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A Scattershot Approach to Host Location: Uncovering the Unique Life History of the Trigonalid Hyperparasitoid *Orthogonalys pulchella* (Cresson)

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Trigonalid wasps are a remarkable group of hyperparasitoids with a curious strategy for locating their hosts. While most parasitoids and hyperparasitoids lay their eggs directly on or in their host, trigonalids lay their eggs on foliage, where these eggs are incidentally ingested by herbivorous insect hosts. Other parasitoids have adopted this "scattershot" approach to host location, but their larvae consume their herbivorous host after hatching in the herbivore's digestive tract. Trigonalids, however, require a third party; larval development requires that the host herbivore simultaneously host a (primary) parasitoid larva of another species. Although the framework for this unusual life history has been described previously, the identities of the herbivorous and parasitoid hosts of trigonalids have remained elusive. Here we present the first host records for the temperate trigonalid hyperparasitoid *Orthogonalys pulchella* and discuss the evolution of this unusual life history strategy.

Trigonalid wasps are hyperparasitoids that are intimately associated with three other organisms over the course of their life cycle: host plant, host caterpillar, and host primary-parasitoid larva. Female trigonalids lay their numerous eggs on foliage (host plant) almost at random in what we call a "scattershot" approach. These eggs are incidentally consumed by herbivorous caterpillars (host caterpillar) as they feed on the host plants. For the trigonalid larva to survive, the host caterpillar has to be parasitized by another parasitoid species (host primary-parasitoid); the trigonalid larva then completes its development by feeding on the host primary-parasitoid (Fig. 1). Hyperparasitoids have not been well studied (Hawkins 1994, Brodeur 2000) and the life histories of trigonalids in particular are almost completely unknown (Carmean and Kimsey 1998). For most trigonalids, it is a mystery as to which hosts (plant, herbivore, and primary-parasitoid) they use in nature. In this article, we present the results of natural history fieldwork in which we were able to elucidate, for the first time, what host plants, host caterpillars, and host primary-parasitoid the trigonalid *Orthogonalys pulchella* uses to complete its development.

Background on Parasitoid Biology

Parasitoids are insects that, as larvae, feed on the bodies of other living arthropods. Similar to predators, parasitoids kill their prey; this differentiates them from many parasites. Unlike predators, which require numerous prey items to survive and complete their development, a parasitoid larva requires only a single host to complete its development; in this regard, parasitoids are more similar to parasites than predators (Godfray 1994). Most parasitoids belong to one of two insect orders, the Hymenoptera (ants, bees, and wasps) and the Diptera (flies), although there are a few examples of parasitoids in the Coleoptera (beetles), Lepidoptera (butterflies and moths), and Neuroptera (lacewings) (Godfray 1994). Most parasitoids are fairly host-specific, and this feature appears to be associated with high rates of evolutionary diversification (Hochberg and Ives 2000).

In general, an adult female wasp or fly parasitoid will locate a host and lay one to many eggs either on the host or within it using her ovipositor. An astounding array of host location strategies and modes of attack exist, however, making parasitoids excellent subjects for comparative study of insect evolutionary ecology. Moreover, the important ecological roles played by parasitoids in suppressing herbivore populations in natural and agricultural systems highlight their economic utility as biological control agents (e.g., Cardinale et al. 2003).

Parasitoids feed either internally (endoparasitoids) or externally (ectoparasitoids) on their host and exploit a variety of insects and life stages. Parasitoid species are often categorized by which life stage they attack (e.g., the egg, larva, pupa, or adult stage of a typical holometabolous insect); the life stage that is killed by the developing parasitoid sometimes differs from the life stage that was attacked (e.g., larval–pupal parasitoids oviposit in larvae but emerge and kill host pupae). Parasitoids have been reared from herbivores in all feeding guilds, including leaf chewers, sap feeders, gallers, borers, and root feeders. Concealed feeders, gall formers, and leaf miners tend to experience exceptionally high attack rates from parasitoids compared with other feeding guilds (Hawkins 1988; Hawkins 1994), but all feeding guilds are attacked to some extent.

