

**INCISALIA HENRICI (GROTE AND ROBINSON) (LEPIDOPTERA:
LYCAENIDAE) REARED ON REPRODUCTIVE AND NON-REPRODUCTIVE
TISSUES OF THREE DIFFERENT PLANT SPECIES**

GORDON F. PRATT AND CECILIA L. PIERCE

Department of Entomology, University of California, Riverside, CA 92521, U.S.A.

Abstract.—Larvae of the small hairstreak butterfly, Henry's Elfin (*Incisalia henrici*), feed on a wide variety of plants and plant parts. The larvae of this Elfin along the eastern coastal plain feed on young leaves and flowers of hollies (*Ilex* sp.). Throughout much of the interior southeast the major food plant is believed to be flowers, flower buds, and young leaves of redbud (*Cercis canadensis*). While in the northern part of its range larvae have been found feeding on the fruits of a variety of plants including blueberries (*Vaccinium* sp.) and cherries (*Prunus* sp.). The effects of food plant species (hollies, redbud, and cherry) and plant parts (leaves vs. flowers) were studied on percent survival, pupal weights, and development times. Larvae survived well on the different test host plants and host plant parts. The *Ilex* reared pupae, despite being reared on the natal host, were significantly lower in weight than pupae of larvae reared on the other two plant species. Larvae reared on *Cercis* flowers and flower buds performed best in all categories. We conclude the subspecies utilizing *Ilex* as a food plant did not become adapted to this plant because larvae perform better than on other plants, but due to other variables such as perhaps the availability or abundance of plants in the habitat.

Key Words: Lycaenidae, hairstreaks, host races, Theclinae, foodplant effects

It has been suggested that some lycaenids, particularly eumaeine hairstreaks, which feed on a broad variety of plants, are able to do so because they specialize on the flowers and fruits of their hosts (Pratt and Ballmer 1991). Presumably these reproductive tissues exhibit a higher proportion of amino acids and protein to that of alkaloids and other secondary plant compounds (Chew and Robbins 1984, Pratt and Ballmer 1991). Specializations to multiple food plants can be either as separate species or by local adaptations of a single species that is capable of feeding on a broad variety of plants (Fox and Morrow 1981). Lycaenid butterflies fit both types from species with restricted host ranges to generalists that have become locally specialized (Ballmer

and Pratt 1989). For instance some lycaenid genera, such as *Celastrina* that feed on a broad variety of plants, exhibit both monophagous species and generalists with local specialization in food plants as geographic races (Pratt et al. 1994). In contrast some species, such as *Strymon melinus* Hubner, not only feed on a broad variety of plants locally, but on a variety of plant parts as well (Ballmer and Pratt 1989).

Henry's Elfin, *Incisalia henrici* (Grote and Robinson), is an interesting model species to test larval adaptations, since it feeds on the flowers, fruits, and leaves of a broad variety of plants and exhibits a number of geographic races (Pavulaan 1998, Gatrell 1999). It uses six host families in nature: Aquifoliaceae [*Ilex cassine* L., *I. opaca*

Ait., *I. vomitoria* Ait., *Nemopanthus mucronatus* (L.) Trel.]; Caprifoliaceae [*Viburnum acerifolium* (L.)]; Ebenaceae [*Diospyros texana* Scheele]; Ericaceae [*Vaccinium pallidum* Ait., *Vaccinium corymbosum* L., *Leucothoe racemosa* (L.) A. Gray, *Gaylussacia baccata* (Wangenn.)]; Fabaceae [*Cercis canadensis* L., *Lupinus texensis* Hook., *Sophora secundiflora* (Ort.) Lag ex. DC.]; Rhamnaceae [*Rhamnus frangula* L.]; and Rosaceae [*Prunus virginiana* L., *Prunus domestica* L., *Prunus pennsylvanica* L. f., *Prunus americana* Marsh., *Prunus serotina* J. F. Ehrh.] (Gifford and Opler 1983, Opler and Krizek 1984, Scott 1986, Pratt, personal observations, Pavulaan and Wright, in litt.). Larvae can be collected from the leaves and flowers of *Ilex opaca* (Pratt, pers. obs.), leaves of *Cercis canadensis* (Wright, pers. comm.), or fruits of *V. corymbosum* and *P. virginiana* (Pratt pers. obs.).

