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LARVAL FEEDING BEHAVIOR AND ANT ASSOCIATION IN FROSTED ELFIN, *CALLOPHRYS IRUS* (LYCAENIDAE)

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ABSTRACT. *Callophrys irus* is a rare and declining lycaenid found in the eastern U.S., inhabiting xeric and open habitats maintained by disturbance. Populations are localized and monophagous. We document a previously undescribed larval feeding behavior in both field and lab reared larvae in which late instar larvae girdled the main stem of the host plant. Girdled stems provide a unique feeding sign that was useful in detecting the presence of larvae in the field. We also observed frequent association of field larvae with several species of ants and provide a list of ant species. We suggest two hypotheses on the potential benefits of stem-girdling to *C. irus* larvae: 1) Stem girdling provides phloem sap as a larval food source and increases the leaf nutrient concentration, increasing larval growth rates and providing high quality honeydew for attending ants; 2) Stem girdling reduces stem toxicity by inhibiting transport of toxins from roots to the stem.

Additional key words: *Baptisia tinctoria*, girdle, feeding sign, Massachusetts, phytochemical defense

The frosted elfin, *Callophrys irus* (Godart, 1824) (Lycaenidae), is an oligophagous butterfly that is reliant on disturbance-dependent habitats (Scott 1986, Schweitzer 1992, Opler 1998). During the past century, the eastern North American range of *C. irus* extended from Ontario to Florida, and west to Texas and Wisconsin (Opler *et al*. 1995, Layberry 1998). The species is univoltine and non-migratory, and although it has a broad geographic distribution, it typically occurs in small, localized populations. *C. irus* appears to be in decline, as indicated by its extirpation in Canada and two US states, and its listing as endangered, threatened or of special concern in 11 of the 27 U.S. states in which it is still found (Packer 1998, NatureServe 2006). Many *C. irus* populations have disappeared or declined in the past 50 years, and remaining populations are limited to xeric sand barrens and savanna habitat with an open vegetation structure, often maintained by anthropogenic activities in the absence of other disturbance (Wagner *et al*. 2003).

A taxonomic account of the immature stages of *C. irus* is beyond the scope of this paper, however, it should be noted that much of the early literature failed to recognize this species as distinct from *Callophrys henrici* (Grote & Robinson, 1867) (Lycaenidae). Many of the early accounts of the immature stages and larval host plants of *C. irus* actually refer to *C. henrici*. For example, Cook (1906) attributes original description of the larva and pupa of *C. irus* to Boisduval & Le Conte (1829–[1837]), however these descriptions (from John Abbot's notes) and figures (by Abbot) are actually of *C. henrici* (Calhoun 2004). Descriptions of the second, third, and fourth-instar larva, pupa, larval hosts, and feeding habits of *C. irus* in Scudder (1888–1889) are from W. H. Edwards' notes on *C. henrici* (Cook 1906), and the larva and pupa figured in Scudder (1888–1889) are reproduced from Abbot's drawings of *C. henrici* in Boisduval & Le Conte (1829–[1837]) (Calhoun 2004). Recently, color photographs of the larva and pupa of *C. irus* have been published by Allen (1997), Allen *et al*.

(2005), and Minno (2005).

The larval host plants of *C. irus* are all legumes (Fabaceae), with most populations feeding on either wild indigo *Baptisia tinctoria* (L.) or wild lupine *Lupinus perennis* (L.), but not both (Schweitzer 1992, Wagner *et al*. 2003). *Baptisia australis* (L.) and *Crotalaria sagittalis* (L.) have also been reported as occasional hosts (Scott 1986). Geographic patterns of host use and concordant morphological differences among populations have led to the suggestion that populations of *C. irus* feeding on *L. perennis* may not be conspecific with those feeding on *B. tinctoria* (Schweitzer 1992). Cook (1906) provided the first detailed life history observations of *C. irus*, from a population feeding on *L. perennis* in the Pine Bush east of Albany, New York. However, little has been published on the life history of *C. irus* populations feeding on *B. tinctoria*.

