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Preference and performance of the wild indigo duskywing (*erynnis baptisiae*) on its native host yellow wild indigo (*baptisia tinctoria*) and on the introduced plant crown vetch (*securigera varia*)

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PREFERENCE AND PERFORMANCE OF THE WILD INDIGO DUSKYWING

(*Erynnis baptisiae*) ON ITS NATIVE HOST YELLOW WILD INDIGO (*Baptisia*

tinctoria) AND ON THE INTRODUCED PLANT CROWN VETCH (*Securigera varia)*

by

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Thesis

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Ypsilanti, Michigan

DEDICATION

This work is dedicated to my parents, Ed and Jean McMahon. Without their consistent support and encouragement, this accomplishment would not have been possible. Sadly, my father passed away prior to the completion of this project; however, his spirit remains with me and I hope this work would make him proud.

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ABSTRACT

The Wild Indigo Duskywing butterfly (*Erynnis baptisiae*) shifted from its native host plant Yellow Wild Indigo (*Baptisia tinctoria*) to the introduced plant Crown Vetch (*Securigera varia*). This study examined the effects of this host shift by comparing butterfly preference (larval feeding and female oviposition) and performance (pupal weight and pupation success) of two distinct butterfly populations, on both native and introduced plants. Caterpillars reared on the native plant had significantly greater pupal weight regardless of the population origin. Larval feeding preference was significantly affected by the plant fed upon; larvae from both populations strongly preferred to feed on the native plant. Neither population origin nor host plant significantly affected pupation success or oviposition preference. Greater performance on and feeding preference for the native plant emphasizes that increasing the *B. tinctoria* population will likely increase the butterfly population.

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INTRODUCTION

A host plant shift occurs when a phytophagous insect transfers from its traditional host plant to a novel plant species. Host shifts occur for a variety of reasons, including abundance of a novel plant combined with rarity of the native host, chemical similarity of plants, and females laying eggs on the incorrect plant species (Strong et al., 1984; Bernays and Chapman, 1994). Insects may innately have the ability to utilize various host plants. Alternatively, insects may evolve physiological or behavioral means to exploit a novel plant as a host plant over time. An example of an evolutionary response is the Australian soapberry bug, *Leptocoris tagalicus*, that evolved 5-10% longer mouthparts, allowing the insect to feed on the fruits of an invasive species, which has much larger fruit than its native host (Carroll et al., 2005).

Advantages of a host plant shift include the potential for range expansion, escape from natural enemies, an extended flight season, and the potential of a host plant with fewer toxins as with agricultural and horticultural plants (Erlich and Raven, 1964; Tabashnik, 1983; Bernays and Chapman, 1994; Graves and Shapiro, 2003; Murphy, 2004). Swallowtail butterfly caterpillars from the *Papilio machaon* group have been found to have greater survival on novel host plants in the absence of natural enemies than with natural enemies present on their typical host plant (Murphy, 2004). Many insects expanded their native host range by incorporating agricultural plants and thereby became pests. For example, *Colias* butterflies whose native host plants include indigenous legumes, such as American Vetch (*Vicia americana*), switched to the legume forage crop Alfalfa (*Medicago sativa*). The shift by *Colias* butterflies took as little as 100 generations

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(less than 50 years) for adaptations, which apparently granted *Colias* caterpillars feeding on Alfalfa greater efficiency digesting Alfalfa than the native host plant *V. americana* (Tabashnik, 1983). The shift by the phytophagous ladybird beetle *Epilachna yasutomii* from Wild Blue Cohosh to cultivated potato resulted in a range expansion, higher population growth rate, shorter development time, and larger females, which enabled this species to become an agricultural pest (Shiral and Morimoto, 1999). The Colorado Potato Beetle (*Leptinotarsa decemlineata*) shifted to cultivated potato and became one of the most destructive agricultural insects in North America as well as Europe (Hare, 1990).

Disadvantages of a host plant shift may include longer development times, risks to growth and reproduction, presence of natural enemies, decreased insect survival, or larval death (Graves and Shapiro, 2003). Even a closely related host plant species may require adaptations for an insect to successfully switch hosts, as shown for the milfoil weevil *Euhrychiopsis lecontei* Deitz. This weevil was raised on two native milfoil species (*Myriophyllum sibiricum* and *M. veticillatum*) and two invasive milfoil species (*M. spicatum* and *M. aquaticum*). Results indicated that female weevils laid eggs on all four species but completed development on only three of the four species. One of the exotic species was apparently toxic since weevils failed to develop further than the larval stage (Solarz and Newman, 2001). In addition, Byers et al. (1986) found reduced pupal weight and significantly higher larval mortality rates when fruitworms fed on compounds extracted from the introduced plant Crown Vetch (*Securigera varia*).

Any host shift to a novel plant species presents the phytophagous insect with a new complement of chemical compounds. The expected result of a host shift should

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include longer development times, slower larval growth rate, and decreased pupal weight. Insects with a greater affinity for utilizing a variety of host plants may evolve adaptations to cope with a host shift more quickly, whereas specialized insects shifting hosts may experience a much longer transition. Some insects have the ability to use a variety of host plants, yet ovipositing females select only one species. Graminivorous sawfly larvae survive well on three species of grass; however, females exhibited a strong oviposition preference for one grass species. Sawfly oviposition preference was closely correlated with maximum larval performance (Barker and Maczka, 1996). Approximately 34% (82) of the 236 butterfly species in California either feed upon or lay eggs on non-native plants. In addition, three species of butterflies lay eggs on plants that are toxic to larvae (Graves and Shapiro, 2003).

The most extreme outcomes of host plant shifts are host race formation and, ultimately, speciation. Elements leading to sympatric host race formation include habitat preference, host plant preference, and greater fitness (Bush, 1994). Mounting evidence demonstrating the occurrence of sympatric speciation exists. One of the most well studied cases involves the tephritid fruit fly complex (*Rhagoletis pomonella* spp.) that formed a new host race through a host shift to domestic apples (Bush, 1994; Schwarz et al., 2005).

An increasingly common means for insects to encounter new combinations of plants is via the presence of introduced or invasive plant species (Wilcove et al., 1998). Most nonindigenous plant species were introduced for agricultural or ornamental purposes (Pimentel et al., 2000). Wilcove et al. (1998) demonstrated that the presence of non-indigenous species presents a serious threat to indigenous species, and the number of invasive and introduced species continues to increase at an alarming rate. The disturbing

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trend toward decreasing populations of native host plant species and increasing populations of invasive plant species allows study of insect host shifts to novel host plants. For example, the aquatic plant, Eurasian Watermilfoil (*Myriophyllum spicatum*), is believed to have been introduced to North American in the 1940s (Sheldon and Jones, 2001). A native North American weevil raised on the Eurasian Watermilfoil exhibited a preference for laying eggs on the exotic and showed greater fecundity on the exotic than the native watermilfoil species (*Myriophyllum sibiricum*). This host shift occurred in less than 11 years (33 generations), which represents a very fast shift to a novel host species (Sheldon and Jones, 2001). Pimentel et al. (2000) estimated the number of introduced plants that escaped and established wild populations in the United States alone in excess of 5000 species. California alone is estimated to have 1057 introduced plant species (Graves and Shapiro, 2003). Despite this trend, few studies have examined the response and evolution of native species in response to introduced and invasive plant species.

