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A FLORIDA CATERPILLAR AND OTHER ARTHROPODS INHABITING THE WEBS OF A SUBSOCIAL SPIDER (LEPIDOPTERA: PYRALIDAE; ARANEIDA: THERIDIIDAE)

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ABSTRACT

Caterpillars of *Tallula watsoni* Barnes & McDunnough regularly occur in the webs of the subsocial spider *Anelosimus studiosus* (Hentz) in south Florida. The caterpillars have not been found outside of the spider webs. Caterpillars feed on living and dead leaves that are on twigs incorporated into the webs of the spiders. A wide variety of trees and woody shrubs are accepted. In the laboratory caterpillars did not attack spiders or their prey. Spiders did not normally attack the caterpillars in the laboratory, but did so on two occasions. Pupation occurs in the spider web. We speculate that the spider web provides the caterpillars some protection from generalist predators and parasitoids. We suspect that *T. watsoni* is an obligate inquiline of *A. studiosus*. Other inquilines in the spider webs include 13 species of spiders and 10 species of insects. Two insects may have close or obligate relationships with *A. studiosus*: *Ranzovius clavicornis* (Knight) (Miridae), a scavenger, and *Zatypota crassipes* Townes (Ichneumonidae), a parasitoid of *A. studiosus*.

Key Words: *Tallula watsoni*, *Anelosimus studiosus*, inquilines, *Zatypota crassipes*.

RESUMEN

Los gusanos de *Tallula watsoni* Barnes & McDunnough a menudo se encuentran en las telas de la araña subsocial *Anelosimus studiosus* (Hentz) en el sur de Florida. Los gusanos no han sidos encontrados fuera de las telas de estas arañas. Los gusanos se alimentan sobre las hojas vivas y muertas sobre las ramas incorporadas dentro de las telas de las arañas. Una variedad amplia de árboles y arbustos estan asociados. En el laboratorio los gusanos no atacaron las arañas o sus presas. Normalmente, las arañas no atacaron los gusanos en el laboratorio, sin embargo paso en dos ocasiones. Los gusanos empupan en la tela de araña. Nosotros especulamos que la tela de araña provee a los gusanos con alguna protección de los depredadores y parasitoides generalistas. Nosotros sospechamos que *T. watsonie* es un inquilino obligado de *A. studiosus.* Otros inquilinos en las telas de estas arañas incluyen 13 especies de arañas y 10 especies de insectos. Dos insectos pueden tener una relación cercana u obligatoria con *A. studiosus*: *Ranzovius clavicornis* (Knight) (Miridae), un oportunista y *Zatypota crassipes* Townes (Ichneumonidae), un parasitoide de *A. studiosus*.

The insect world abounds with evolutionary opportunists stealing resources from fierce predatory arthropods. Camp-follower silverfish and wasps scurry beside raiding army ants (Hölldobler & Wilson 1990), milichiid flies land beside the fangs of spiders and sip the blood of crushed stink bugs (Eisner et al.1991), and satellite flies dart in to deposit larvae on the prey of fly-eating digger wasps (Evans 1966). This paper portrays another apparently risky relationship: a caterpillar that makes its home and finds its food in the communal webs of a subsocial spider.

Tallula watsoni Barnes & McDunnough (Fig. 1) is a moth in the subfamily Epipaschiinae of the family Pyralidae. It is known from Maryland through Florida (Adams 2003). To our knowledge, the only published host record is "larvae on oranges" (Kimball 1965), presumably referring to caterpillars feeding on orange tree foliage, not fruits. At the Archbold Biological Station (ABS) in south-central Florida we have repeatedly raised adult moths from caterpillars feeding on leaves incorporated into the webs of the spider *Anelosimus studiosus* (Hentz). This spider, whose range extends from New England to Argentina (Jones & Parker 2002), spins irregular, tangled webs in vegetation; at the ABS the webs are always on outer twigs of trees and shrubs. The web is begun by a single female, who is eventually accompanied by her offspring, including up to 50 individuals (Brach 1977, Furey 1998). The larger webs may be inhabited by inquilines, including a mirid bug, *Ranzovius clavicornis* (Knight), which scavenges on dead insects (Wheeler & McCaffrey

