

THE SINGING REAPER: DIET, MORPHOLOGY AND VIBRATIONAL SIGNALING IN THE NEARCTIC SPECIES *FENISECA TARQUINIUS* (LEPIDOPTERA: LYCAENIDAE, MILETINAE)*

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Abstract – A survey at fourteen sites in Eastern North America of populations of the carnivorous lycaenid butterfly, *Feniseca tarquinius*, confirmed that the sole prey item on *Alnus rugosa* (Betulaceae) for this species in these regions was *Paraprociophilus tessellatus* (Homoptera: Aphidoidea: Pemphigidae). Overwhelmingly, these aphids were tended by ants in the subfamily Formicinae. These results are compiled with all earlier records of prey aphids, their host plants and attendant ants for this species. SEM examination of a 4th instar larva of *F. tarquinius* supported Cottrell's (1984) observation that the dorsal nectary organ and tentacle organs are absent in the 4th instar of virtually all Miletinae. Larvae of *F. tarquinius* were found to produce substrate-borne vibrations that possess a long pulse length and narrow bandwidth when compared with other lycaenid calls. The possible function of these calls is briefly discussed.

Resumen - Un estudio llevado a cabo en poblaciones de la mariposa carnívora *Feniseca tarquinius* (Lycaenidae) provenientes de 14 localidades del Este de Norte America confirma que la única presa consumida por esta especie sobre *Alnus rugosa* (Betulaceae) en estas regiones es *Paraprociophilus tessellatus* (Homoptera: Aphidoidea: Pemphigidae). La gran mayoría de estos áfidos es atendida por hormigas en la subfamilia Formicidae. Estos resultados han sido analizados junto con observaciones para esta especie relativas a áfidos presa, plantas hospedadoras y hormigas asociadas compiladas anteriormente. Observaciones realizadas en la larva del cuarto estadio mediante un microscopio electrónico de barrido (SEM) apoyó la observación de Cottrell (1984) que indica que el órgano productor de néctar ubicado dorsalmente y los órganos tentáculos están ausentes en el cuarto estadio larval de prácticamente todas las Miletinae. Se encontró que las larvas del cuarto estadio producen vibraciones transmitidas a través del sustrato que se caracterizan por presentar una gran longitud de pulso y pequeña amplitud de banda comparadas con llamadas emitidas por otras Lycaenidae. Se discute brevemente la posible función de estas llamadas.

Key words: Larval behavior, life history, carnivory, Betulaceae, Homoptera, Formicinae, Syrphidae, Neuroptera, *Taraka*.

INTRODUCTION

Life history

The life-history of the only known carnivorous North American butterfly, *Feniseca tarquinius* Grote (Lycaenidae: Miletinae), the harvester, has been known for over a century (Edwards, 1886; Riley, 1886; Scudder, 1889, 1897), yet little has appeared recently on the ecology of this enigmatic species. *F. tarquinius* is encountered sporadically across its range, from Florida in the south to Nova Scotia in the north, and extends as far west as Texas in the south to Manitoba in the north (Opler and Krizek, 1984.). Up to 8 broods have been reported for *F. tarquinius* in Virginia (Clark and Clark, 1951). More typically, however, it is known to have two to three broods, the first appearing in early May, the second in mid to late July, and occasionally, a third in August or September. The butterfly lays its eggs among clumps of woolly aphids (Aphidoidea: Pemphigidae), on which the emergent larvae obligately feed (Scott, 1986) (Table 2). The homopteran prey is typically attended by ants which have been observed to be distinctly hostile to the lycaenid larvae (Scudder, 1889). This possibly explains why young instar larvae tend to live in concealed locations under the aphids until fully grown, even spinning a silken web among the aphids (Clark, 1926; Cottrell, 1984). As frequently noted in the literature, the shape and markings on the pupa (Figure 3. C) make it resemble a miniature monkey's head (Scudder, 1897; Balduf, 1939; Hinton, 1974; Krizek, 1995). Development appears to be relatively rapid, lasting approximately three weeks from egg to adult (Scott, 1986).

Morphology

Myrmecophilous lycaenid larvae use an array of chemical, behavioral, and secretory cues to form and maintain associations with attendant ants that protect them from predators and parasites. These caterpillars may possess at least three organs assisting in this process: the dorsal nectary organ (DNO) found on the 7th abdominal segment, the tentacular organs (TOs), found on either side of the 8th abdominal segment and the pore cupolae organs (PCOs) found scattered dorsally along the length of the cuticle (Hinton, 1951; Cottrell, 1984). Kitching and Luke (1985) coined the term 'myrmecoxeny' to describe those lycaenid species that do not produce visible secretions harvested by ants but are nevertheless protected chemically against their attacks. In the Miletinae, which is almost entirely myrmecoxenous, the DNO is lacking, and in most species, the TOs as well (Cottrell, 1984). The PCOs however, do exist, though reduced in numbers relative to those in myrmecophilous counterparts (Cottrell, 1984).

