POSSIBLE FUNCTION OF SPATULATE SETAE SURROUNDING THE PAPILLAE ANALES OF SAROTA BUTTERFLIES (RIODINIDAE: HELICOPINI)

Additional key words: Camouflage, Costa Rica, Ecuador, epiphylls, oviposition

Lepidopteran eggs can face high levels of mortality due to a variety of factors including environment, predators, and parasitoids (e.g., Hilker 1994; Obermaier et al. 2006; Sansone & Smith 2001). Ovipositing females are thought to show various traits that may help escape these pressures, including egg placement, shell toxins, and chemical crypsis (e.g., Obermaier et al. 2006; Scoble 1992).

During the course of fieldwork in Central and South America, we observed oviposition by several species of Sarota (Riodinidae) butterflies. As far as is known, larvae of this genus feed on tiny epiphyllic lichens, mosses, and liverworts growing on the surface of tropical leaves (DeVries 1988, 1997). We observed a distinctive behavior associated with egg laying in S. subtessellata (Costa Rica, n = 1), S. gyas (Ecuador, n = 2), and S. chrysus (Ecuador, n = 1). After landing on a leaf, females walked slowly across its surface, dragging the tips of their abdomens, sometimes for up to five minutes before depositing an egg (Fig. 1). They occasionally walked to the lower surface of the leaf, sometimes pausing for several minutes, but always returning to oviposit on the upper surface. Upon close examination of the eggs, we noted that each was entirely covered with scraps of epiphylls glued to the chorion. Subsequently, when observing the external morphology of female genitalia of these and other Sarota spp., we noted the obvious presence of strange, stiff, apically-re curved, spatulate setae surrounding the papillae anales. These have been described and illustrated by Hall (1998), though he indicated their function remains a mystery. Although these setae are considered a synapomorphy of the Helicopini, encompassing Helicopis, Sarota, Anteros, and Ourocnemis (Hall 1998), similar structures are present in some moths in the Geometridae and Tortricidae (Pellmyr 1980; Scoble 1992). For Sarota, we also clearly observed the spine-like setae described by Hall (1998), located between the spatulate setae and the ostium bursae.

In at least one tortricid moth these spatulate scales are considered to facilitate covering eggs with debris (Scoble 1992). In concert with these assertions, our observations strongly suggest that spatulate and spine-like scales and setae of Sarota are used to scrape and gather scraps of epiphylls, which are then glued to the egg. This behavior likely provides effective visual and chemical camouflage for eggs deposited on their epiphyll-covered oviposition substrates. Future observations and experiments on the covering of eggs with debris by lepidopterans may yield important clues as to the effectiveness of this behavior in deterring ants and/or egg parasitoids. Similarly, observations on the function of these structures in other genera within the Helicopini may shed light on their evolutionary origin.

ACKNOWLEDGEMENTS

We thank J. O. Stireman III for help with literary sources and J. P. W. Hall for confirmation of species identifications. We are grateful to the owners and staff of La Selva Lodge and Hakuna Matata Lodge for their hospitality in Ecuador, and the Smithsonian Tropical Research Institute for support in Panama. HFG acknowledges the support of Matt Kaplan & John V. Moore. This study was funded in part by NSF grants DEB-0346729 and DEB-0527441. This is publication no. 193 of the Yanayacu Natural History Research Group.

LITERATURE CITED

Scores of insects use the resources provided by goldenrod plants (Solidago spp.). In the Finger Lakes Region of New York alone, Root & Cappuccino (1992) documented 138 species of insects that feed on leaves, stems, or sap of tall goldenrod, Solidago altissima L. With its prodigious flowering display in late summer and early autumn, S. altissima is also visited by numerous species of pollen-, nectar-, flower-, and seed-feeding insects (Gross and Werner 1983; Sholes 1984). Therefore, I was not surprised during my studies of goldenrod in Virginia to see adults of the red-spotted purple, Limenitis arthemis astyanax, making repeated visits to S. altissima in early September—until I realized that the plants had yet to open any flowers. A closer examination of the interaction revealed a very unusual behavior: The butterflies were imbibing spittle excreted by the nymphs of spittlebugs (Cercopidae) that were abundant on S. altissima (Fig. 1).