Henry's Elfin exhibits an interesting pattern of host utilization throughout its range. From the southern Appalachians of North America west to the Prairies it seems to specialize on *Cercis*, while along the coastal plain it specializes on the evergreen *Ilex* species. To the north of the range of these hosts in eastern Canada it specializes on a different variety of hosts particularly *Prunus* and *Vaccinium* species. Therefore this butterfly could exhibit local adaptations to the different plant species or may be adapted to a broad variety of plants and using specific plants locally because of food plant availability (Fox and Morrow 1981).

Gatrelle (1999) separates the subspecies of Henry's Elfin into two groups, those that are *Ilex* feeding and those that are non-*Ilex* feeding. He suggested that these groups could have already separated into sibling species, since larvae of one race of the *Ilex* feeding group had poor survival when fed *Cercis* (redbud). Redbud is a major food plant of the non-*Ilex* feeding group. Pavulaan (1998) supported Gatrelle's conclusions since he found holly-associated females from Prince George's County, Mary-

land, when set up on *Cercis* would not oviposit, yet immediately did so when transferred to *Ilex opaca*. Pavulaan also found that larvae of *Incisalia henrici viridissima* Pavulaan, a race that belongs to the *Ilex* feeding group, survived poorly on *Cercis*.

Host race adaptations are believed to have played an important role in the speciation of many insects, particularly in sympatry (Tauber and Tauber 1989). These adaptations involve traits that relate to fitness within the different groups of the Henry's Elfin as suggested by Gatrelle (1999). If the different races have made adaptations to their different food plants, then their survival and fecundity on their natural food plants should be higher than on food plants of the other races. The objectives of this paper are to determine how the coastal race of *I. henrici* adapted to *Ilex* performs as to survival, weight, and development time on its natal versus host plants of its other races.

MATERIALS AND METHODS

Ova ($n > 350$) of *I. henrici* were field collected on April 20 1992 from *Ilex opaca* at Nanticoke Wildlife Refuge, 10 km west of Laurel, Sussex Co., Delaware. Ova were easily found by scanning the upper surface of older leaves (often near the midrib). First instar larvae which eclosed from these ova two days later were separated into six groups of 50 each and reared either on flowers or leaves of the following plants: *Cercis canadensis* (Fabaceae), *Ilex opaca* (Aquifoliaceae), and *Prunus serotina* (Rosaceae). The newly eclosed larvae were transferred prior to any larval feeding via a camel hairbrush to their respective test host and reared in groups of 50 within square plastic storage containers (10 × 10 × 6 cm) at room temperature (23°C).

Branches of *Prunus* and *Ilex* were obtained from Nanticoke Wildlife Refuge, and *Cercis* were collected from a woodlot at the University of Delaware, Newark, DE, and maintained in refrigerated plastic Ziploc® bags until needed. Larvae that were fed

flowers (from male plants for *Ilex*) were given branches stripped of leaves, while larvae fed leaves were given branches stripped of flowers. Due to the season of the year, at which the butterfly occurs, most of the leaves and flowers larvae were reared on were fresh young growth of all three plant species. Fresh and old plant parts were added and removed daily, and the containers were cleaned twice daily at 12-hour intervals. When larvae reached fourth instar, to reduce the quantity of frass buildup in each container, they were divided in two equal groups and reared on the same host and plant part in two storage containers.

Development times in days and number that survived to pupation and to adult were recorded for each of the six treatments. Two weeks after the last larva pupated, all pupae were weighed to the nearest milligram. On October 15, 1992, all pupae were placed on moist sterilized sand at 4°C for a four-month period. The pupae were removed in mid February 1993, and placed at 20–22°C in an incubator with 24 h of darkness until all live pupae eclosed.

The data were analyzed by the SAS general linear models procedure (SAS Institute 1990). Data were grouped by treatments (*Cercis* leaves, *Cercis* flowers, *Ilex* leaves, *Ilex* flowers, *Prunus* leaves, and *Prunus* flowers), by host species, and by plant part (leaves and flowers). Means and standard errors were calculated for each group. Significance between groups for larval development time to pupation, pupal weights, and adult eclosion time and adult percent survival were determined by Tukey's Studentized Range (RSD) Test.