Sound

Larvae of Lycaenidae (including Riodininae) are capable of producing substrate-borne vibrations (DeVries 1990, 1991). With several apparent exceptions [e.g. *Deudorix diovis* Hewitson (De Baar 1984), *Caleta roxus* Godart (Fiedler 1994)], most lycaenids that can produce vibrational signals associate with ants as larvae (DeVries 1990, 1991, but see Downey; 1966; Downey and Allen, 1978). Travassos and Pierce (2000) have demonstrated that

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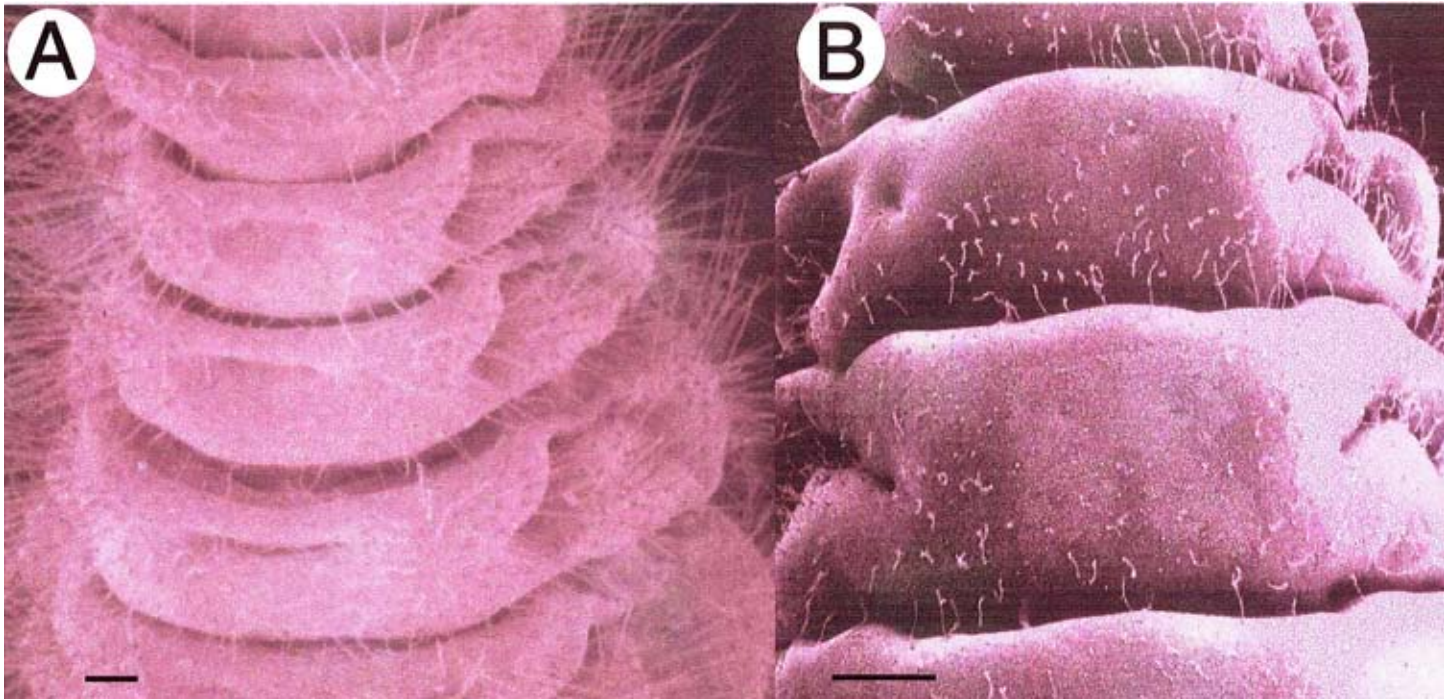


Figure 1. Anterior segments of last instar larvae under SEM to show relative pilosity. A. *Feniseca tarquinius* (X 18). B. *Taraka hamada* (X 33).

larvae of the Australian lycaenid *Jalmenus evagoras* Donovan (Lycaenidae) significantly increase call production in the presence of their attendants ants.

The ability to produce vibrational signals appears to be widespread in the Lycaenidae (DeVries 1991; Fiedler *et al.* 1995; Heath 1998, Heath and Claassens 2003). In the first description of sound production in the Lycaenidae, Dodd (1916) mentioned *Miletus* among the genera he had heard produce calls as larvae; without a species name, however, it is difficult to know whether the *Miletus* he was describing would be classified as a miletine today. Heath (personal communication) has found that fourth instar larvae of *Thestor yildizae* Koçak, a South African miletine that lives in *Anoplolepis custodiens* ant nests, produce faint sounds in response to a disturbance.

MATERIALS AND METHODS

Life history

Field surveys of *Alnus* spp. (Betulaceae) were undertaken across 14 site localities in New Brunswick, Maine, New Hampshire, and Massachusetts (Table 1) between June and September 1998, and between July and September 1999. Larvae at different instar stages found among the woolly aphids were collected, and at one site (the Arnold Arboretum), adults were also collected. The presence of ants attending the prey populations was noted, as were predators competing for the same prey base with the lycaenid larvae, such as syrphid flies (*Syrphus* spp.) and neuropteran lacewings (*Chrysopa* spp.). The larvae and associated predators and prey were collected and reared to adulthood under constant conditions (24°C) in a growth room. Wings were removed as voucher specimens and adult bodies were preserved in 100% ethanol and stored at -80°C.

