8–10 | (12) |
| | Lincoln Co., Oregon | 8–9 | (9) | 9–10 | (10) |
| | Lane Co., Oregon | 7–9 | (7) | 8–10 | (9) |
| *hippolyta*-like | Del Norte Co., California | 9–13 | (8) | 12–14 | (7) |
| | | 8–9 | (5) | 9–10 | (7) |
| | | 10–13 | (6) | 11–13 | (8) |
| *behrensii* | Curry Co., Oregon | 7–8 | (5) | 8–9 | (9) |
| | | 7–8 | (2) | 9 | (5) |
| *gloriosa* | Josephine Co., Oregon | 7–8 | (11) | 8–10 | (12) |
| | | 7–8 | (7) | 9–10 | (6) |
| *myrtleae* | Marin Co., California | 7–8 | (11) | 8–10 | (14) |
| | | 7–9 | (11) | 8–10 | (10) |
| | | 8–9 | (12) | 8–10 | (12) |

McCorkle 1980). Rapid ovarian development is also thermodependent (Watt 1968).

*Speyeria* use a dorsal basking position in which the wings are extended in a horizontal plane from the body, thus exposing the dark basal suffusion to solar radiation. In dorsal basking butterflies, heat first absorbed by the basal part of the wings is then absorbed by the thorax, and usually a thick coat of long hairs serves as insulation for retention of thoracic heat (Douglas 1978, McCorkle 1980). Douglas (1978:43) suggests that large butterflies are at a disadvantage under cool conditions because they heat up more slowly, while smaller butterflies warm quickly to an adequate thoracic temperature. In a cold, windy environment, small butterflies also have a second advantage because the smaller wingspan allows flight closer to the ground where wind velocity is lower. Wind is a problem in maintaining body temperatures because heat is lost from the body surface by forced convection (Douglas 1978:69).

Since most *Speyeria* require high body temperatures for normal activity, they usually fly only in full sunshine, or under cloudy conditions when the air temperature is higher than 21°C (70°F). However, field observations of *S. z. hippolyta* revealed that it engages in normal activity under cloudy or foggy conditions with air temperatures as low as 16°C
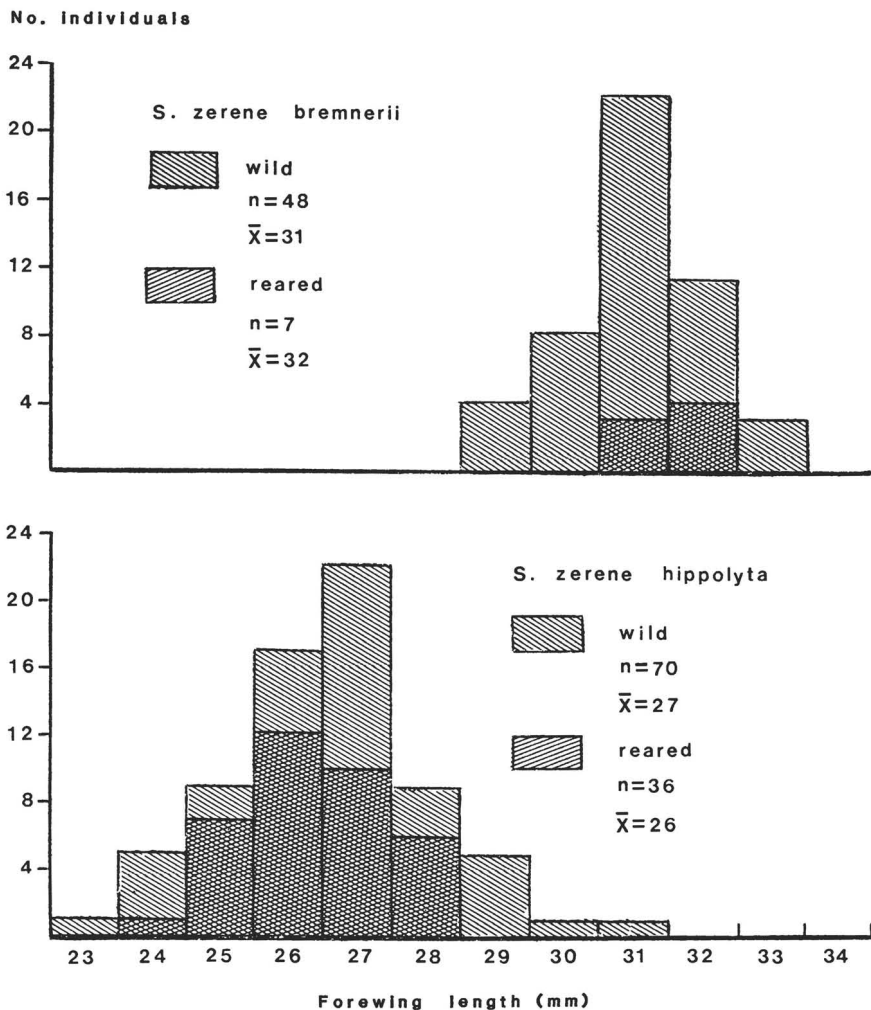
No. individuals