Indeed, some parasitoids even prey upon other parasitoids as "hyperparasitoids" or "secondary parasitoids." Most hyperparasitism occurs when a parasitoid lays her egg in an insect that is currently host to another parasitoid, referred to as the primary parasitoid. Facultative hyperparasitoids are capable of feeding on both herbivore and primary-parasitoid tissues whereas obligate hyperparasitoids feed exclusively on the primary parasitoid and cannot complete development on unparastized hosts. In contrast to the pattern observed for primary parasitoids, herbivores that feed externally on plant tissue (leaf chewers, rollers, and webbers) are attacked by more hyperparasitoid species than are herbivores that feed internally on plant tissue (leaf miners, gallers, and borers) (Hawkins 1994). Primary parasitoids are relatively well studied, but hyperparasitoids have received comparatively little attention (Hawkins 1994, Brodeur 2000) even though they comprise an important component of the fourth trophic level in many terrestrial communities (Montoya et al. 2003) and are of interest because of their potential mitigating role in biological control efforts (Sullivan and Volkl 1999).

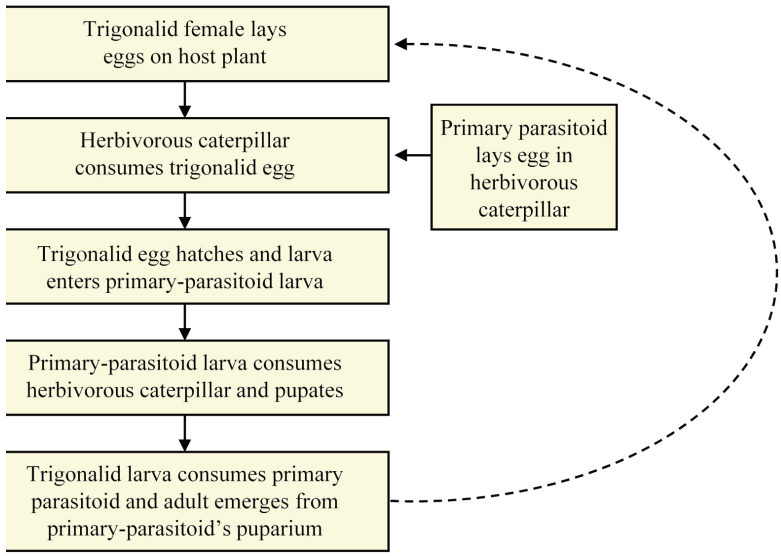

Fig. 1. A diagram describing the life stages of the trigonalid hyperparasitoid *Orthogonalys pulchella*.

Unique Life History of Trigonalid Hyperparasitoids

Members of the wasp family Trigonalidae have an extremely unusual life history that makes them interesting even among hyperparasitoids (Fig. 1). Unlike most parasitic hymenopterans, trigonalids do not lay their eggs in or on their hosts, but instead lay their eggs on a variety of plants and rely on appropriate herbivorous hosts to incidentally ingest their eggs as they consume the foodplant. Some trigonalids lay more than 10,000 tiny eggs to ensure that some of them will be ingested (Godfray 1994). The strategy of laying thousands of "microtype" eggs on foliage has evolved at least twice within the Tachinidae (Stireman et al. 2006), but these tachinid flies are strictly primary parasitoids whereas trigonalids are hyperparasitoids.

The trigonalid eggs will not hatch unless they are consumed by an herbivorous larva, usually a caterpillar or sawfly larva with a highly alkaline gut pH (Weinstein and Austin 1991). Although a few trigonalids may be facultative hyperparasitoids, most are obligate hyperparasitoids that must complete yet another complicated step once they have been ingested to finish their life cycle. At least one species of trigonalid in the western United States parasitizes vespid wasps. After the wasps attack a caterpillar that has ingested trigonalid eggs, they take the caterpillar back to their nest, where they feed it to their offspring; when the vespid offspring eat the dead caterpillar, they also consume the trigonalid larvae that are inside and become parasitized (Carmean 1991). Other hyperparasitoid trigonalids, including the one that we are studying, require that the herbivorous caterpillar that has eaten the egg from the foliage be either already or subsequently parasitized by a primary parasitoid, usually a tachinid fly or ichneumonid wasp, which will serve as the host for the developing trigonalid (Smith 1996).