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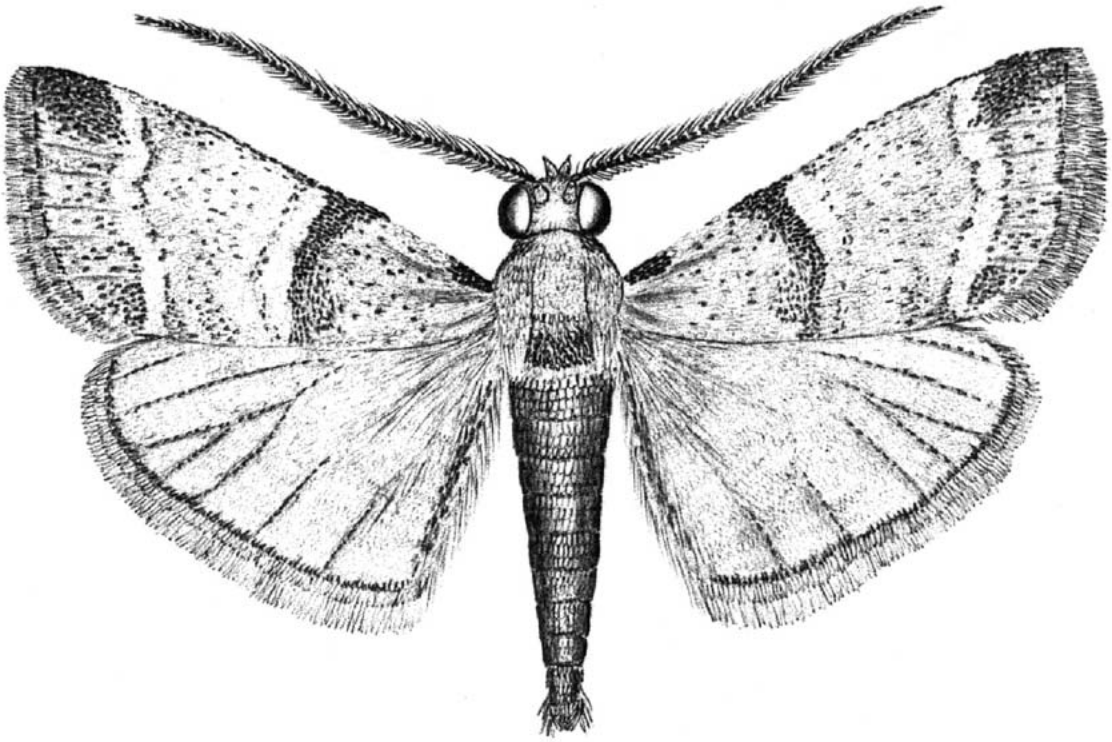


Fig. 1. *Tallula watsoni*, adult male; wingspread 16.0 mm.

1984). Vincent Brach, whose 1977 paper was based on work done at the ABS, mentions that the webs may be "shared by a host of other arthropods." The "pyralid webworms" that he found were almost certainly *T. watsoni*. In our paper we present some details of the natural history of *T. watsoni* and consider some implications of its inquiline life style.

Materials and Methods

The Archbold Biological Station, Highlands County, in south-central Florida has several plant associations where *A. studiosus* regularly occurs, including seasonal ponds with woody *Hypericum* species, Florida rosemary (*Ceratiola*) barrens, and oak scrub around the margin of a lake. For details of the vegetation of the ABS, see Abrahamson et al. (1984). Twenty-eight assemblages of spiders and caterpillars were kept in the laboratory by clipping the twigs in which the webs were constructed and placing the twigs in small jars of water. A plastic bag was placed over the twigs to maintain humidity and to retain the spiders' prey, wild-caught *Drosophila* sp. Caterpillars were also removed from the twigs and reared on foliage without spiders. Thirty-nine webs were removed from the field and completely dissected in the laboratory, with tabulation of the arthropod species found in the web system. Between February and April, 1997, we surveyed *A. studiosus* webs in the field for presence/absence of caterpillars. Parasitoids of the spiders also were surveyed.