A unique and reliable feeding sign can be useful in detecting the presence of a larva on a host plant and may be used as a surrogate for direct observations of larvae during research on rare Lepidoptera (Swengel 1995, Smith *et al*. 2002, Albanese *et al*. in preparation). A feeding sign is especially useful when it is persistent and consistent in form and location. In this paper we provide observations on larval feeding behavior of *C. irus* on *B. tinctoria*, including documentation of an unusual feeding sign that is present throughout most of the year and can be used to determine the presence of the species.

Associations between lycaenids and ants (Formicidae) are not unusual, with approximately 75% of the species known to associate with ants. These associations range from loose facultative to obligate (Pierce *et al*. 2002). The costs and benefits of interacting with ants vary among lycaenid species (Fiedler & Saam 1992, Wagner 1993, Cushman *et al*. 1994). With regard to the benefits of ant attendance, two hypotheses have been proposed: appeasement and protection (Pierce *et al*. 2002). Larvae may appease potentially aggressive ant species with food rewards. Ants may also protect larvae from predators and parasitoids because larval secretions are a valuable food resource (Atsatt 1981, Pierce & Mead 1981, Pierce *et al*. 1987, Peterson 1993). Providing food rewards to ants can negatively affect both larval development and adult reproductive success (Robbins 1991, Fiedler & Hölldobler 1992, Wagner 1993, Wagner & Kurina 1997), and the selection of legumes or other protein-rich host plants by ant-attended lycaenids may serve to offset this increased nutritional cost (Pierce *et al* 1985, Fiedler 1996). Such complex interactions between host plants, larvae, and ants are of immense importance and interest in the study of lycaenid ecology and evolution, and the documentation of ant association is an important step in furthering the conservation of rare lycaenid species (Pierce *et al*. 2002). In this paper we report the association of *C. irus* larvae with several ant species.

METHODS AND RESULTS

We conducted field and laboratory studies from 2002 through 2005 as part of a larger research project designed to assess the multi-scale habitat requirements of *C. irus*. The fieldwork was conducted at four sites in southeastern Massachusetts, U.S.: 1) Crane Wildlife Management Area (WMA), Barnstable County; 2) Gavins Pond Municipal Water Authority (MWA) property, Norfolk County; 3) Myles Standish State Forest (SF), Plymouth County; and 4) Noquochoke WMA, Bristol County. All of these areas are on the coastal plain and are characterized by xeric, sandy soil and relatively flat topography.

In results reported below, we use the terms early-, mid- and late-instar to describe larvae when the exact instar was not determined. Relative to the four larval instars of *C. irus*, early-instar = first or second instar, mid-instar = second or third instar, and late-instar = third or fourth instar. Results of statistical analyses are presented as the mean ± SE.

Larval behavior: Field observations. Late-instar *C. irus* larvae produced "feeding rings" on host plants at all study sites. Larvae produce rings by consuming the epidermis near the base of the main stem of the *B. tinctoria* plant (Fig. 1). Feeding continued around the circumference of the stem until the outer tissue (epidermis and cortex) was completely consumed, exposing the inner vascular tissue in a complete ring, effectively "girdling" the main stem of the host plant (Fig. 2). Although a single stem typically had only one complete feeding ring, in some cases two or more rings were present. Only late-instar larvae were observed feeding in this manner. Host plants developed scar tissue in the area of the feeding ring, causing it to persist throughout the growing season. For 15 of the 198 late-instar larvae found between 2003 and 2005, we did not inspect the host plant stems for feeding rings. Of the 183 remaining host plants, feeding rings were present in 172 cases (94%). It is possible that the 11 larvae found on plants without feeding rings were encountered prior to commencement of stem-feeding, and that we have underestimated the number of larvae that produced feeding rings prior to pupation.

At Gavins Pond, from 13 to 18 June 2005, 20 larvae not used in other parts of the study were found in the second instar, and their host plants were flagged to allow

Fig. 1. Late-instar *Callophrys irus* larva beginning to feed on the epidermis of a *Baptisia tinctoria* stem.