It is unknown how the trigonalid larva gets into the primary parasitoid larva; the trigonalid larva may either be ingested by the primary parasitoid as it consumes the herbivore or the trigonalid larva may burrow through the herbivore's gut wall and then into the primary parasitoid (Weinstein and Austin 1991). Once the trigonalid larva has entered the primary parasitoid larva, however, the trigonalid halts development until the primary parasitoid has pupated (Weinstein and Austin 1991). The trigonalid then consumes the primary parasitoid and emerges from the primary parasitoid's puparium. A life history that relies on eggs being ingested by caterpillars is unusual in its own right, but to require that the herbivorous caterpillar is also parasitized by yet another parasitoid to complete development is remarkable.

Novel Host Records and Host Biology

As part of an ongoing project investigating diet evolution of caterpillars in the family Limacodidae, we have reared field-collected caterpillars in the laboratory for the past several years; many of the caterpillars are parasitized by tachinid flies and hymenopteran wasps from a number of families. In eastern North America, the larvae of ~20 species of moths in the family Limacodidae feed during late summer and early autumn in deciduous forests (Covell 1984). The larvae of these species are well known for their unusual morphologies, which often include intricate color patterning and various types of protuberances on their dorsal surfaces (Fig. 2). Many species also possess stinging setae for all or a portion of their larval development (Dyar 1899) and can be quite painful to touch. Their common name, slug caterpillars, derives from their unusual locomotory habit, characterized by a high degree of ventral contact with the substrate, the use of abdominal "sucker" appendages in movement, and the secretion of semifluid silk that serves to enhance substrate contact (Epstein 1995). The larvae are also highly polyphagous, feeding on trees and shrubs in more than a dozen plant families, but appearing to favor plants with glabrous leaves (Epstein 1988, Wagner 2005, Lill et al. 2006). Smooth leaf surfaces are believed to facilitate caterpillar adhesion and movement upon leaf surfaces (Epstein 1995).

Although detailed host lists are generally not available for most species, common host plant genera of eastern North American limacodids include *Acer*, *Asimina*, *Betula*, *Carya*, *Cercis*, *Cornus*, *Fagus*, *Fraxinus*, *Malus*, *Nyssa*, *Ostrya*, *Prunus*, *Quercus*, *Salix*, *Sassafras*, and *Tilia*. The larvae are slow moving, have long development times (7–8 wk to pass