Results and Discussion

Distribution of Caterpillars in the Field

At the ABS we disassembled and examined 503 webs of *A. studiosus*, of which 34 (6.8%) contained one or more caterpillars of *T. watsoni*; a total of 63 caterpillars were found. Up to four caterpillars occurred in a web system. Caterpillars fed on leaves from a wide variety of trees and shrubs whose leaves were incorporated into the spider webs. Plant hosts were: Empetraceae: *Ceratiola ericoides* Michaux; Fagaceae: *Quercus geminata* Small, *Q. chapmanii* Sargent, *Q. myrtifolia* Willdenow, *Q. virginiana* Miller; Myricaceae: *Myrica cerifera* L.; Asteraceae: *Baccharis halimifolia* L.; Ericaceae: *Lyonia fruticosa* (Michaux); Hypericaceae: *Hypericum edisonianum* (Small) Adams & Robson; Ulmaceae: *Celtis laevigata* Willdenow.

Behavior of Caterpillars and Spiders in Webs

The following observations on *T. watsoni* were made in the field and in the laboratory. Caterpil-

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lars in the field were associated with gnawed leaves and with frass caught up in the webbing. In the laboratory, caterpillars fed on dead leaves as well as living leaves. In the field, dead leaves that fell from shrubs into the spider webs sometimes showed damage and associated frass, as if the caterpillars had fed on them. In the laboratory, caterpillars made a loose network of webbing, both when isolated from spiders and when kept together with spiders. We never found caterpillars in the field that had set up webs independently, without spiders. Spiders and caterpillars were often adjacent to each other in a web (Fig. 2D); we do not know whether the spiders move into, or utilize in any way, the webbing spun by the caterpillars. In the laboratory, caterpillars apparently did not respond to spiders or their prey. They spent most of the day suspended motionless in the web, with the head cocked back in a distinctive way (Fig. 2C). On two occasions, when a caterpillar was being introduced into a spider colony, the spiders attacked and ate the caterpillars. Pupation occurs in the web (Fig. 2B); we observed no interaction between spiders and pupae. Adults emerging in the laboratory always escaped from the spiders' web. During the day, adults assume a characteristic posture with the wings partially furled (Fig. 2A). We did not observe mating or oviposition. Caterpillars are occasionally (five instances out of 63 caterpillars) attacked by a parasitoid wasp, *Apanteles* sp. (Braconidae). One caterpillar produced a parasitoid wasp in the family Chalcididae: *Brachymeria hammari* (Crawford). At the ABS this wasp has also been reared from *Antaeotrichia vestalis* (Zeller) (Oecophoridae), whose caterpillars make retreats of leaves sewn together with silk. *Brachymeria hammari* is a widely distributed species known to be a primary parasitoid of caterpillars in the families Pyralidae, Gelechiidae, and Tortricidae (Burks 1960).

As far as we know, *T. watsoni* is an obligate inquiline of *A. studiosus*, at least at the ABS. We also suspect that larval *T. watsoni*, unlike the mirid *Ranzovius clavicornis* studied by Wheeler & McCaffrey (1984), is exclusively phytophagous. There is no evidence that it scavenges on dead insects in the manner of caterpillars of *Neopalthis madates* Druce (Noctuidae) in the webs of the tropical social spider *Anelosimus eximius* Simon (Robinson 1977).

There is no reason to suspect that *T. watsoni* has any positive or negative effect on *A. studiosus*. The caterpillars contribute webbing that might entangle passing insects that then fall into the spiders' web, but it seems unlikely that this occurs to any significant extent, or that the ability to produce webbing is limiting to the spiders. The spiders often shelter or hide below leaves in the web, but we have not seen cases in which the caterpillars removed all such leaves, depriving the spiders of shelter. We offer no hypothetical adaptive reason why the spiders should tolerate edible caterpillars in their webs. The simplest hypothesis is that the caterpillars avoid triggering predatory responses, possibly by remaining motionless when the spiders approach. It is reasonable to suppose that communal spiders are somewhat less reactive to movement in their web than are solitary spiders (Wheeler & McCaffrey 1984). This would help explain the variety of inquilines, including *T. watsoni*, that inhabit webs of *A. studiosus* at the ABS (see list below).