Adults of the genus Limenitis are known to have rather eclectic feeding habits. In addition to nectar, they also feed on rotting fruit, dung, and carrion (Downes 1973). They have also been reported to feed on sap exuding from woodpecker holes in trees and on honeydew excreted by aphids (Rosenberg 1989). However, there are apparently no previous reports of L. a. astyanax or any other species of butterfly, utilizing the excretions of spittlebugs. It is quite possible that this behavior has not been officially documented for any insect.

It might seem like a small step from feeding on aphid honeydew to spittlebug excretions, as both aphids and spittlebugs tap into the flow of plant sap and excrete copious amounts of liquid waste. However, the similarities end there. Aphids feed on phloem sap, which is rich in sugars manufactured by the plant through photosynthesis. Because aphids obtain more carbohydrates than they need from phloem sap, their excretions (honeydew) are rich in sugars. Many insects, most notably ants, are able to take advantage of this honeydew as a source of sugar.

In contrast to aphids, spittlebugs ingest xylem sap, which is relatively dilute, with small amounts of inorganic nutrients and amino acids and smaller amounts of sugar (Wieght 1964a; Horsfield 1977). Spittlebug nymphs introduce bubbles into their liquid excrement and cover their bodies with the foamy spittle, which may serve as protection from predation or dessication (Guilbeau 1908; Weaver and King 1954; Wieght 1964a; Whittaker 1970; Turner 1994). Spittlebugs extract most of the sugars and other nutrients from the xylem sap, such that spittle is expected to be of little nutritional benefit to other insects (Wieght 1964b). It has been suggested that the spittle may be toxic to other insects due to the presence of ammonia (Turner 2000).

The fact that L. a. astyanax repeatedly returned to spittle masses raises several questions. For instance, do the butterflies sip spittle to their own detriment, or do they gain a net benefit from it? If the latter, then what is the nature of the benefit? Are there undigested amino acids from the xylem or nutrients from decaying exuviae and small organisms trapped in the spittle, or do the butterflies simply use the spittle as a source of moisture? Would the costs and benefits of sipping spittle differ depending on the species of cercopid producing the spittle?

The most abundant spittlebug nymph on S. altissima in Virginia in September is the sunflower spittlebug (Clastoptera xanthocephala Germar), a rather polyphagous species that is best known for feeding on plants in the Asteraceae. Nymphs of two other cercopid species, Philaenus spumarius (L.) and Lepronyia quadrangularis (Say), are common on S. altissima during the late spring and early summer, but I have not observed...
L. a. astyanax visiting goldenrods when these spittlebugs were present. This difference in L. a. astyanax behavior may be caused by differences in the physical or chemical properties of the spittle created by the different species, or it may simply be a result of changing needs of the butterflies from spring to fall. Notably, the weather in the period in which I observed the spittle sipping was particularly warm and dry. Changes in plant size or chemical constituents of xylem as the season progresses could also affect the attractiveness of cercopid spittle to L. a. astyanax. It would be interesting to determine if the butterflies feed on spittle derived from plants other than goldenrods.

Finally, in order to characterize the ecological interaction among the butterflies, spittlebugs, and goldenrod, it would be necessary to know whether spittle sipping by butterflies affects the fitness of the spittlebug nymphs. My observations suggest that L. a. astyanax only takes a small proportion of available spittle per feeding bout from any given spittle mass, and thus a single visit is likely to have only a minor effect on the nymphs. If the butterflies were to return frequently, then they might shrink a spittle mass faster than the nymphs can replace it. In addition, a butterfly’s proboscis might disturb a nymph’s feeding, causing it to leave the spittle mass to relocate elsewhere on the plant. During the time period needed to re-establish its spittle mass, the nymph would be vulnerable to desiccation and predation (Wise et al. 2006). Clearly, the observation of spittle sipping by L. a. astyanax introduces a number of interesting physiological and ecological questions that will require further study to resolve.