Erynnis baptisiae, commonly called the Wild Indigo Duskywing, is an indigenous butterfly of the skipper family Hesperiidae, subfamily Pyrginae. This butterfly species is considered globally secure; however, it is a species of special concern in Michigan and has populations in only four counties (Fig. 1; MNFI; NatureServe, 2007). Michigan forms part of the northern boundary of the geographic range for *E. baptisiae*, which is partially why the butterfly is relatively rare in the state. Host plants of *E. baptisiae* that are native to Michigan include *Astragalus canadensis* (Canadian Milk Vetch), *Baptisia leucantha* (White Wild Indigo), *Baptisia tinctoria* (Yellow Wild Indigo), *Crotalaria sagitallis* (Rattlebox), and *Lupinus perennis* (Wild Lupine; Scott, 1986). However, Michigan populations of the Wild Indigo Duskywing have not been observed utilizing

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host plants other than those within the *Baptisia* genus and *Securigera varia* (Nielsen, 1999). Wild Indigo Duskywing females lay eggs singly on host plants (Scott, 1986). This species is multivoltine and typically has 2-3 generations per season (Gochfeld and Burger, 1997). In Michigan, the first generation appears in mid to late April, the second generation appears in July, and the third generation appears in September. Very little research on this species exists, and the impacts of utilizing the introduced plant *S. varia* as a host plant remained unknown. In addition, very few sites remain where the Wild Indigo Duskywing is able to use the native *B. tinctoria* as its host plant.

Baptisia tinctoria, commonly referred to as Yellow Wild Indigo, is a perennial plant in the pea family (Leguminosae) with a native distribution throughout eastern North America (Voss, 2001). *Baptisia tinctoria* populations declined over the last 10 years due partially to commercial demand of the plant for homeopathic purposes (Carroll and Feist, 2004). A recent review found evidence that ingestion of *B. tinctoria* root extracts greatly reduced the duration and intensity of symptoms of the common cold (Roxas and Jurenka, 2007). Although considered globally secure, *Baptisia tinctoria* populations are rare and are present in only 10 Michigan counties (USDA, NRCS; NatureServe, 2007). *Baptisia tinctoria* was the primary host plant of the local populations of the Wild Indigo Duskywing butterfly, *Erynnis baptisiae*, until some populations switched to the introduced plant *Securigera varia* (Shapiro, 1979; Nielsen, 1999).

The Wild Indigo Duskywing butterfly (*E. baptisiae*) shifted to *Securigera varia* fairly recently (Shapiro, 1979; Scott, 1986; Nielsen, 1999). *Securigera varia*, commonly called Crown Vetch, is a non-indigenous perennial plant in the pea family (Leguminosae) that was introduced to North America from Europe after 1890 as an erosion control

agent, a crop or ground cover plant, and sometimes as a livestock forage plant (Shapiro, 1979; Voss, 2001; USDA, NRCS). *Securigera varia* spread rapidly and now has a distribution in 48 states (USDA, NRCS). The species has been in Michigan for a maximum of 120 years. The first published observation of the Wild Indigo Duskywing using *S. varia* as a host plant was in 1974 (Shapiro, 1979). No detailed information concerning the growth, reproduction, or survival of the Wild Indigo Duskywing on the introduced host species is available.

Objectives

The primary objective of this study was to gain knowledge about the Wild Indigo Duskywing to provide sound management recommendations to increase populations of the species. The Wild Indigo Duskywing has not been well-studied, and critical information about the biology of the species on both its native host, *Baptisia tinctoria*, and the introduced host, *Securigera varia*, is not documented in the literature.

This study compared the preference and performance of two distinct butterfly populations, one using the native plant *B. tinctoria* and one using the introduced plant *S. varia*. One population is at Petersburg State Game Area, Monroe County, where adult females lay eggs on the native plant *B. tinctoria* (no *S. varia* was present). The second population is at Olson Park, Ann Arbor City Park, Washtenaw County, where females lay eggs on the introduced plant *S. varia* (no *B. tinctoria* was present). To examine preference and performance, the following questions were addressed.

Preference

- Does oviposition preference differ between females from the two populations when offered a choice of *B. tinctoria* or *S. varia*?

- Does feeding preference differ between larvae from the two populations when offered a choice of *B. tinctoria* and *S. varia*?

- Does the plant species on which a female lays an egg influence subsequent larval feeding preference?

Performance

- Do larval and pupal development (growth rate, pupal weight, and pupal success) differ for larvae from the two populations when reared on *B. tinctoria* versus *S. varia*?

Colias butterflies that shifted to introduced Alfalfa performed better on Alfalfa, while those remaining on the native vetch performed better on vetch, both in terms of greater pupal weight and shorter development time (Tabashnik, 1983). Thus, butterflies appeared to be diverging from one another as evidenced by better performance on one of the host plants. If the two *E. baptisiae* butterfly populations evolved specialization on their particular hosts, then it would be expected that (1) females should prefer to lay eggs on the plant on which they were reared, (2) larvae should exhibit a preference for feeding upon the plant species used by their original population, (3) the plant upon which an egg was laid should influence feeding preference, and (4) the plant upon which larvae feed should affect larval and pupal development times. If specialization has evolved, then butterflies from Olson (introduced host plant) should consistently show preference for

and perform better on the introduced plant *S. varia*, while Petersburg (native host plant) butterflies should consistently show preference for and perform better on the native plant *B. tinctoria*. Conversely, a lack of specialization by the two populations would demonstrate shorter development time and greater pupal weight on *B. tinctoria*, and longer development time on and lower pupal weight on *S. varia*.

METHODS

Larval Performance

During the 2005 field season, I conducted a 2X2 factorial experiment in the greenhouse at the Terrestrial and Aquatic Research Facility of Eastern Michigan University where growth rates of larvae were compared as a function of (1) population origin (*B. tinctoria* or *S. varia*) and (2) host plant on which larvae were reared (*B. tinctoria* or *S. varia*). *Baptisia tinctoria* plants were grown either from seed or bare root plants and planted in topsoil within pots in the greenhouse. The introduced plant *S. varia* was obtained from local wild sources, and these plants were also planted in topsoil within pots in the greenhouse.

Wild Indigo Duskywing larvae were collected between July 7 and August 11, 2005, from two field sites: (1) Petersburg State Game Area, Monroe County (where butterflies use the native host plant *B. tinctoria*), and (2) Olson Park, Ann Arbor City Park, Washtenaw County (where butterflies use the introduced host plant *S. varia*). The caterpillars from each of these two distinct populations were offered no choice of host plant and were reared on either *B. tinctoria* or *S. varia*. Eight caterpillars from the native *B. tinctoria* were reared upon *B. tinctoria*; 9 caterpillars from the native *B. tinctoria* were reared upon the introduced plant *S. varia*; 16 caterpillars from the introduced plant *S.*

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varia were reared upon *S. varia*; and 12 caterpillars from *S. varia* were reared upon the native plant *B. tinctoria*. Once placed on a plant, larvae were enclosed in lightweight, white mesh bags to ensure they remained on the no-choice host plant. Larval length was measured to the nearest millimeter and documented approximately every five days in the greenhouse. The third generation of *E. baptisiae* over winters in the larval state, and consequently all research was conducted on the first or second generation of butterflies.

In addition to the controlled greenhouse experiment on larval performance, five larvae were monitored at both field sites. Similar to the greenhouse experiment, larvae were enclosed in a lightweight mesh bag on the plant (*B. tinctoria* at Petersburg; *S. varia* at Olson), and larval length was measured to the nearest millimeter approximately every 5 days after the start of experiment. At Olson, larvae on *S. varia* in the field ranged in length from 2.0 to 7.0 mm upon initial measurement. At Petersburg, larvae on the native *B. tinctoria* initially ranged in length from 6.0 to 12.0 mm upon initial measurement.

The pupal weight of butterflies and moths can be an indicator of adult fitness, with greater pupal weight associated with greater adult fecundity and fitness (Tammaru et al., 2002; Murphy, 2004; Moreau et al., 2006). As a result, once larvae formed pupae, the wet pupal weight was recorded to the nearest hundredth gram, in both the greenhouse and field experiments.