It is easier to speculate about possible advantages and disadvantages of its peculiar life style to *T. watsoni*. An obvious disadvantage is that the polyphagous caterpillars forego all but a tiny fraction of potential host material by confining its consumption to vegetation within the web of a particular spider. There is also the possibility that some caterpillars may fall prey to spiders, or that they may restrict their feeding and movements in order to prevent triggering a predatory response from the spiders. An advantage to living in a spider web might be protection by the spiders and their web from local predators that may be reluctant to enter spider webs, such as certain Formicidae, Vespidae, Tachinidae, Ichneumonidae, Braconidae, and Chalcidoidea. While this seems a likely benefit, it has not been tested.

We provisionally classify *T. watsoni* in a general category of inquilines associated with well-defended hosts that are presumed to be defended by those hosts, even though studying the inquiline in the absence of its host is not practical. There are familiar examples of this, such as the relationship between clown fish and stinging sea anemones. There are four additional species of *Tallula* in North America, and it is possible that one or more of these species is free-living and could be used in a comparative study of relative mortality.

Other Inquilines of *A. studiosus* at the Archbold Biological Station

As mentioned by Brach (1977), a wide variety of arthropods can be found in the webs of *A. studiosus* and on the vegetation incorporated into the webs. At the ABS 39 webs were removed from the field and fully dissected, with all species of arthropods noted from each web. In the following list, the number following the name of an arthropod indicates the number of samples (out of 39) that had the arthropod listed; numbers of individuals are not tallied. Araneida: Araneidae: *Metazygia* sp. (3), *Eustala* sp. (1); Linyphiidae: *Florinda coccinea* (Hentz) (2); Salticidae: *Hentzia palmarum* (Hentz) (1), *Hentzia* sp. (5), *Peckhamia* sp. (1); Anyphaenidae, unidentified to genus (8); Clubionidae: *Castianeira* sp. (1); Theridiidae: *Dipoena* sp. (1); *Argyrodes trigona* (Hentz) (4); Tetragnathidae: undetermined to genus (6); Mimetidae: *Mimetus* sp. (2); Oxyopidae: *Peucetia viridans* (Hentz) (2);