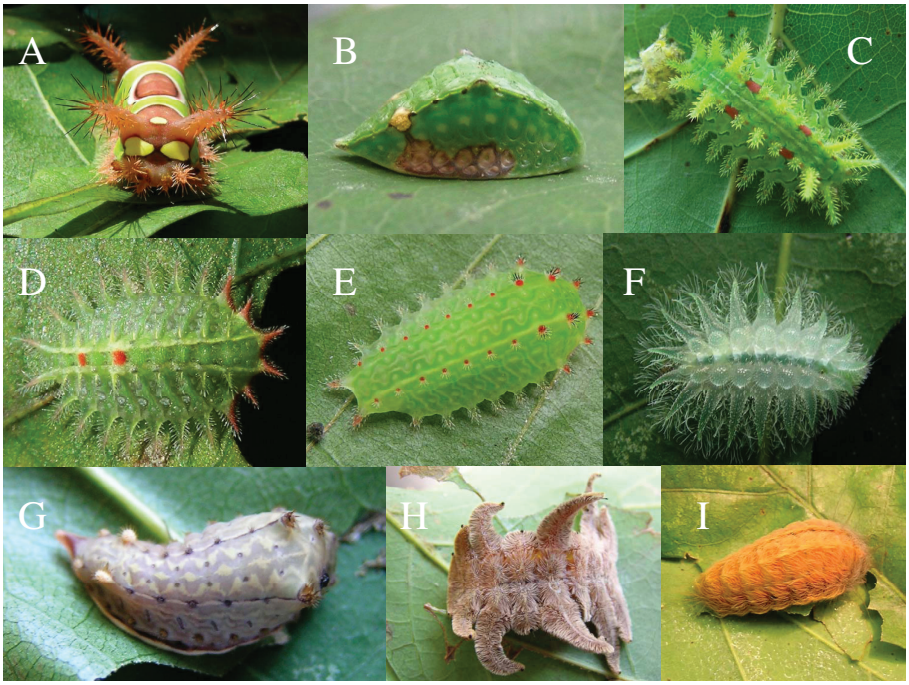

Fig. 2. Slug caterpillars are well known for unusual morphologies, which often include intricate color patterns and various types of protuberances on their dorsal surfaces: (A) *Acharia stimulea*, (B) *Prolimacodes badia*, (C) *Euclea delphinii*, (D) *Isa textula*, (E) *Natada nasoni*, (F) *Isochaetes beutenmuelleri*, (G) *Parasa chloris*, (H) *Phobetron pithecium*, and (I) *Megalopyge crispata*. Species A–H are members of the family Limacodidae; species I, *M. crispata*, belongs to the closely related family Megalopygidae.

through 6–10 instars; JTL, unpublished data), and are functionally restricted to a single plant for the duration of their development. Thus, while limacodids are generalists at the species level, individuals are in effect specialists.

When we collect a limacodid larva from the field, we can often tell if it has been parasitized by a hymenopteran parasitoid because the larva fails to grow and soon a single or several small wasps emerge from the deflated larva (wasps in the family Eulophidae are the most common parasitoids). By contrast, when we collect a limacodid larva that has been parasitized by a tachinid fly, there is some slight discoloration on the dorsum, but the host larva continues to grow, completing most of its development before the tachinid larva consumes the host, emerges, and pupates (Fig. 3A). The tachinid adult usually emerges the following spring (Fig. 3B). Sometimes, however, instead of a tachinid adult, a large trigonalid wasp, *Orthogonalys pulchella* (Cresson) (Trigonalidae), emerges, usually after overwintering inside the tachinid puparium (Fig. 4). One individual *O. pulchella*, therefore, is intimately associated with at least three other organisms over the course of its life cycle: host plant, host caterpillar, and host primary—parasitoid larva.

For 13 years, Smith (1996) collected almost 4,000 *O. pulchella* adults in Malaise traps in eastern forests. While much was learned about the habitats in which *O. pulchella* are likely to be found, it was not known what species of Lepidoptera they used as hosts. There is only a single record in the literature of an *O. pulchella* specimen for which the tachinid host has been identified (*Archytas aterrimus* Robineau-Desvoidy), but there is no information about what caterpillar species the tachinid had parasitized (Carlson 1979). Of the thousands of pinned *O. pulchella* specimens in the National Museum of Natural History entomology collection (Smithsonian Institution, Washington, DC), not a single specimen has a host record to indicate what type of caterpillar or tachinid species it used as hosts. It is not uncommon for host records to be unknown for trigonalid specimens, and very little is known about their biology in general (Carmean and Kimsey 1998). Indeed, hosts are known for <20% of the almost 100 trigonalid species found worldwide (Carmean 1991).

Since 2003 we have collected seven *O. pulchella* individuals from three sites in the Washington, DC, metropolitan area (Table 1). We reared these individuals from caterpillars that we collected from the field, and thus we know for the first time what species of lepidopteran larva *O. pulchella* parasitize and even what food plant the larva was feeding on when it was parasitized because limacodids rarely move between trees as larvae (JTL and SMM, unpublished data). We reared *O. pulchella* from four caterpillar species in