Oviposition Preference

During the field season of 2006, the following preference and development time experiments were conducted. Two wooden framed cages approximately 1.5m^3 were constructed and covered with white lightweight polyester netting. The cages were

anchored to the ground with stakes, and both the interior and exterior perimeters of the bottom of the cage were lined with sand to prevent butterfly escape. These cages were housed on the grounds of the University of Michigan Matthaei Botanical Gardens in Ann Arbor, MI. This location excludes the range of both butterfly populations studied. Permission to use this site was granted by the Director.

Four potted plants, two native *B. tinctoria* and two introduced S. *varia*, were placed in the corners of the cages. Native and introduced plants were staggered within the cage, as in native-introduced-native-introduced, so the same species were not adjacent to one another. Plants were primarily grown from bare root stocks, along with some plants remaining from experiments conducted in 2005. All plants were grown in 8-inch green plastic pots with growing medium of topsoil and MiracleGro Potting Soil® mix in a 3:1 ratio, respectively.

Gravid females were obtained from each of the two distinct butterfly populations, Petersburg (native host) and Olson (introduced host). Once captured, a gravid female was placed in a cage with two *B. tinctoria* and two *S. varia* plants in an experiment to test female oviposition choice. Natural and artificial nectar sources were available for females during experiments. A total of 10 females were captured from Petersburg, and 22 females were captured from Olson. Nine of the ten females from Petersburg were from the second generation (early to mid-July), and one female was from the third generation (late August). Two of the 22 gravid females from Olson were from the first generation (late May to early June); 16 females were from the second generation (mid-July); and 4 females were from the third generation (early September). Females were housed in the cages for a period of 24 hours and then released at their natal field site. There were a few

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exceptions to the 24-hour rule, based on conditions at the time of the experiments. Two females from the second Olson generation were held in cages for 48 hours; two females from the Olson third generation were held for 48 hours. Only one female from the third generation at Petersburg was held for a period of 48 hours. The plants selected by the female, and the number of eggs laid on each plant were recorded.

Larval Feeding Preference

Eggs obtained from the oviposition preference experiment were utilized to assess larval feeding preference. Eggs were left on the original plant where laid and were placed in a mesh bag along with a branch of the opposite plant (native or introduced). The amount of herbivory on each damaged leaf in the mesh bag was determined 11, 18, 26, 32, and 39 days after the start of each experiment, using a standard damage estimate scale (see Bach and Kelly, 2004), where 0=0% leaf area removed, 1=1-5%, 2=6-25%, 3=26-50%, 4=51-75%, 5=76-99%, and 6=100% leaf area removed.

Development Time

Since very little life history information on *Erynnis baptisiae* is documented in the literature, it was of interest to gain knowledge of approximate development times for the 2-3 butterfly generations. The dates on which eggs were laid at each site were recorded, as well as the dates of emergence of adult butterflies. *E. baptisiae* over winters in the larval stage and, as a result, development time data can only be obtained with the 2nd and 3rd generations of butterflies that complete their entire life cycle within a single season.

Data Analysis

   Larval Performance. Two-way ANCOVAs were conducted on the pupal weight and growth rates, testing for the effects of population origin (native or introduced), plant upon which larvae were reared (native or introduced), an interaction between plant reared upon and the population origin, with a covariate of original larval length (mm). Larval growth rate was determined by subtracting the original length from the final length and dividing by the number of days the larva was alive.

   Oviposition Preference. Since a single female from Petersburg (native host) completed the oviposition preference experiment, the oviposition preference of the two populations could not be compared statistically. A t-test was conducted to determine whether females from Olson (introduced host) exhibited an oviposition preference for *B. tinctoria* (native) or *S. varia* (introduced).

   Larval Feeding Preference. Data from days 18 and 26 after the start of the larval feeding choice experiment were used to statistically analyze larval feeding preference. Butterflies from Petersburg (native host) emerged earlier than those from Olson (introduced host). Days 18 and 26 had the largest sample sizes and the maximum larval feeding overlap of the two populations. Two aspects of larval feeding preference were analyzed: (1) number of damaged leaves, and (2) mean amounts of damage on damaged leaves. Mean amounts of leaf damage were calculated by utilizing the midpoint for the amount of leaf damage within each damage category (0-6) for each damaged leaf. The proportion damage data were arcsine transformed prior to data analysis. Two-way

ANOVAs tested for effects of original population, plant fed upon, and any interactive effects.

In order to test whether the plant upon which the egg was laid affected larval feeding preference, the only sufficient sample size originated from the Olson population. Again, for days 18 and 26, two-way ANOVAs were used to test for effects of the plant upon which the egg was laid, plant larvae fed upon, and an interactive effect. All analyses of variance were conducted using SYSTAT 5.0 software (Wilkinson, 1990).

RESULTS

Larval Performance

Results from the larval performance experiment conducted in the greenhouse demonstrated significantly greater pupal weight when the native plant *B. tinctoria* was the host plant regardless of the original host plant (P=0.030; Table 1, Fig. 2). The population origin (native or introduced) and the interactive effect lacked significance (Table 1). The covariate of original length did not significantly affect pupal weight (Table 1).

Daily larval growth rate was significantly affected (P=0.022) by both the population origin (native or introduced) and the original length (P=0.000, Table 2, Fig. 3). Interestingly, the population origin (native or introduced) had a greater effect on growth rate than did the plant larvae fed upon. Larvae from the introduced population grew significantly faster than those from the native population (Fig. 3). Although growth rates were greater on the introduced plant than on the native plant (Fig. 3), this difference lacked statistical significance (P=0.210). There also was no significant interactive effect on growth rate (Table 2).

The total number of larvae that pupated was 21 of 45, approximately 47% (Table 3). The greatest percentages of pupation success occurred with larvae originally from one plant (native or introduced) that were reared on the opposite plant (50% if reared on *B. tinctoria*; 66% if reared on *S. varia*); however, these data lacked statistical significance. Less than 40% of larvae successfully pupated when reared on the same plant as their original population. Larvae originating on *S. varia* that fed on either plant were more successful at emerging as adult butterflies (33% if reared on *B. tinctoria*; 31% if reared on *S. varia*; Table 3). However, there was no significant difference in pupation success for larvae oviposited on one plant and reared on the opposite plant versus larvae oviposited on one plant and reared upon that same plant (χ^2=1.84, df=1, P>0.05).

Of the 10 larvae (five at each site) monitored at both Petersburg (native host) and Olson (introduced host) field sites, only three (from the Petersburg site) pupated.

Oviposition Preference

Females from Olson did not exhibit a significant preference for laying eggs on the native versus the introduced plant (t= -0.039, df=6, P=0.97, Fig. 4). In fact, four females laid more eggs on *S. varia* than on *B. tinctoria*, and three females laid more eggs on *B. tinctoria* than on *S. varia*. The single female from Petersburg showed a preference for *B. tinctoria*.

Larval Feeding Preference

When feeding preference was measured as the number of damaged leaves, there was a significant preference for feeding upon the native plant, *B. tinctoria*, on day 18 (P=0.014; Table 4, Fig. 5). The lack of a significant interaction indicates that larvae from both populations preferred *B. tinctoria* (although there appears to be a stronger preference exhibited by the *B. tinctoria* population). There were no significant effects on the number of leaves eaten on day 26 (Table 4, Fig. 5). When feeding preference was measured as the mean amount of damage per damaged leaf, there was a clear effect of population origin on preference on Day 18 (Table 5). Larvae from the native population caused about twice as much leaf damage as those from the introduced population (Fig. 6). There was no preference for either species for plant fed upon and no interactive effect (Table 5, Fig. 6). On day 26, there were no significant effects on mean damage per damaged leaf (Table 5).