FIG. 6.   Frequency distribution of male forewing length in wild and reared *S. zerene hippolyta* (central Oregon coast) and *S. z. bremnerii* (Willamette Valley).

(60°F), although the butterflies retreat to shelter under windy conditions. For example, during early September 1982, we observed approximately a dozen males in mate-searching flight, six males and females nectaring on flowers, and three females engaged in oviposition under windless, cloudy-foggy conditions with air temperature only 16°C (60°F). Similar observations have been made consistently during subsequent years. In sharp contrast, observations of the similarly colored *S. a. atlantis* (Edwards) in the Appalachians of West Virginia during 1977 revealed

virtually no evidence of similar activity under cool, cloudy conditions. These adults (N = 100+) engaged in nectaring and flight only in full sunshine, and retreated to shelter in trees when clouds covered the sun at a temperature of approximately 21°C (70°F). In more dramatic contrast, the large S. *idalia* (Drury) favors minimum air temperatures of 24–27°C (75–80°F) for normal flight activities based on observations (N = 100+) in Nebraska during 1983, and continues to fly at temperatures of 41°C (105°F) or more. This species exhibits little basking behavior in the field, and the basal wing areas completely lack dark suffusion. Even the black hindwings of S. *idalia* are mostly pale orange at the wing base.

Because S. *a. atlantis* and S. *zerene hippolyta* are nearly identical in their dark basal suffusion, and are of similar small size, the expected thermal regulation and behavioral activity of these species should be similar. Therefore, the above observations suggest that S. *z. hippolyta* employs an additional mechanism that allows activity under low temperatures and cloudy conditions. This mechanism might include changes in enzyme systems that would allow normal physiological function at low body temperatures, but this possibility has not yet been studied.

Finally, S. *z. hippolyta* along the central Oregon coast is also highly unusual in that adult emergence in the field extends over a long period of some 8 weeks from early July to early September, and it requires 7–14 weeks to complete larval and pupal development in the laboratory (Figs. 4, 5). These developmental patterns appear to be an additional adaptation to the coastal environment. By contrast, most western *Speyeria* emerge over a relatively short period of about three to four weeks in June and July. For example, the Willamette Valley form of S. *z. bremnerii* usually emerged during late June and early July in the field, and required only 5–9 weeks to complete larval and pupal development in the laboratory. As shown in Figs. 4 and 5, the sharp differences in the developmental patterns between S. *z. hippolyta* and S. *z. bremnerii* are maintained consistently both in field and laboratory, suggesting that a strong genetic component is involved.