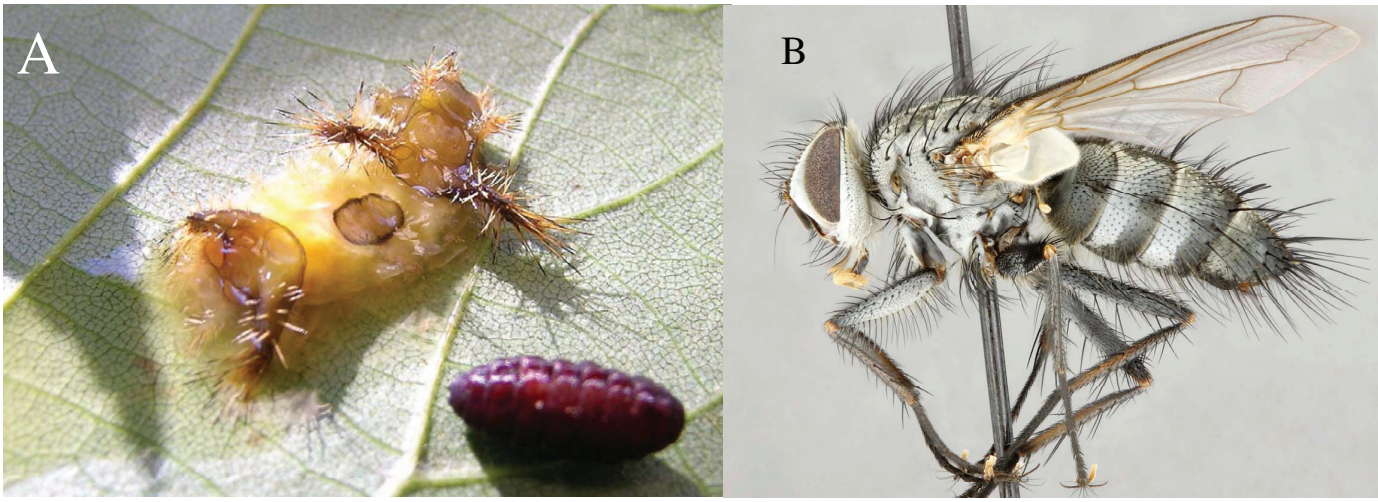

Fig. 3. (A) The remains of an *Acharia stimulea* caterpillar that was parasitized by *Uramya pristis*, a tachinid fly that has pupated next to the caterpillar. (B) A pinned *Uramya pristis* adult. Photo credit: Katja Seltmann, Morphbank.

Fig. 4. A pinned *Orthogonalys pulchella* adult. Photo credit: Katja Seltmann, Morphbank.

three families: Limacodidae, Megalopygidae (a sister family to the Limacodidae), and Noctuidae. We now know that *O. pulchella* females lay their eggs on at least four plant species: American beech (*Fagus grandifolia* Ehrh.), chestnut oak (*Quercus prinus* L.), white oak (*Quercus alba* L.),. and red oak. We can also add a second name to the list of tachinid fly species that serve as hosts for *O. pulchella*. From all of our field collections, we have only found one species of tachinid that is a larval parasitoid of eastern Limacodidae, *Uramya pristis* (Walker); we have successfully reared three dozen individuals of this fly species from an assortment of Limacodidae hosts. All of our *O. pulchella* adults have emerged from *U. pristis* pupae. There is a second tachinid parasitoid *(Austrophorocera* n. sp.*)* that attacks Limacodidae, but it is a larval–pupal parasitoid (it parasitizes the larva but emerges from the caterpillar's pupa the following spring). To date, no *O. pulchella* have emerged from *Austrophorocera*; additional rearing efforts are needed, however, to determine the host range of *O. pulchella* within the Limacodidae.

All but one of our *O. pulchella* adults emerged from tachinid pupae that had attacked caterpillars we collected late in the season (late August, early September); in each case, the *O. pulchella* larva overwintered inside the tachinid puparium before it killed its host and emerged the following summer. In 2007, however, we collected an *Acronicta increta* (Noctuidae) caterpillar on July 19, a tachinid emerged from the larva and pupated on July 23, and then an *O. pulchella* adult emerged from the tachinid puparium later that same summer (the exact date is unknown because we were not expecting this and were not monitoring this container closely). *O. pulchella* has always been thought to be univoltine, but this single host record suggests that it may sometimes be bivoltine. Because we reared this individual from an *A. increta* larva that we collected in July, we know that the parasitoid's mother was flying sometime between May and early July. Our reared *O. pulchella* emerged later that same summer and thus, in the wild, would have been part of the second flight and would have had the opportunity to hyperparasitize late-season lepidopteran larvae, such as limacodids or the fall generation of *A. increta*.