There was a significant interactive effect of the plant the egg was laid upon and plant the caterpillar fed upon on feeding preference measured as the number of leaves damaged for the Olson (introduced host) population on Day 18 (P=0.027; Table 6, Fig. 7). There were no significant main effects of the plant egg laid upon and the plant fed upon (Table 6). Similarly, feeding preference based on the number of damaged leaves on Day 26 for the Olson population indicates a significant interactive effect of the plant the egg was laid upon and plant upon which the caterpillar fed (P=0.013, Fig. 7). Again, the plant the egg was laid upon and the plant the caterpillar fed on were not significant effects (Table 6). These interactive effects clearly show larvae preferred to feed on the plant upon which they were laid (Fig. 7).

Feeding preference based on the proportion of leaves damaged for the Olson

population revealed no significant differences for Days 18 and 26 (Table 7). Caterpillars

from eggs laid on the native plant *B. tinctoria* fed more on the native plant; conversely,

caterpillars from eggs laid on the introduced plant *S. varia* fed more on the introduced

plant; however, the differences lacked statistical significance (Table 7, Fig. 8).

Development Time

The most important finding related to larval development time was that in the

field, the timing of different life stages varied between the Petersburg (native host) and

Olson (introduced host) populations. Adult butterflies at Petersburg preceded those at

Olson by nearly 2 weeks during the second (July) generation in 2006 (Fig. 9). The

shortest development time coincided with the highest ambient temperature for both

populations. Development times represent combined transition dates for several eggs laid

by females from each population (Fig. 9). Combined transition dates represent the earliest

date of occurrence of life stage transitions for all eggs laid by a female on a single plant

(Fig. 9).

DISCUSSION

Erynnis baptisiae had significantly greater pupal weight when *B. tinctoria*

(native) was the host plant regardless of the original host plant. These results are

interesting because they strongly suggest that neither population performs as well on the

introduced host, *S. varia*. Population decreases of *B. tinctoria* may present a serious

obstacle for increasing the butterfly population and thus eliminating its status as a species

of special concern in the state.

The Olson butterfly population has not had access to the native plant *B. tinctoria* for approximately 30 generations or 10 years (Natural Area Preservation Division). The possibility that these distinct populations developed host plant specialization exists. Evidence of host plant specialization would demonstrate greater performance on the native plant by the Petersburg (native host) population and greater performance on the introduced plant by the Olson (introduced host) population. However, this study revealed no evidence for host plant specialization by these populations.

Larvae from Olson grew at a faster rate than larvae from Petersburg, which is likely due to the difference in the development timing between these two populations. Caterpillars from Olson were younger and apparently growing at a faster rate as a result. Although larvae from Olson grew faster, pupal weight of caterpillars reared on *S. varia* was significantly less than those reared on the native *B. tinctoria*. Greater pupal weight correlates with greater adult fecundity and fitness, suggesting that *E. baptisiae* fitness and fecundity will increase by increasing the population of the native plant *B. tinctoria* (Tammaru et al., 2002; Murphy, 2004; Moreau et al., 2006).

The percentages of larvae that successfully pupated (37.5% - 66.6%) and pupae successfully emerging as adults (12.5%-33.3%) were surprisingly low, particularly considering that larvae and pupae were protected to a much greater degree in mesh bags in the greenhouse compared with those in the field consistently exposed to natural enemies. Larvae monitored at the two field sites had the lowest proportion of larvae successfully pupating, and presumably a greater number of these caterpillars escaped from bags, desiccated, or were killed by natural enemies. The possibility that caterpillars escaped from bags in the field and subsequently pupated exists, but seems unlikely.

Caterpillars from eggs laid on the native plant *B. tinctoria* strongly preferred feeding on *B. tinctoria* as measured by the number of leaves damaged. Interestingly, caterpillars from eggs laid on the introduced plant *S. varia* also preferred feeding on the native plant *B. tinctoria*. Although *S. varia* is an adequate host plant for larval development, early instar larval feeding preference is consistent with better larval performance on the native plant *B. tinctoria*. Considering that the number of leaves damaged on *B. tinctoria* was much greater than on *S. varia*, it was interesting that the mean amount of damage per damaged leaf did not differ. The Petersburg (native host) population developed more quickly and at an earlier date than did the Olson (introduced host) population. The greater amount of damage for the native population may result from differences in the development times between the two populations, and larval feeding preference on *B. tinctoria* on day 18 likely indicates a stronger preference for the native plant earlier when larvae are less developed.

Feeding preference of caterpillars from the Olson population revealed only that the plant upon which the egg was laid influenced subsequent larval feeding preference. Caterpillars from eggs laid on the native plant *B. tinctoria* preferentially fed on the native plant, while caterpillars from eggs laid on the introduced plant *S. varia* preferred feeding on the introduced plant. The total number of eggs laid was nearly equal (70 on the native *B. tinctoria*; 65 on the introduced *S. varia*), which eliminates a potentially confounding factor of significantly more eggs laid on one plant species.

Based on observations gained from the field, there was a disparity in the timing of life stages (i.e. egg, larva, pupa, adult) between the Petersburg (native host) and Olson (introduced host) populations. An adult male butterfly was discovered at Petersburg on

July 4, 2006. The first adult from the oviposition experiment with the first generation from Olson emerged on July 15, 2006. This suggests that larvae feeding on *S. varia* have a longer development time, which may increase exposure to natural enemies and reduce adult fitness (Nylin and Gotthard, 1998). Again, this suggests that large *B. tinctoria* populations will result in a stronger *E. baptisiae* population, which may lead to butterfly population stability. An alternative is that *S. varia* may act as a host plant largely free of natural enemies, which may provide a benefit, counteracting longer development time (Murphy, 2004). This may be of greater importance if natural enemies (i.e. parasitoids) of larvae present the greatest threat to growth and development.

Female butterflies select suitable host plants based on visual cues, olfactory responses, and contact chemical cues upon landing on a plant (Murphy and Feeny, 2006). Additionally, a female should select the most beneficial plant for larval growth and development when laying eggs (Stanton, 1982). The oviposition study revealed that female butterflies from Olson showed no consistent preference for either the native *B. tinctoria* or the introduced *S. varia*, yet individual females showed preference (3 preferred *B. tinctoria*; 4 preferred *S. varia*). Gratton and Welter (1998) found that a specialist leafminer showed oviposition preference for established host plants over novel hosts. Barker and Maczka (1996) demonstrated that oviposition preference strongly correlated with larval performance for sawflies. It is likely that the butterflies at the Olson site have not had access to their native host plant *B. tinctoria* for at least 10 years (Natural Area Preservation Division). The fact that females selected *B. tinctoria* as often as the introduced *S. varia* is intriguing, and demonstrates no evidence for specialization, measured by oviposition preference.

The possibility exists that these distinct butterfly populations are genetically distinct. *Colias* butterflies shifted from established host plants to Alfalfa within 100 generations, and those who shifted to Alfalfa apparently lost some ability to develop on the established host plant *Vicia americana* (Tabashnik, 1983). The well-documented host race formation by *Rhagoletis* presents an intriguing example of steps toward speciation based on host plant preference (Bush, 1994). Yet evidence for genetic divergence via host race formation in *Erynnis baptisiae* was not demonstrated during this study.

The host shift of *E. baptisiae* from the native plant *B. tinctoria* to the introduced plant *S. varia* most likely occurred because *B. tinctoria* became largely unavailable. *Securigera varia* is within the pea family, to which the most primitive members of the skipper subfamily Pyrginae are restricted (Scott 1986). In addition, *S. varia* is a highly palatable forage plant and fixes nitrogen in the soil (USDA, NCRS). The host shift to *S. varia* may provide many benefits to *E. baptisiae*, including providing a corridor between *B. tinctoria* populations, particularly considering that *S. varia* was frequently planted along roadways. Additionally, *S. varia* may act as a buffer and provide a suitable host plant in the event of further decreases in the *B. tinctoria* population. It is also possible that *S. varia* may allow the *E. baptisiae* population to expand its geographic range.