ACKNOWLEDGEMENTS
I thank the University of Virginia’s Blandy Experimental Farm for providing housing and access to field sites. I also thank Netta Dorchin of the Museum Koenig in Bonn, Germany and the community of entomologists on the ENTOMO-L Listserv for anecdotes and leads to information regarding spittle feeding in insects.

LITERATURE CITED

LIFE HISTORY OF THE DOUBLE TUFTED WASP MOTH, DIDASYS BELAE GROTE
(EREBIDAE: ARCTINAE)

Additional key words: sedge, wasp mimicry, Fuirena

The Double Tufted Wasp Moth, Didasys belae Grote (Fig. 1), is one of eastern North America’s most beautiful tiger moths. Adults are scarce in collections, in large measure because the species is extremely local, but also because Didasys is believed to be diurnal or crepuscular and closely tied to its hostplant, Fuiarena scirpoidea Michaux (southern umbrella sedge). Despite the moth’s broad distribution in Florida, the early stages of Didasys were unknown prior to this report (Heppner 2007).

Didasys belae occurs from Monroe County north to Escambia County, Florida. There is also a specimen from Delchamps, Mobile County, Alabama collected in August 1933 (Vernon A. Brou, Jr. personal communication). While adults are seen in a variety of habitats, the species is most frequently encountered in marshlands (Kimball 1965) and other wetlands. The adults occur nearly year-round in southern Florida. JS discovered the larva by scouring a marsh along Lake Mary Jane in Orange County (Fig. 2), where the adults can be found flying or resting on various plants including the host. Larvae were found resting upon and were reared to maturity on Fuiarena scirpoidea. Below we describe the insect’s early stages, emphasizing the last instar larva, and provide notes on the insect’s life history.

Description of immature stages: Egg. 0.86–0.92 mm in diameter by 0.63–0.66 mm high (n=3), hemispherical, pale cream, without obvious surface sculpturing (Fig. 3). First instar. Pale red-orange, shiny, with long dark primary setae borne from raised pinacula; T2 thickened; D and SD setae on T2, T3, and A8 grouped onto a single pinaculum (Fig. 4). Middle instars. Ground color dark to nearly black with white dorsal and subspiracular stripes, both of which become obscure rearward of A8; both stripes may include ill-defined yellowish patches in intersegmental areas of the first eight abdominal segments; T1 with numerous forward-directed setae; T2 enlarged with hyper trophyed setae that extend well forward of head; A7 and A8 elongate, nearly half again as long as preceding segments; long, caudally directed setae on A8–A10 extend beyond abdominal terminus (Fig. 5). Last Instar. Length: 27 mm. Body modestly compressed dorsoventrally with prominent black and creamy yellow striping (Figs. 6, 7). Thick middorsal, broad lateral, and narrow subventral black stripes separate thick yellowish dorsal and mostly white subspiracular stripes. Yellow dorsal stripe includes both the D1 and D2 verrucae; mostly white subspiracular stripe narrower than dorsal and infused with more yellow. T1 with reduced secondary setae and verrucae. Dorsal verrucae fused on T2 and T3. T2 with subdorsal verrucae bearing elongate, black, splayed hairpencils that project forward of head. A9 and A10 with elongated black setae that project behind body; No setae gathered into pencils. Venter dusky orange on segments bearing legs and prolegs; intervening segments more yellow. Most setae pale but longer ones darkened at mid-length and becoming nearly black by apices. Setae with conspicuous barbs; elongate black setae somewhat feathery in appearance.