Fig. 2. In the foreground, a late-instar *Callophrys irus* larva rests on a *Baptisia tinctoria* stem. This larva previously consumed the epidermis and cortex layers of the stem to produce a characteristic "feeding ring." In the background, another late-instar larva feeds on different stem.

periodic field observation of feeding behavior. The lengths of all 20 larvae were < 4 mm (3.4 ± 0.2) at the commencement of observations. During each observation, we relocated each larva and examined the host plant for evidence of feeding. Early-instar larvae skeletonized young leaves on the apical shoots of the host plants. Middle- and late-instar larvae fed on entire leaves, frequently initiating feeding on the younger foliage near the tips of branches and sequentially consuming leaves while descending a branch. Larvae often defoliated an entire branch top before ascending a new apical shoot. We monitored 13 of the 20 larvae until the final instar; by this time all 13 had produced a feeding ring. The body length of final-instar larvae was 14.9 ± 0.7 mm (n = 13), and the development time from commencement of observations to the final instar was 25.2 ± 0.6 days (range = 21–30 days).

Larval behavior: Captive rearing observations. At Myles Standish SF, on 25 May 2002, we observed an adult female *C. irus* oviposit on the new apical growth of a *B. tinctoria* plant. The plant was dug up and potted for rearing in a screen cage, and kept outdoors in a shaded location. The egg hatched on 30 May (5 days after oviposition), the larva exiting through a small hole, leaving the remainder of the egg shell intact. The first-instar larva fed preferentially on new apical growth, skeletonizing the surface of the leaves. In the second instar the larva began to feed at the edges of leaves. During the third instar the larva and potted host plant were brought indoors for more frequent observation. In the third and fourth instars the larva consumed entire leaves, and feeding was concentrated on a particular branch of the plant, leaving it defoliated (as noted in observations of late-instar larvae in the field). The fourth-instar larva produced a feeding ring near the base of the main stem of the host plant. In this stage the larva spent most of its time at the base of the main stem, either resting or feeding on the stem, although it would periodically ascend to the top of the plant to consume leaves, later returning to its position at the base of the main stem. On 1 July the larva escaped through the open top of the cage and was not located for several days. When found it was beneath a wicker basket about 1 m from the potted plant, and had spun a small amount of silk around itself in preparation for pupation. The larva was transferred to a plastic vial where it pupated on 6 July (total larval period = 36 days).

On 4, 10, and 19 July 2003, we collected three larvae from *B. tinctoria* at Myles Standish SF. These larvae were reared on separate potted *B. tinctoria* plants, each enclosed in a large acrylic tube covered at the top with fine-mesh netting and kept outdoors in a shaded location. In the fourth instar, all three larvae produced feeding rings near the base of the main stem of the potted host plants, with one larva producing two separate rings. Like the larva reared in 2002, all three fourth-instar larvae would rest and feed at the base of the main stem, periodically ascending to the top of the plant to consume leaves. After 13, 8, and 4 days in captivity, respectively, each of the larvae ceased feeding and moved about the inside of their enclosure for 1–2 days before burrowing into the dry *Sphagnum* moss provided as a substitute for leaf litter. Several weeks later, it was observed that all three larvae had pupated at the surface of the soil, beneath 5–7 cm of dry *Sphagnum*. Each was resting on a thin pad of silk, dorsal side down, with surrounding pieces of moss held together with a few strands of silk, forming a loose chamber around the pupa.

In 2005 we collected five adult female *C. irus* from

the Gavins Pond site, brought them to the laboratory, and placed them in an enclosure with branches of *B. tinctoria* and 15 hours of natural and supplemental light per day. Within 48 hours, we observed > 25 ovipositions on *B. tinctoria*, and left the eggs undisturbed. We detected the first larvae within leaves of the apical shoots eight days following oviposition. After 2–5 additional days of development, we removed the larvae from the oviposition enclosure, and transferred each to a separate 480-ml, covered plastic cup. Larvae were provided with fresh *B. tinctoria* leaves and a 4–6 cm section of stem daily. Eighteen of the larvae were successfully reared to pupation. First and second larval instars skeletonized young developing leaves. Second through fourth instars consumed entire leaves. None of the larvae consumed the epidermis of a *B. tinctoria* stem until the fourth instar, at which time 17 of the 18 larvae produced a feeding ring. Stem-feeding damage of laboratory-reared larvae was typically less extensive than that observed in the field. Body length of the fourth-instar, lab-reared larvae was 12.8 ± 1.0 mm. Larval development time from initial detection of a first instar to pupation was 33 ± 0.3 days (range = 30–36 days). The larvae attached themselves with several strands of silk at the bottom of the cup, on the side of the cup, or to a piece of *B. tinctoria* before pupation.