RESULTS

The lack of significant differences between development times of larvae on leaves and flowers suggests that the plant parts did not consistently affect the rate of development in the same way across species, yet there were significant differences of larvae reared on flowers and leaves within some species (*Cercis* and *Prunus*) (Table

Table 1. *Incisalia henrici* larval development and proportion survival to pupation on different hosts and plant parts.

| Host | Part | N | Mean Development* | Survival (percent) |
|---------------|---------|----|-------------------|--------------------|
| <i>Cercis</i> | Flowers | 50 | 15.98 (0.80) A | 100 |
| <i>Cercis</i> | Leaves | 43 | 17.91 (0.97) C | 86 |
| <i>Ilex</i> | Flowers | 42 | 16.36 (1.78) AB | 84 |
| <i>Ilex</i> | Leaves | 46 | 16.68 (1.14) AB | 92 |
| <i>Prunus</i> | Flowers | 48 | 18.85 (1.54) D | 96 |
| <i>Prunus</i> | Leaves | 31 | 17.00 (1.48) B | 62 |

* Means that are followed by a different letter are significantly different ($P < 0.05$). The standard deviations are in parentheses beside the mean development times.

1). Larvae reared on flowers and leaves of the same food plant were not significant ($P > 0.05$). The mean development times of larvae reared on *Prunus* were significantly slower than that of the other hosts ($P < 0.05$). The differences between species were in large part due to the long development times of larvae reared on *Prunus* flowers (Table 1). Most of the variations in development times amongst the six rearing treatments were between flowers of the different hosts, with larvae reared on *Cercis* flowers taking the shortest time to pupate and those on *Prunus* flowers taking the longest.

The pupae of larvae reared on the natal host *Ilex opaca* weighed significantly less from those reared on the other hosts ($P < 0.0001$). Pupal weights of larvae reared on flowers were not significantly different from those reared on leaves ($P > 0.05$). The heaviest mean pupal weights were of larvae reared on *Cercis* flowers and *Prunus* leaves, which were significantly different from the other four treatments but not from each other (Table 2).

The highest percent survival to adult was on *Cercis* flowers (98%), which was significant from all other treatments (Table 3). The percent survivals of the other five treatments were not significant from each other. Adult eclosion times of *I. henrici* pupae from larvae reared on *Prunus* were signif-

Table 2. Mean pupal weights of *I. henrici* reared on different hosts and plant parts.

| Host | Part | N | Mean Weight* |
|---------------|---------|----|----------------|
| <i>Cercis</i> | Flowers | 50 | 0.099 (0.01) A |
| <i>Cercis</i> | Leaves | 37 | 0.089 (0.01) B |
| <i>Ilex</i> | Flowers | 38 | 0.085 (0.01) B |
| <i>Ilex</i> | Leaves | 41 | 0.082 (0.01) B |
| <i>Prunus</i> | Flowers | 36 | 0.088 (0.01) B |
| <i>Prunus</i> | Leaves | 29 | 0.104 (0.02) A |

* Means that are followed by a different letter are significantly different ($P < 0.05$). The standard deviations are in parentheses beside the mean weights.

icantly shorter than those reared on the other two hosts ($P > 0.0005$). Also the eclosion times of pupae of larvae reared on flowers of a respective host were significantly different from pupae of larvae reared on leaves of the same host ($P < 0.05$).

DISCUSSION

In our model system, *Incisalia henrici* thrived best on *Cercis* flowers. This treatment yielded the quickest larval development time (Table 1), a very high mean pupal weight (Table 2), and the greatest survival to adult (Table 3). It has been suggested that flowers may provide advantages to lycaenid larvae due to their higher ratio of nutritional resources (amino acids and proteins) to non-nutritional resources (alkaloids and other secondary chemicals) (Chew and Robbins 1984, Pratt and Ballmer 1991). The family Fabaceae (which includes *Cercis*) is known to have some of the highest ratios of amino acids and proteins to carbohydrates, most likely due to their association of nitrogen-fixing bacteria. Members of the Fabaceae are thought to be great nutritional resources to lycaenid larvae (Pratt and Ballmer 1991).