Life History Notes and Discussion. So far as known, southern umbrella sedge (Fuiarena scirpoidea) is the only host. We observed a female oviposit on this sedge and we have found six larvae perched on this...
plant in the wild. In 2007 we were able to rear a cohort of ex ova larvae through to maturity on southern umbrella sedge. Our efforts to switch the larvae to other sedges, grasses, or rushes were unsuccessful—larvae nibbled on *Carex stricta*, but straggled and died. Late instars perch conspicuously on stems, often about midway up a given stalk. In a crude fashion, the larvae resemble the white flower or seed heads of *Fuirena scirpoidea*. We are uncertain if larvae consume inflorescences, although one larva was found perched at the top of a stalk that showed signs of feeding. Larvae tend to occur in low numbers—we logged more than eight hours searching stems of southern umbrella sedge to recover six wild larvae.

Larvae displayed different defensive behaviors. When initially disturbed, caterpillars held their grip, but if further molested dropped to the ground and curled into a C or scurried off into vegetation, wedging their

body into a hideaway, in a fashion common to other ground-dwelling arctiines (see Wagner 2009). Some displayed an animated alarm response after being touched, repeatedly snapping the anterior end of their body back towards the caudal end of the body—a response that would surely dislodge small invertebrate natural enemies (e.g., parasitic flies or ants).

Females flew low to the ground in a fashion similar to the flight of some wasps seen in the same habitat. Males tended to fly higher but were also noted to land head down on scattered sedge and plant stems. JS saw one mating pair in the late afternoon in June of 2008. Mindy Conner observed a single adult male feeding at dusk on the roots of a dog fennel plant (*Eupatorium capillifolium*) that had been pulled and hung up at the Archbold Biological Station to attract *Cosmostoma myradora* (Dyar) and other PA-collecting arctiids (Goss 1979; Conner & Jordan 2009; Mindy Conner personal communication).

We saved a single cocoon for study. While we endeavored to carefully extract the pupa from the wispy cocoon, a large portion of the cocoon wall tore free, attached to the cremaster, when the shell was removed for study. Upon microscopic examination, we noted that silk and setae from the cocoon wall had been tightly wound about the base of the cremaster, indicating that the pupa had spun repeatedly (in a single direction) while in the cocoon. The extent to which this represents an anomalous observation, or an adaptive behavior to ensure that the pupa is locked into the cocoon wall or that larval setae accompany the pupa should the pupa be ripped free of the cocoon, is worthy of further investigation.

The prominent orange and black patterning of the pupal shell and open nature of the cocoon suggest that the pupa enjoys some form of either physical or chemical protection. Such is common among ctenuchids (Subtribe Euchromiina) (see Wagner 2009). The fact that the cocoon is spun exposed on a stem, rather than secreted among dense vegetation or litter, also suggests that the pupa (and/or cocoon) is somehow protected. The basis of any chemical protection that the caterpillars and pupae might enjoy, presumably, would be based on self-manufactured defensive substances, as sedges are not known to produce defensive substances that could be sequestered by arctine larvae.

**ACKNOWLEDGEMENTS**

DLW described the immature stages and prepared the text; JRS discovered the larva and hostplant, reared a cohort for *D. belae* larvae on umbrella sedge, and carried out the field work. Mindy and Bill Conner alerted JRS to the presence of *Didasys* at Archbold Biological Station, which catalyzed our efforts to discover the early stages of this seldom seen tiger moth. It was Don Stillwaugh that first discovered *Didasys belae* at the Lake Mary Jane site and who guided us to the marsh where the caterpillars were first found. Moria Robinson and one anonymous reviewer offered suggestions for improvements of an earlier draft. We thank Patti Anderson and Richard Weaver of the University of Florida Herbarium, who identified the plants mentioned in this note. Plates were assembled by Amy Fernald.

**LITERATURE CITED**


David L. Wagner, Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3043, USA; email: david.wagner@uconn.edu, and Jeff R. Slotten, Research Associate McGuire Center and FSCA, Gainesville, Florida. 5421 Northwest 69th Lane, Gainesville, FL 32653, USA; email: jslotten@bellsouth.net

Received for publication 21 July 2009, revised and accepted 14 January 2010.