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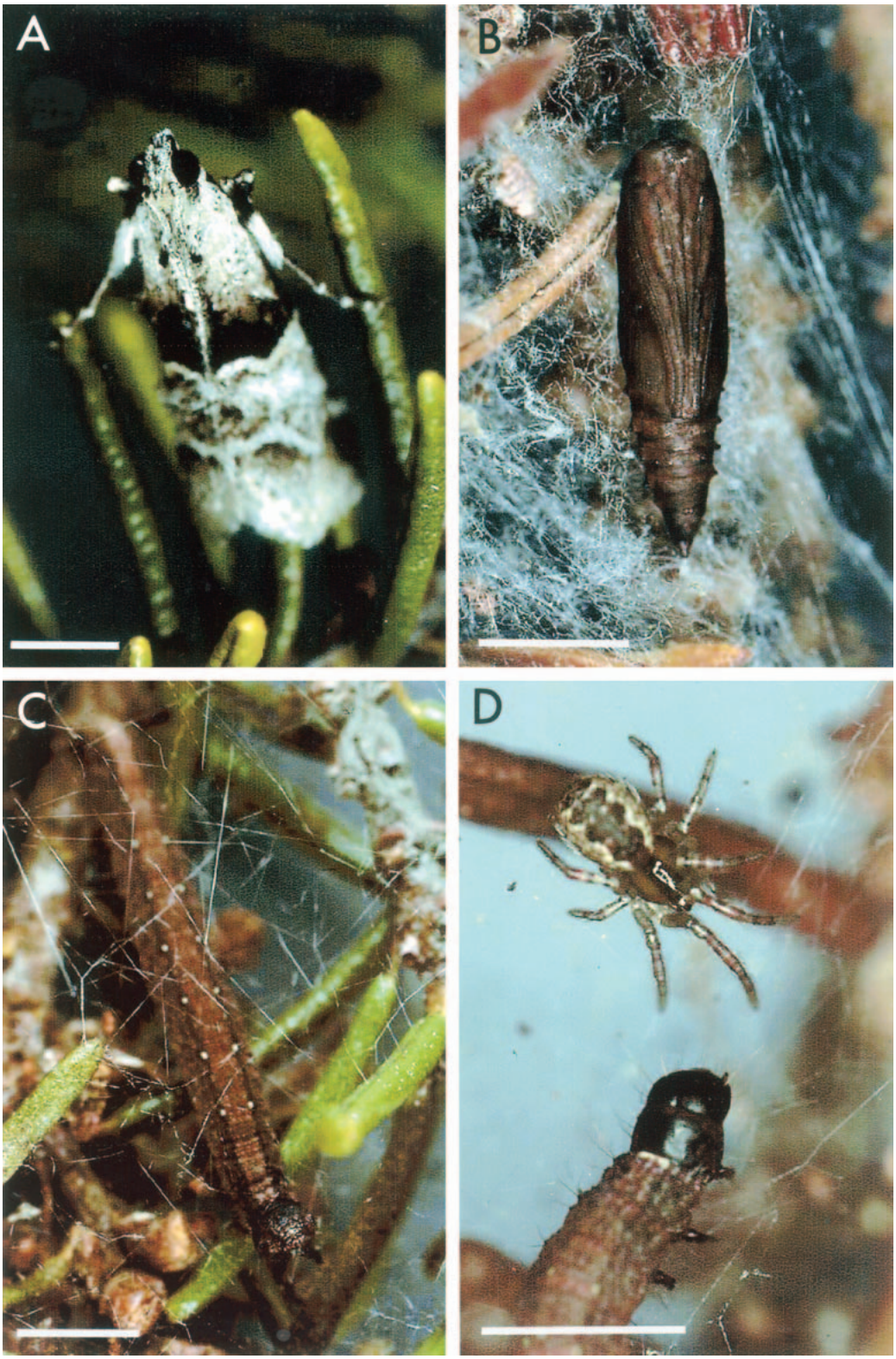


Fig. 2. *Tallula watsoni*: A: Adult; B: Pupa suspended in webbing; C: Larva in webbing; D: Larva in webbing with *Anelosimus studiosus*. Lines = 2 mm.

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Heteroptera: Tingidae: *Corythuca floridana* Heidemann (1); Miridae: *Ranzovius clavicornis* (16); Diptera: Empididae: *Drapetis* sp. (2); Psocoptera: unidentified to family (12); Collembola: Entomobryiidae: unidentified to genus (15); Hymenoptera: Formicidae: *Monomorium viride* Brown (1), *Crematogaster ashmeadi* Mayr (1); Lepidoptera: Pyralidae: *Tallula watsoni* (8); Coleoptera: Tenebrionidae: *Epitragodes tomentosus* (LeConte) (1).

During the survey of 503 webs, wasp larvae (Ichneumonidae) were found feeding externally on five spiders. Four females and one male of *Zatypota crassipes* Townes were reared from these larvae. This appears to be the first record of *Z. crassipes* from any host spider. Members of the genus *Zatypota* are all presumed to be external parasitoids of spiders (Townes & Townes 1960). The cocoon of *Z. crassipes* is pale brown and covered with semi-erect loops of silk. Several other species of *Zaptypota* also have loops of silk covering their cocoons (Townes & Townes 1960); the function of these loops is unknown.

Aside from *T. watsoni*, the mirid *Ranzovius clavicornis* and the wasp *Z. crassicornis*, it is unlikely that many of the arthropods listed above have a close or obligate relationship with *A. studiosus*. Some may even be potential prey items with short persistence in the webs. Further studies at other sites might help distinguish between casual inquilines, habitual inquilines, and inquilines that are dependent on *A. studiosus*. There might also be oligolectic phytophagous inquilines that require plants that are absent from the ABS. The web inhabitants of *A. studiosus*, if studied throughout the range of the spider, could present an interesting model of the transitions between opportunism and specialization.

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