Ant associations. Of the 198 late-instar *C. irus* larvae found at the four field sites between 2003 and 2005, 55 (28%) were observed interacting with ants (Table 1). We collected 13 ants from the dorsal surface of 13 different *C. irus* larvae at two of the sites between 1 and 15 July 2005. Specimens were preserved in 70% ethyl alcohol, identified to species and deposited at the University of Connecticut Insect Collection. The 13 specimens consisted of five ant species, of which only one, *Tapinoma sessile* (Say, 1836), was collected at both sites (Table 1). Due to small sample size, we likely underestimated the number of ant species associating with *C. irus* larvae across sites.

We observed ants interacting with *C. irus* larvae in the field for several minutes and interpreted and categorized the interactions according to the descriptions in Pierce *et al*. (2002). We classified all but one ant association as loose facultative and mutualistic, though it is unknown whether the ants defended the larvae from predators or parasitoids. The single non-mutualistic association observed was predatory, and consisted of 10–20 ants (species undetermined) overwhelming and killing a single *C. irus* larva.

We typically observed ants on the dorsal surface of late-instar larvae with their heads proximal to the larva's posterior end in the area of the seventh abdominal segment and dorsal nectary organ (Fig. 3). We never observed ants associating with early-instar larvae. Ant-tended larvae were often located on the main stem of a host plant, feeding on the epidermal and cortex tissues, or resting. Ants frequently circled the dorsal surface of a larva, intermittently stopping to tap the larva with their antennae or mouthparts. Ants often approached the larva's head and then returned to the area of the seventh abdominal segment, presumably to receive a secretion from the dorsal nectary organ. One to several ants often tended a single larva for several minutes. In one case we observed a single ant (*Formica dolosa* Buren, 1944) tending a larva for over two hours, but such long-term observations were seldom performed for logistical reasons.

DISCUSSION

The outer tissue of the stem of *B. tinctoria* is presumably more difficult to consume and digest, and lower in nutrients than newly-flushed apical leaves. Therefore it seems likely that the nearly universal behavior of stem-feeding among late-instar *C. irus* larvae serves a purpose other than directly deriving nutrition from stem tissue. We hypothesize two possible benefits to larvae following stem girdling of *B. tinctoria*: 1) increased access to water and carbohydrates; and 2) improved feeding conditions due to deactivation of an induced phytochemical defense.

Access to water and carbohydrates. The "honeydew" secreted by the dorsal nectary organ of lycaenid larvae provides ants with water containing a

Table 1. Listed ant species were observed associating with late-instar *Callophrys irus* larvae on *Baptisia tinctoria* at two study sites in 2005. Ant specimens were collected from the dorsal surface of *C. irus* larvae and preserved for later identification. Total number of late-instar larvae found from 2003 to 2005, and the number of larvae associated with ants at each of four study sites, is given in the last row of the table.

Species of ant (Formicidae)	Crane WMA	Gavins Pond MWA	Myles Standish SF	Noquochoke WMA
Crematogaster lineolata (Say, 1836)		X		
Formica dolosa (Buren, 1944)				X
Lasius neoniger (Emery, 1893)		X		
Tapinoma sessile (Say, 1836)		X		X
Tetramorium caespitum (L., 1758)				X
Total larvae (total ant-associated larvae)	47 (7)	109 (26)	11 (1)	31 (21)

Fig. 3. *Formica dolosa* in a typical position on the dorsal surface of a late-instar *Callophrys irus* larva. The ant's head is positioned proximal to the larva's dorsal nectary organ. The larva is at the base of a *Baptisia tinctoria* stem.

relatively high concentration of carbohydrates and amino acids (Pierce *et al*. 2002). Growing caterpillars also need carbohydrates, amino acids, and other nutrients, and water obtained from food is often at a premium (Slansky 1993). This is especially true for larvae of *C. irus*, because their habitat is typically very dry and warm during the latter half of larval development. It therefore seems likely that *C. irus* larvae girdle the stem of their host plant in order to tap phloem sap, thereby obtaining additional water and nutrients. Although phloem sap could be obtained by simply chewing a hole in the stem, complete girdling of a vascular plant stops phloematic flow back to the roots, resulting in accumulation of carbohydrates (soluble sugar and starch) in the portion of the plant above the girdle (Noel 1970).