In nature redbud (*Cercis*), is not the naturally available host for this model population of *I. henrici*. *Cercis canadensis* and *Ilex opaca* are utilized by *I. henrici* almost everywhere they occur. Yet these hosts do not exhibit much distributional overlap in nature (Gatrelle 1999). *Prunus virginiana* is

Table 3. *I. henrici* mean adult eclosion times from pupae and proportion survival from first instars to adults on different hosts and plant parts.

| Host | Part | N | Mean Eclosion* | Survival (percent) |
|---------------|---------|----|----------------|--------------------|
| <i>Cercis</i> | Flowers | 49 | 9.67 (2.15) A | 98* |
| <i>Cercis</i> | Leaves | 37 | 6.81 (1.02) B | 74 |
| <i>Ilex</i> | Flowers | 35 | 6.91 (1.29) B | 70 |
| <i>Ilex</i> | Leaves | 37 | 9.51 (1.84) A | 74 |
| <i>Prunus</i> | Flowers | 30 | 7.73 (1.48) B | 60 |
| <i>Prunus</i> | Leaves | 27 | 6.67 (0.78) B | 54 |

* Means followed by an asterisk or a different letter are significant at $P < 0.05$. The standard deviations are in parentheses beside the mean eclosion times.

common in many localities of both races, but does not appear to be used as a food plant, except in the northern part of the range where *Cercis canadensis* and *Ilex* species are both absent. *Euphydryas editha*, a butterfly that has had extensive research for over 30 years, has this type of host utilization, since when its natural host is absent the butterfly will switch to other available food plants that are not normally used (Singer et al. 1992, Singer and Thomas 1996).

Interestingly, *Incisalia henrici* is quite abundant in areas where it utilizes hollies as food plants, while the butterfly is generally uncommon in areas where the species is believed to be using redbud (Pratt, personal observation, Pavulaan, personal communication). This observation suggests there could be advantages of feeding on holly over that of redbud. Also, *Cercis* flowers are not likely used to a great extent even in populations specifically adapted to *Cercis*. *Cercis* blooms early in nature before the leaves (probable larval food in the field) break bud and well before most adult butterflies eclose from over-wintering pupae.

The success of natural *Ilex*-feeding *I. henrici* larvae on *Cercis* in the laboratory may be explained by 1) the ancestral food plant is redbud and holly is a recent adaptation, 2) the ratio of nutritive to non-nutritive resources in redbud flowers is higher

than its own food plant, 3) redbud flowers are devoid of growth toxins present in other hosts, and/or 4) unknown factors unmasked by laboratory conditions. In nature the ability to feed and thrive on a specific plant is an obvious adaptive trait, but it may not be the only variable that makes one food plant better than another. *Cercis* may harbor large numbers of predators and parasites, especially around young budding leaves where most eggs on *Cercis* are laid. In *Ilex* populations, *Trichogramma* (Hymenoptera: Trichogrammatidae) parasitized eggs may be far less frequent on the old *Ilex* leaves and have a distinct advantage over eggs oviposited upon flowers, flower buds, or leaf buds (Pratt, personal observation). Old *Ilex* leaves on the other hand can't feed first instar larvae, so newly hatched larvae must travel great distances in search of developing leaves. If there were no advantage to ovipositing on these old leaves, this adaptation would therefore be counterproductive to the species. These sort of adaptations made by insects to escape parasitization have been observed in other host/parasite systems (Moore 1989, Schreiber et al. 2000).

It would seem from the data in this study that *Incisalia henrici* has not formed sibling species based on host adaptations as suggested by Gatrell (1999). If the *Incisalia henrici* races adapted to these different plants had formed species, the model population adapted to *Ilex* would be expected to do better on *Ilex* than on either *Cercis* or *Prunus*. Instead this population adapted to *Ilex* did best on *Cercis* flowers, rather than on the natal host, *Ilex opaca*. Instead *Incisalia henrici* appears to fit more the pattern of a generalist that is able to feed on a broad variety of plants and has made local adaptations to local food plants (Fox and Morrow 1981). As expected in this model there was actually little differences in performance of larvae on the different food plants.

Our *I. henrici* model system showed no significant differences in the developmental

parameters between larvae reared on flowers versus those reared on leaves. This elfin is adapted to a variety of food plants and plant resources. It does not appear to be adapted to any specific plant or plant part. The adaptations made by this species are broad in that it is able to feed on the flowers, fruits, and leaves of many plant species and it is not particularly specialized. That a butterfly with this capacity has formed distinct localized races suggests that it has made localized adaptations independent of its ability to feed and grow on locally available food plants.

ACKNOWLEDGEMENTS

We thank David M. Wright and Harry Pavulaan for reading the manuscript and all of their thoughtful suggestions provided throughout this study. Two reviewers, Robert K. Robbins and anonymous reviewer, also provided much helpful editing and suggestions. We also thank John Pesek at the University of Delaware for his help with the statistics. We also acknowledge the late lepidopterist Ben Zeigler for his deep interest in the food plant utilization of the Henry's Elfin and other butterflies found in North America.

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