The hyperparasitoid *O. pulchella* presumably attacks a variety of lepidopteran larvae, likely from other families in addition to the three we have documented; in this sense, it may be considered a generalist. *O. pulchella* is constrained, however, in that it cannot complete development without a tachinid host. In the collections of *O. pulchella* at the National Museum of Natural History, the size of the adult specimens varies greatly (4.0–10.2 mm; head and body, antennae excluded); the size of an individual wasp is likely to be determined directly by the size of its tachinid host and indirectly by the size of its herbivore host if tachinid size is also resource dependent. Because of their passive approach to host location, some degree of developmental plasticity is expected in trigonalids, which would allow them to complete development on a range of hosts that vary in size and nutritional quality.

Evolution of an Unusual Life History

How might such an unusual and risky life history have evolved? The optimum lifetime fecundity (number of eggs) for most species of parasitoids is predicted to converge on the maximum number of unparasitized hosts a female is likely to encounter during her lifetime (Godfray 1994). Yet trigonalids, along with the many tachinid fly species that use a similar strategy of laying "microtype" eggs on vegetation instead of on or near herbivorous hosts (Stireman et al. 2006), benefit by inundating their environment with eggs. For these species, the more eggs a female lays, the greater the odds that at least a few of her eggs will be ingested by an appropriate host. Although this scenario readily explains the large number of laid eggs recorded for trigonalids, the details of how the "scattershot" approach to host location evolved (i.e., ovipositing without regard to potential host cues such as leaf damage) is as yet unresolved. For tachinids, it has been suggested that laying eggs on foliage

Table 1. Host records for the seven *Orthogonalys pulchella* specimens that we have collected.

Date Collected	Field Site[a]	Larval Host Species[b] (Family)	Food plant	Emergence year
9/9/03	PNWR	*Megalopyge crispata* (Megalopygidae)	White oak	2004
9/6/05	PNWR	*Isochaetes beutenmuelleri* (Limacodidae)	Beech	2006
8/29/05	RCP	*Isa textula* (Limacodidae)	Chestnut oak	2006
9/15/06	RCP	*Isa textula* (Limacodidae)	Chestnut oak	2007
9/15/06	RCP	*Isa textula* (Limacodidae)	Chestnut oak	2007
7/19/07	LBRP	*Acronicta increta* (Noctuidae)	Beech	2007
9/6/07	LBRP	*Isa textula* (Limacodidae)	Red oak	2008

[a]PNWR, Patuxent National Wildlife Refuge (Beltsville, MD); LBRP, Little Bennett Regional Park (Clarksburg, MD); RCP, Rock Creek Park (Washington, DC).
[b]The larval host species is the identity of the larva that originally ate the *O. pulchella* egg after it was laid on the larval host food plant. The larval host was either already or subsequently parasitized by a tachinid fly, and it is from the pupal case of the tachinid that the *O. pulchella* adult emerged.

may have originally evolved as a means of attacking otherwise inaccessible hosts, such as nocturnal or well-defended caterpillars; in addition, this strategy is hypothesized to reduce the amount of time a female needs to spend searching for hosts and the risk of injury during host encounters while ovipositing (Stireman and Singer 2003). As the life history details for additional species of trigonalids are uncovered, taxa comparisons within a phylogenetic framework may shed light on this question for the Trigonalidae as well.

How hyperparasitism may have evolved is a little more straightforward, and Godfray (1994) suggests two possible routes to becoming an obligate hyperparasitoid. Obligate hyperparasitoids may have evolved from facultative hyperparasitoids that fed on the herbivorous host and/or the primary parasitoid if the host was parasitized. The step from facultative to obligate hyperparasitoid requires only that the parasitoid lose the ability to feed on the herbivorous host, which would most likely occur when host parasitism by other primary parasitoids is frequent. Alternatively, obligate hyperparasitoids may evolve by means of a host shift; they may have shifted from being a primary parasitoid of an herbivorous host to a hyperparastoid of a primary parasitoid that is closely related to the original herbivorous host. For instance, hyperparasitoids that attack hymenopteran primary parasitoids may have evolved from primary parasitoids of sawflies, which are also members of the Hymenoptera. Given the phylogenetic diversity of hyperparasitoids, hyperparasitism is likely to have multiple evolutionary origins and may have evolved through other, more complicated mechanisms (Brodeur 2000). Whatever the mechanism, feeding on a member of a higher trophic level, such as a primary parasitoid instead of an herbivore, may be advantageous because of the increased nutritional quality of carnivorous hosts relative to herbivorous hosts (Denno and Fagan 2003).