Therefore, stem-girdling of *B. tinctoria* by *C. irus* probably provides both phloem sap and leaf tissue with greater concentrations of carbohydrates. The larva obtains these carbohydrates (and water) by consuming phloem sap at the girdle, and by periodically ascending the plant to consume leaves. Water, amino acid, and protein content of the leaves remains the same because water and nitrogen transport from the roots through the xylem is unaffected by girdling (Noel 1970). Although herbivore growth is usually limited by dietary nitrogen (Mattson 1980), *B. tinctoria* is a nitrogen-fixing legume and its leaves presumably have a relatively high nitrogen concentration (especially the young, growing leaves preferred by *C. irus*). Therefore larvae may be more limited by access to carbohydrates. Larval consumption of excess water and carbohydrates may allow production of honeydew without adversely affecting their own growth and metabolism by compensating for the loss of these resources. The greater availability of water and carbohydrates may also enable larvae to produce honeydew in greater quantity or of higher quality (greater carbohydrate concentration), thereby attracting a larger "standing guard" of ants to protect them from predators and parasitoids (Pierce *et al*. 2002).

Deactivating phytochemical defense. Plants have a diversity of chemical defenses (Arnason *et al*. 2004), and the mechanism of these defenses may be either direct, such as toxicity to an herbivore, or indirect, such as release of volatile chemicals that attract parasitoids (Turlings & Wäckers 2004). Furthermore, phytochemical defenses may be either constitutive (always expressed in the plant), or induced (expressed following an herbivore attack). While many induced defenses are synthesized locally in the tissue damaged by an herbivore, some involve a long-distance signal-transduction pathway that triggers transport of a defensive compound from another part of the plant (Karban & Baldwin 1997). One such example is the induction of nicotine defense in tobacco (*Nicotiana* spp.). When the leaves of a tobacco plant are damaged, a chemical signal is sent from the leaves, via the phloem, to the roots of the plant where nicotine is synthesized. This signal results in a dramatic increase in the amount of nicotine exported from the roots, through the xylem, back to the leaves. Karban & Baldwin (1997) note that an herbivore could "short-circuit" such a defense by girdling the plant, thereby blocking the phloem-borne signal from leaves to roots. We suggest that *C. irus* larvae may girdle *B. tinctoria* stems to deactivate a phytochemical defense induced by leaf consumption. Since only late-instar larvae girdle the host plant, induction of such a defense may require more extensive tissue damage than produced by early-instar larvae. It is also possible that the fresh leaf tissue fed upon by early-instar larvae is low in defensive compounds, and if a plant is not girdled by the time larvae are in final instars, the plant will have synthesized and accumulated a sufficient concentration of defensive compounds to be detrimental to larvae.

These two hypotheses are not mutually exclusive. For example, it is possible that stem-girdling by *C. irus* larvae reduces attack rate by parasitoids via three separate yet simultaneous mechanisms: 1) reduction in larval development time due to increased consumption of nutrients; 2) increased protection from ants due to a greater quantity and quality of honeydew produced; and 3) deactivation of an induced indirect defense of the host plant.

We recommend that further research be conducted on the adaptive significance of host plant stem-girdling by *C. irus* larvae. Nutritional analysis of *B. tinctoria* tissues pre- and post-girdling, and investigation of how

this behavior affects the production, transport, and storage of both nutrients and defensive chemicals in *B. tinctoria* plants would be informative. Further experiments would be needed to link host plant physiology with larval development and survivorship. To further understand the role and importance of ant association in *C. irus*, we recommend more widespread documentation of associated ant species and more detailed observations of larval interactions with ants.

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