There are two apparent reasons for these developmental patterns in S. *z. hippolyta*. In most years, adverse conditions of cold wind, fog, and rain persist along the ocean through May, June, and July, and weather more favorable for adult flight usually does not develop until August and September. The retarded larval development of S. *z. hippolyta* coordinates adult emergence with the best weather conditions in the coastal environment. In addition, adverse stormy weather may develop in some years along the coast during either August or September. The great range of individual variation in developmental rate and adult emergence suggests an additional adaptation to variable and un-

predictable weather conditions. Thus, early emerging butterflies may be more successful in reproduction one year, and late butterflies the next year, depending on each year's storm patterns. Since coastal weather is so variable from year to year, genes for both early and late emergence (fast and slow development) would tend to be maintained.

During the past 20 years, we have reared most of the geographic subspecies recognized in *Speyeria* under similar laboratory conditions at temperatures of 21–23°C (70–72°F). The fastest rate of larval and pupal development was observed in certain forms of *S. atlantis*, *S. egleis* (Behr), *S. callippe* (Boisduval), and Oregon *S. zerene bremnerii*, all of which required only five to six weeks for males and six to seven weeks for females. Most subspecies of *S. zerene* and *S. coronis* required six to seven weeks for males and seven to eight weeks for females. These include Sierran-type *S. z. zerene*, Rocky Mountain *S. z. sinope* dos Passos & Grey, and Great Basin *S. z. gunderi* (Comstock). Even very large-bodied species such as *S. c. cybele* (Fabricius), *S. idalia*, and *S. nokomis caerulescens* (Holland) required only a similar amount of time, while *S. nokomis apacheana* (Skinner), *S. diana* (Cramer), and *S. edwardsii* required seven to eight weeks for males and eight weeks for females.

However, except for typical *S. z. bremnerii* itself, all populations of *S. zerene* within the *bremnerii* subspecies group as defined by Grey and Moeck (1962) exhibit a relatively long developmental time of 7–9 weeks for males and 8–10 weeks for females (Table 1). Our field emergence data (Fig. 5), indicate especially long and variable development times for *S. z. hippolyta* populations along the central Oregon coast from Lane Co. N to Tillamook Co.

Hammond & McCorkle (1983) noted *hippolyta*-like populations of *S. zerene* along the coast of Del Norte Co., California, N of Crescent City. These are disjunct from Oregon *hippolyta*, and are separated by intervening populations of an *S. z. behrensii-gloriosa* intergrade in Curry Co., Oregon. Two of three family lines reared from the Del Norte populations exhibited an extended development time of 10–13 weeks for males and 11–14 weeks for females (Table 1). Thus, the extremely variable developmental rates observed in field emergence of *S. z. hippolyta* are also seen in some family lines reared in the laboratory. In sharp contrast, two family lines of *S. z. behrensii* from Curry Co. to the north, and three family lines of *S. z. myrtleae* from Marin Co., California to the south did not exhibit this extended development. Moreover, wild populations of *S. z. myrtleae* usually emerge in the field during early to mid-July, a full month earlier than the *hippolyta*-like populations. The manner in which these emergence patterns relate to respective local weather is undocumented as yet.

There are two close parallels to *S. zerene hippolyta* within the Argynninae that also exhibit adaptations to cold, wet marine-modified grasslands. One is *S. mormonia bischoffi* (Edwards) in coastal S Alaska from the Kodiak region N to Anchorage. The second is *Fabriciana (Mesoacidalia) aglaja scotica* Watkins in the Hebrides and Orkney Islands N of Scotland. Both species display extensive dark suffusion over much of the dorsal wing surfaces. Ford (1945) indicated that *F. a. scotica* often exhibits reduced wing size on small, wind-swept islands.

In the San Francisco Bay area of California, both *Speyeria c. callippe* and *S. coronis coronis* also have heavy melanic basal suffusion in a cool, foggy coastal environment (Hovanitz 1941), although the California habitat is less severe compared to the northern coastal grasslands occupied by the previous three species.

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