Although *E. baptisiae* can obviously subsist on *S. varia*, it performs better on the native plant *B. tinctoria*. This implies that an increase in the number of *B. tinctoria* plants may increase the fitness of *E. baptisiae*, which, in turn, may lead to an increase in the population of the butterfly. If the butterfly population increases and becomes stable, the species may attain a secure population status in Michigan.

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Table 1

Two-way ANCOVA of pupal weight with covariate of original larval length, as a function of the population origin (native or introduced), the plant larvae were reared upon, and an interactive effect.

Pupal Weight (g)	F	DF	P
Population Origin	0.035	1,16	0.855
Plant Reared Upon	5.660	1,16	0.030
Interaction	0.738	1,16	0.403
Original Length	0.384	1,16	0.544

Table 2

Two-way ANCOVA of daily larval growth rate (mm/day) as a function of the population origin (native or introduced), the plant larvae were reared upon, and an interactive effect.

Larval Growth Rate (mm/day)	F	DF	P
Population Origin	6.330	1,18	0.022
Plant Reared Upon	1.690	1,18	0.210
Interaction	0.677	1,18	0.421
Covariate–Original length (mm)	44.46	1,18	0.000

Table 3

Percentage of larvae that pupated and the percentage of pupae that successfully emerged as adult butterflies from the greenhouse experiment conducted in 2005. Larvae from both original populations (native or introduced) were reared upon either the native (B. tinctoria) or the introduced plant (S. varia).

Original Plant		Plant Reared Upon	N	% of larvae that became pupae	N	% of pupae successfully emerged as adults	N
B. tinctoria	→	*B. tinctoria*	8	37.5%	3	12.5%	1
B. tinctoria	→	*S. varia*	9	66.6%	6	22.2%	2
S. varia	→	*B. tinctoria*	12	50.0%	6	33.3%	4
S. varia	→	*S. varia*	16	37.5%	6	31.3%	5

Table 4

Two-way ANOVA of the number of leaves damaged, based on the population origin (native or introduced), the plant fed upon, and an interactive effect on days 18 and 26.

Day 18	F	DF	P
Population Origin	2.507	1,30	0.124
Plant Fed Upon	6.780	1,30	0.014
Interaction	3.089	1,30	0.089

Day 26	F	DF	P
Population Origin	0.168	1,30	0.685
Plant Fed Upon	0.415	1,30	0.524
Interaction	1.217	1,30	0.279

Table 5

Two-way ANOVA of mean leaf damage on damaged leaves, based on the population origin (native or introduced), the plant fed upon, and an interactive effect on days 18 and 26. Data were arcsine transformed prior to analysis.

Day 18	F	DF	P
Population Origin	36.29	1,25	0.000
Plant Fed Upon	0.194	1,25	0.664
Interaction	1.691	1,25	0.205

Day 26	F	DF	P
Population Origin	0.074	1,25	0.787
Plant Fed Upon	0.031	1,25	0.862
Interaction	0.008	1,25	0.930

Table 6

Two-way ANOVA of the number of leaves damaged based on the plant egg laid upon, plant fed upon, and an interactive effect on days 18 and 26. Data are from the Olson (introduced host) population.

Day 18	F	DF	P
Plant Egg Laid On	1.478	1,20	0.238
Plant Fed Upon	0.226	1,20	0.639
Interaction	5.698	1,20	0.027

Day 26	F	DF	P
Plant Egg Laid On	2.347	1,20	0.141
Plant Fed Upon	0.781	1,20	0.387
Interaction	7.353	1,20	0.013

Table 7

Two-way ANOVA of the mean leaf damage on damaged leaves, based on the plant egg laid upon, plant fed upon, and an interactive effect on days 18 and 26. Data are from the Olson (introduced host) population. Data were arcsine transformed prior to analysis.

Day 18	F	DF	P
Plant Egg Laid On	0.768	1,17	0.393
Plant Fed Upon	0.494	1,17	0.492
Interaction	0.615	1,17	0.444