Studies such as ours demonstrate that relatively simple rearing experiments can lead to new discoveries, often in unpredictable ways. Through our focused rearing efforts, we expected to learn more about host plant use by limacodids but did not realize that we would also be able to fill in a significant gap in knowledge about the natural history of *O. pulchella*. Given the paucity of information about hyperparasitoids in the literature and the limited number of host records, our data greatly enhance understanding of the natural history of *O. pulchella* in particular, but also of trigonalid hyperparasitoids in general.

Acknowledgments

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Appendix: Methods, Field Sites

We collected larvae from three field sites in the Washington, DC, metropolitan area: Patuxent National Wildlife Refuge (Beltsville, MD), Little Bennett Regional Park (Clarksburg, MD) and Rock Creek Park (Washington, DC). Patuxent National Wildlife Refuge (PNWR) is the nation's only designated research refuge. Owned and operated by the U.S. Fish and Wildlife Service, it encompasses more than 5,000 ha of forest interspersed with meadows and wetlands; it is one of the largest remaining forested areas in the mid-Atlantic region. Second-growth stands of oak–hickory and beech forest are common on the refuge, along with more mesic and riparian species such as pawpaw, box elder, willow, and sweetgum. Common understory trees include black cherry, sassafras, redbud, black gum, and saplings of oaks, hickories, and beech.

Little Bennett Regional Park (LBRP) is part of the Montgomery County Park system and is run by the Maryland–National Capital Park and Planning Commission. The park encompasses 1,500 ha of forest, meadow, and riparian habitat. Similar to the forest at PNWR, black cherry, black gum, saplings of oaks, hickories and beech are all common in the understory.

When Rock Creek Park (RCP) was founded in 1890 by the National Park Service, it was on the edge of Washington, DC; today Rock Creek Park is an urban park composed of 710 ha of woodland surrounded by the District of Columbia. The forest is a mix of riparian and upland tree species and is topographically quite heterogeneous. Of the upland tree species found in the higher elevations of the park, there are numerous white oaks, hickories, beeches, and maples.

Field Sampling

During the field season, from July through October, with the help of our field crew, we manually search foliage at least twice a week for limacodid caterpillars at our two main field sites (LBRP and PNWR). Our other site (RCP) is sampled more haphazardly. We primarily search the foliage of six focal plant species: American beech (*Fagus grandifolia* Ehrh.), white oak (*Quercus alba* L.), northern red oak (*Quercus rubra* L.), black cherry (*Prunus serotina* Ehrh.), black gum (*Nyssa sylvatica* Marsh), and pignut hickory (*Carya glabra* Mill.). Each of these species is a known host for a variety of limacodid caterpillar species.

We record the local density of limacodids on each host plant (larvae/m^2 foliage). Whenever we find a limacodid larva, we record its size at collection, which serves as an estimate of larval instar and age (JTL and SMM, unpublished data). We then take it to the laboratory to allow it to complete development.

Laboratory Rearing

Limacodid larvae are reared in the laboratory on excised foliage from their natal host plant. Foliage is replaced as needed, at least every 2–3 d. Each larva is placed in an individual 16-oz. deli container and is monitored regularly until one of four fates arises: the larva dies, hymenopteran parasitoid(s) emerge, a tachinid larva emerges and pupates, or the larva successfully completes development and pupates. Moist peat is added to the tachinid and limacodid pupal containers, and the containers are placed in an environmental growth chamber (Percival Scientific, Perry, IA) where they overwinter (0:24 L:D, 4°C). The following spring, we remove the pupae from the growth chambers and allow them to emerge in the laboratory. For the limacodids, we record whether the pupa has died or emerged as an adult. For the tachinid pupae, we record whether the pupa dies, a tachinid emerges, or a hymenopteran hyperparasitoid (*O. pulchella*) emerges.

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