Day 26	F	DF	P
Plant Egg Laid On	4.22	1,19	0.054
Plant Fed Upon	0.046	1,19	0.833
Interaction	0.222	1,19	0.643
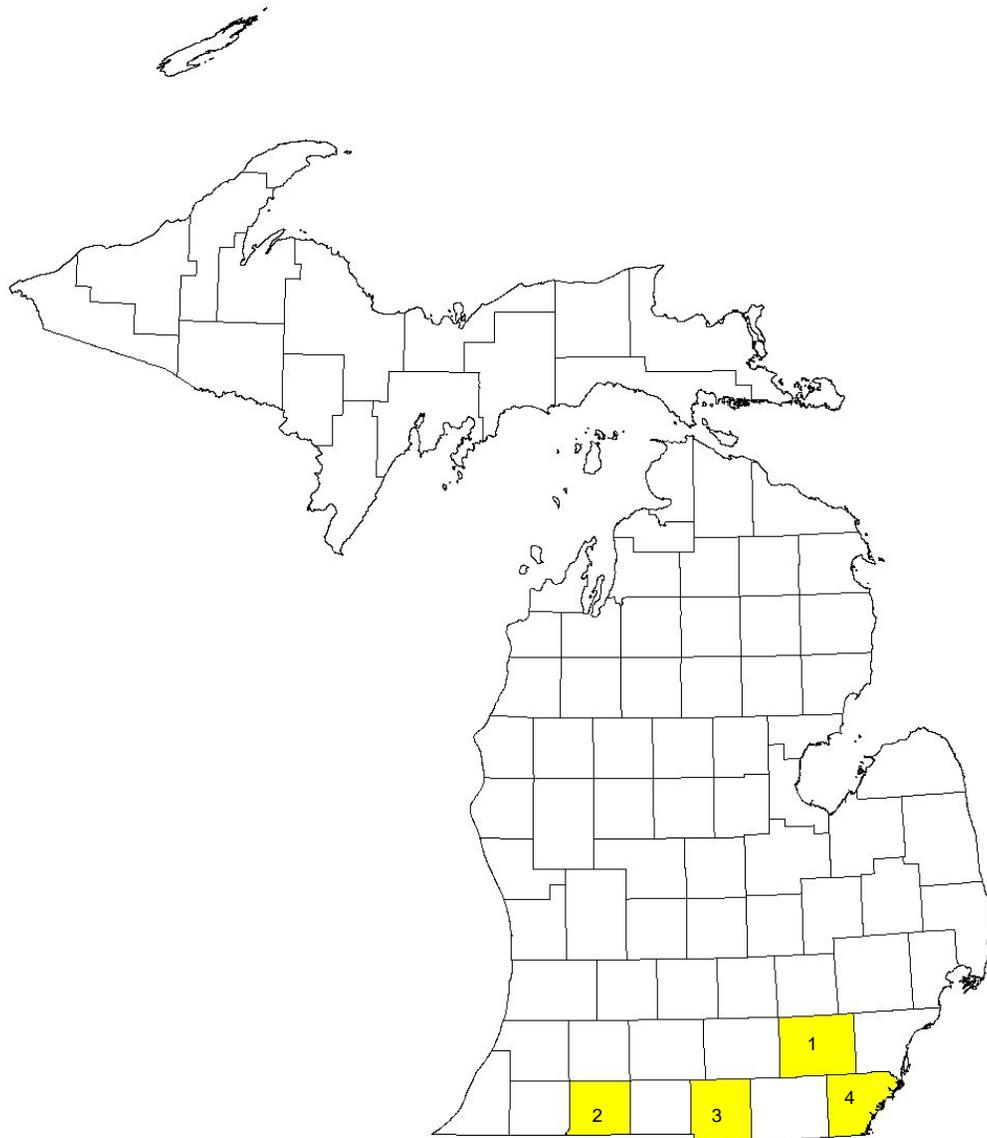
Fig. 1. Distribution of Wild Indigo Duskywing (*Erynnis baptisiae*) populations in Michigan (NatureServe, 2007). 1 – Washtenaw County, 2 – St. Joseph County, 3 – Hillsdale County, 4 – Monroe County.
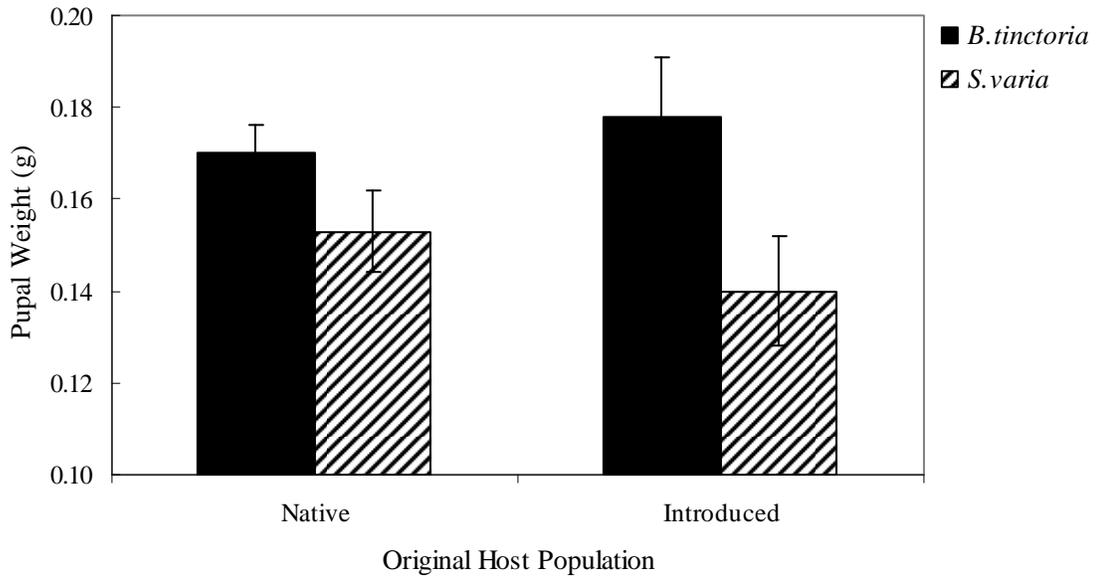
Fig. 2. Pupal weights of larvae from each of the two host populations (native and introduced) grown on the two host plants, *B. tinctoria* (native) or *S. varia* (introduced). Means and SE are represented for pupal weight based on population and plant. *B. tinctoria* → *B. tinctoria* N=3. *B. tinctoria* → *S. varia* N=6. *S. varia* → *B. tinctoria* N=6. *S. varia* → *S. varia* N=6.
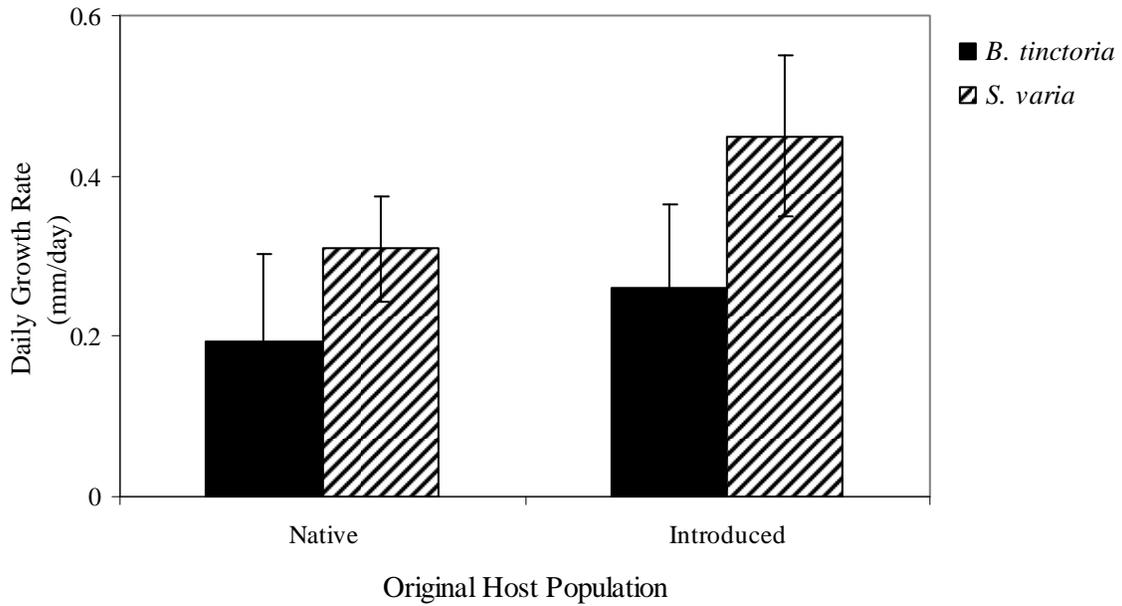
Fig. 3. Daily larval growth rate ([final length – initial length]/# of days) of larvae based on population origin (native or introduced) and plant reared upon, *B. tinctoria* (native) or *S. varia* (introduced). Means and SE are represented for growth rate. *B. tinctoria → B. tinctoria* N=4. *B. tinctoria → S. varia* N=6. *S. varia → B. tinctoria* N=7. *S. varia → S. varia* N=6.
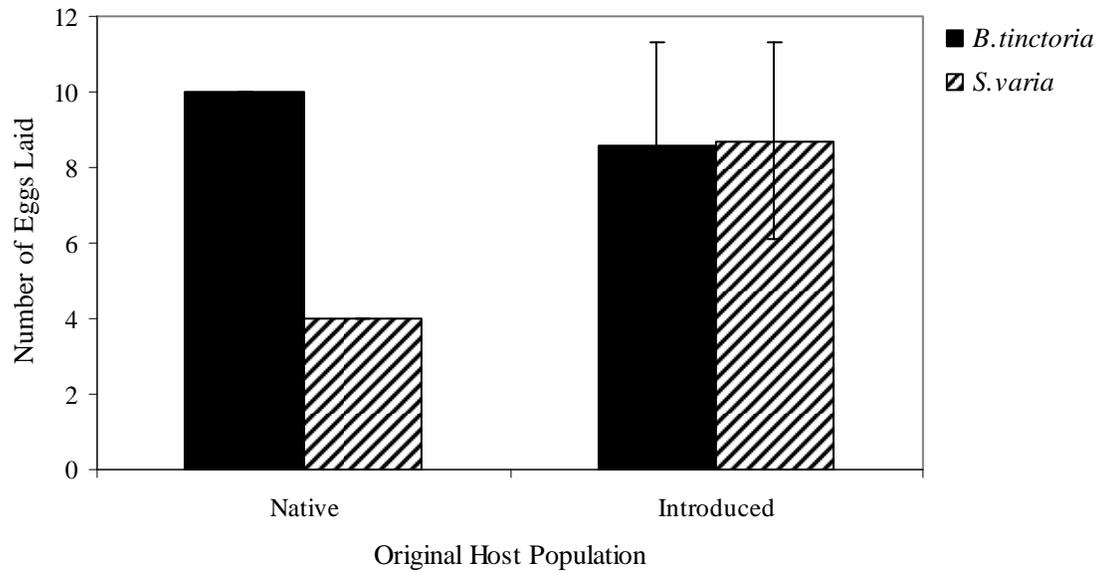
Fig. 4. Number of eggs laid on either the native (*B. tinctoria*) or introduced (*S. varia*) plant, based on original host population. Only a single female from the Petersburg (native host) population completed this experiment, and data show the actual number of eggs laid. Means and SE are represented for females from the Olson (introduced host) population. Native host population: *B. tinctoria* N=1; *S. varia* N=1. Introduced host population: *B. tinctoria* N=7; *S. varia* N=7.
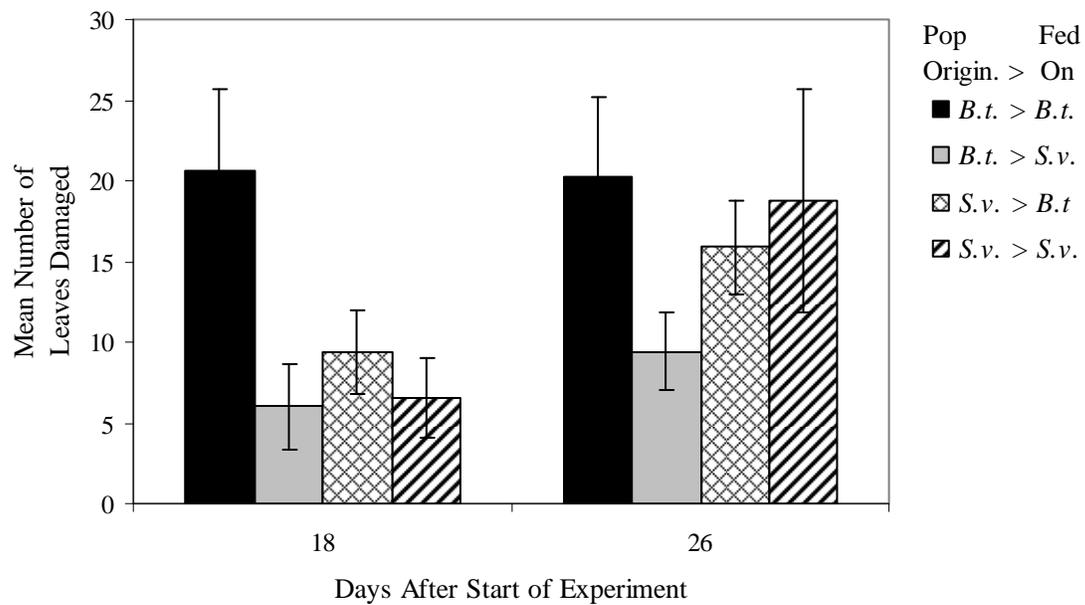
Fig. 5. Damage is shown for caterpillars from the Petersburg (native host) population feeding on *B. tinctoria* (black bars) and *S. varia* (gray bars); and for caterpillars from the Olson (introduced host) population feeding on *B. tinctoria* (diamond bars) and *S. varia* (diagonal bars). Means and SE are represented for the mean number of leaves damaged by both populations (native and introduced). *B. tinctoria* → *B. tinctoria* N=5. *B. tinctoria* → *S. varia* N=5. *S. varia* → *B. tinctoria* N=12. *S. varia* → *S. varia* N=12.
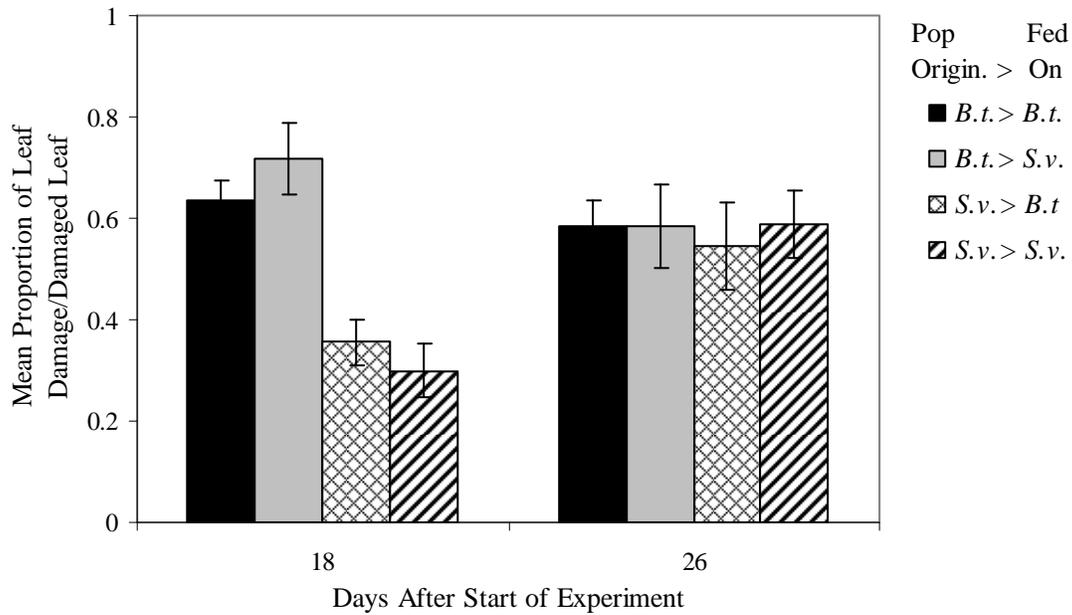
Fig. 6. Damage is shown for caterpillars from the Petersburg (native host) population feeding on *B. tinctoria* (black bars) and *S. varia* (gray bars); and for caterpillars from the Olson (introduced host) population feeding on *B. tinctoria* (diamond bars) and *S. varia* (diagonal bars). Means and SE are represented for the mean proportion of leaf damage per damaged leaf by both populations (native and introduced). Day 18: *B. tinctoria* → *B. tinctoria* N=5. *B. tinctoria* → *S. varia* N=3. *S. varia* → *B. tinctoria* N=10. *S. varia* → *S. varia* N=11. Day 26: *B. tinctoria* → *B. tinctoria* N=5. *B. tinctoria* → *S. varia* N=5. *S. varia* → *B. tinctoria* N=11. *S. varia* → *S. varia* N=12.
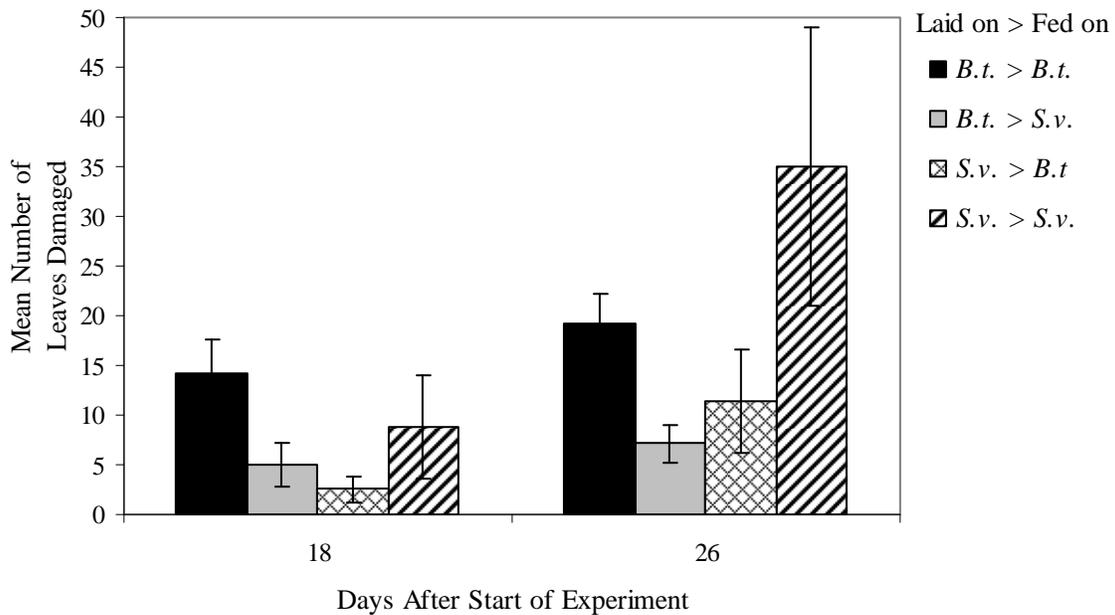
Fig. 7. The number of leaves damaged on days 18 and 26 after the start of the experiment. Data are from the Olson (introduced host) population. Means and SE are represented for the mean number of leaves damaged by the Olson population. Solid black bars indicate eggs laid on *B. tinctoria* (native) and larvae feeding upon *B. tinctoria*. Solid grey bars indicate eggs laid on *B. tinctoria* (native) and larvae feeding upon *S. varia* (introduced). Bars with the diamond pattern indicate eggs laid on *S. varia* (introduced) and larvae feeding upon *B. tinctoria* (native). Diagonal bars indicate eggs laid on *S. varia* (introduced), and larvae feeding upon *S. varia*. *B. tinctoria* → *B. tinctoria* N=7. *B. tinctoria* → *S. varia* N=7. *S. varia* → *B. tinctoria* N=5. *S. varia* → *S. varia* N= 5.
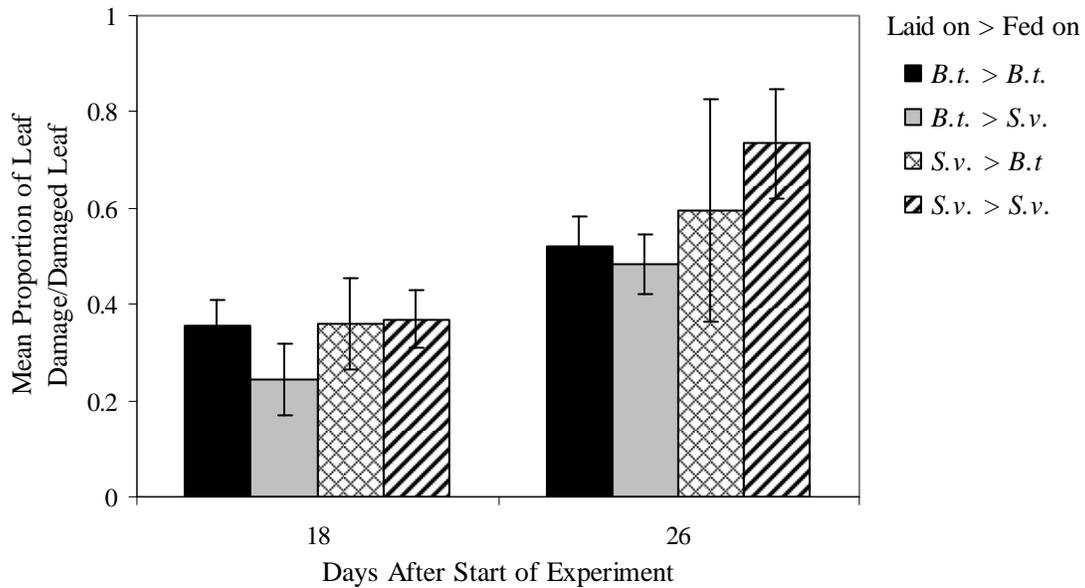
Fig. 8. The proportion of leaf area removed per damaged leaf on days 18 and 26 after the start of the experiment. Data are from the Olson (introduced host) population. Means and SE are represented for the mean proportion of leaf damage per damaged leaf by the Olson population. Solid black bars indicate eggs laid on *B. tinctoria* (native) and larvae feeding upon *B. tinctoria*. Solid grey bars indicate eggs laid on *B. tinctoria* (native) and larvae feeding upon *S. varia* (introduced). Bars with the diamond pattern indicate eggs laid on *S. varia* (introduced) and larvae feeding upon *B. tinctoria* (native). Diagonal bars indicate eggs laid on *S. varia* (introduced), and larvae feeding upon *S. varia*. Day 18: *B. tinctoria* → *B. tinctoria* N=7. *B. tinctoria* → *S. varia* N=6. *S. varia* → *B. tinctoria* N=3. *S. varia* → *S. varia* N=5. Day 26: *B. tinctoria* → *B. tinctoria* N=7. *B. tinctoria* → *S. varia* N=7. *S. varia* → *B. tinctoria* N=4. *S. varia* → *S. varia* N=5.
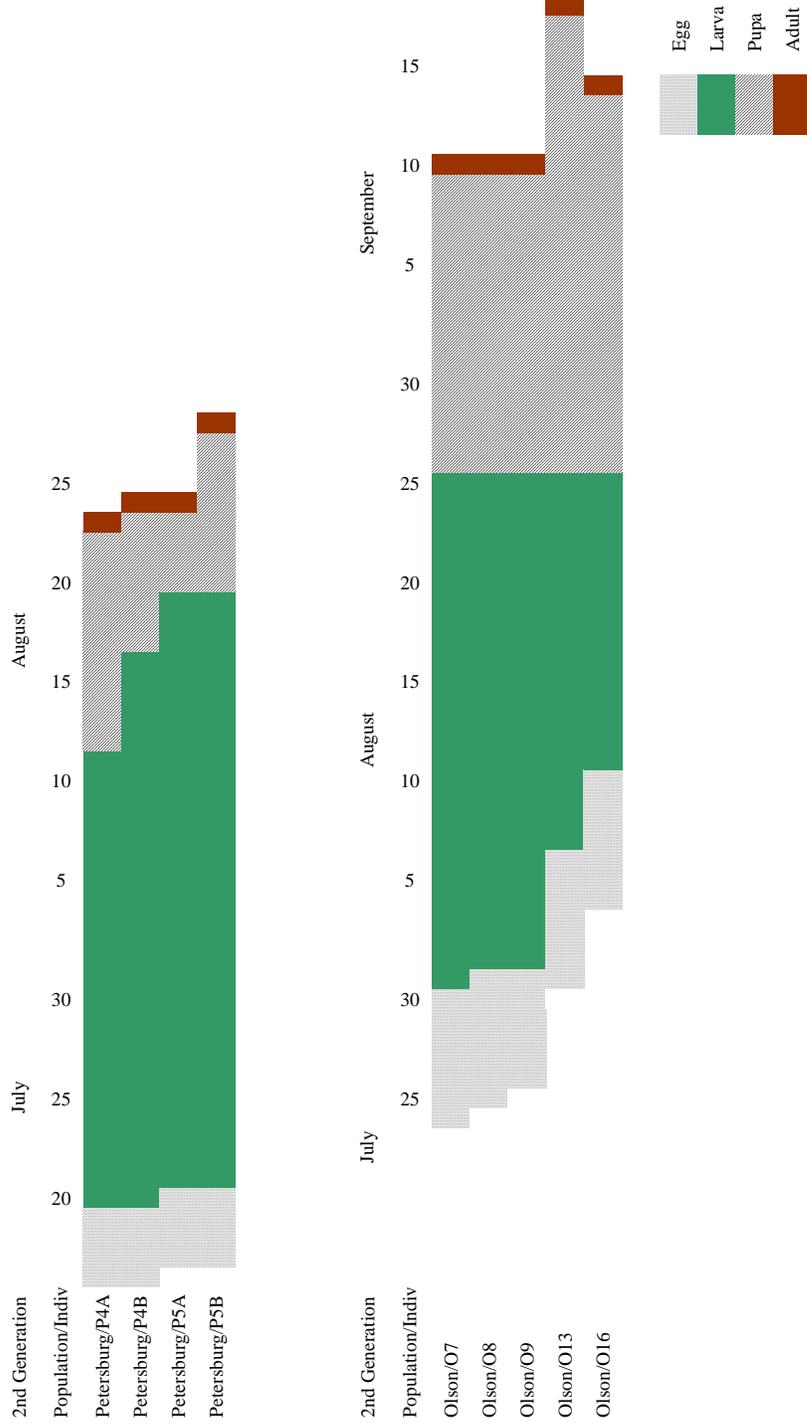
Fig. 9. Approximated development time of the second generation of butterflies from Petersburg (native host) and Olson (introduced host) populations. Each row shows data for all eggs laid by a female on a plant during oviposition experiments in 2006. Life stages represent the first date of occurrence for each transition.