Morphology

The surface features of a single 4th instar *F. tarquinius* larva were studied under SEM (Figure 1. A). The sample was subjected to increasing levels of alcoholic dehydration (40%, 60%, 75%, 90%,

100%), prior to critical point drying with liquid carbon dioxide, employing a Tousimis Samdri PVT-3B. It was then mounted on a metal stub and sputter-coated with gold preparatory to viewing under SEM (JSM-6400).

Sound

Several late instar larvae of *F. tarquinius* were collected in June, 1999, in the Arnold Arboretum in Jamaica Plain, Massachusetts. In the laboratory, each larva was placed on a recording stage that consisted of a paper circle with a 12 cm diameter tightly taped over the opening of an 8 cm tall, 12 cm diameter plastic container so that the stage was taut. A Pfanstiehl P-136 Sonotone 2T phonograph cartridge taped to the recording stage acted as a microphone. Calls were recorded on a Nagra IV-SJ Tape Recorder with maximum gain. We induced larvae of *F. tarquinius* to call by stimulating them with a fine-haired paint-brush. We did not monitor sound production in a more natural context such as when *F. tarquinius* feeds on ant-tended woolly aphids.

Calls were examined with Canary 1.2b 1994, a sound analysis program produced by the Cornell Laboratory of Ornithology (Figure 2). The beginning and end of a call were defined with respect to the background noise level. At least ten call samples were taken for each larva examined, and 33 calls from three larvae were analyzed in total. For each call, three properties were measured: mean dominant frequency, bandwidth, and pulse length. The dominant frequency was calculated as the average of the upper and lower frequency bounds of a call. The bandwidth of a call consisted of the difference between these upper and lower bounds. The pulse length was measured as the duration of a call. Summary statistics are reported as mean \pm one standard error, and counts given refer to the number of larvae sampled.

RESULTS

Life history

Aphids ranged from a few individuals to dense clusters. In all 14 site localities (Table 1), the host aphids, *Paraprociophilus tessellatus* Fitch (Pemphigidae) were found on *Alnus rugosa* Du Rois (Betulaceae), (Figure 3. A, B), with a single exception where they occurred on *Alnus glutinosa* (L.) Gaertn. (Betulaceae). The larvae were typically found burrowing under the aphids, out of reach of the attendant ant-guard. Adults were encountered only four times; on one occasion, a female was seen to extrude what appeared to be a scent gland on the surface of a leaf (Figure 3. D).

Morphology

SEM examination of the surface of the *F. tarquinius* larva at 18X magnification revealed a hirsute dorsum replete with setae and few and scattered PCOs along its length. There was no evidence of a DNO or TOs (Figure 1. A).

Sound

Larvae of *F. tarquinius* produced a call that, depending on the distance from the phonograph cartridge, resembled a mournful sigh, a falling *glissando* of six half-steps from F to middle C, or, at proximity, when amplified, the bleating of a sheep. Larvae called when disturbed with a paintbrush. When calling, a caterpillar lifted its anterior portions, including its head and thorax, off the substrate. The larval call (N=3) of *F. tarquinius* had a mean dominant frequency of 302.1 ± 29.1 Hz, a pulse length of 477.0

± 143.2 ms, and a bandwidth of 79.3 ± 8.4 Hz (Figure 2). In a typical larval call, there was a drop in frequency over the length of the call.

DISCUSSION

Life history

Banno (1997) showed that a close relative of *F. tarquinius* in the Palaearctic, *Taraka hamada* (H. Druce), was responsible for decimating whole colonies of its host aphid, *Ceratovacuna japonica* (Takahashi) (Hormaphididae). In our observations, the larvae of *F. tarquinius* appeared to be remarkably similar. In both cases, competing predators are often present; syrphid flies (Figure 3. A, B), in numbers, and more infrequently, lacewings. The ant species tending the prey aphids of *F. tarquinius* mainly belonged to the Formicinae; this may be a function of the disproportionate abundance of formicine species in the north temperate region (please see data from Wisconsin in Youngsteadt and DeVries, 2005, as well). We did however, record tending by one myrmecine species, *Myrmica incompleta*, which was also observed by Lohman *et al.* (2006), in New Hampshire.

The biocontrol potential of *F. tarquinius* was suggested by Brower (1947) who reported that in Indian Town, Maine, the destructive balsam woolly aphid, *Adelges piceae* (Ratz.) (Adelgidae), was preyed upon by a dozen larvae of *F. tarquinius*. This was, however, a single record for the phenomenon, and little evidence of economic importance has since emerged from this line of pursuit for the species. Another close relative in the Spalgini, *Spalgis epius* (Kirby), however, does play a significant biocontrol role in

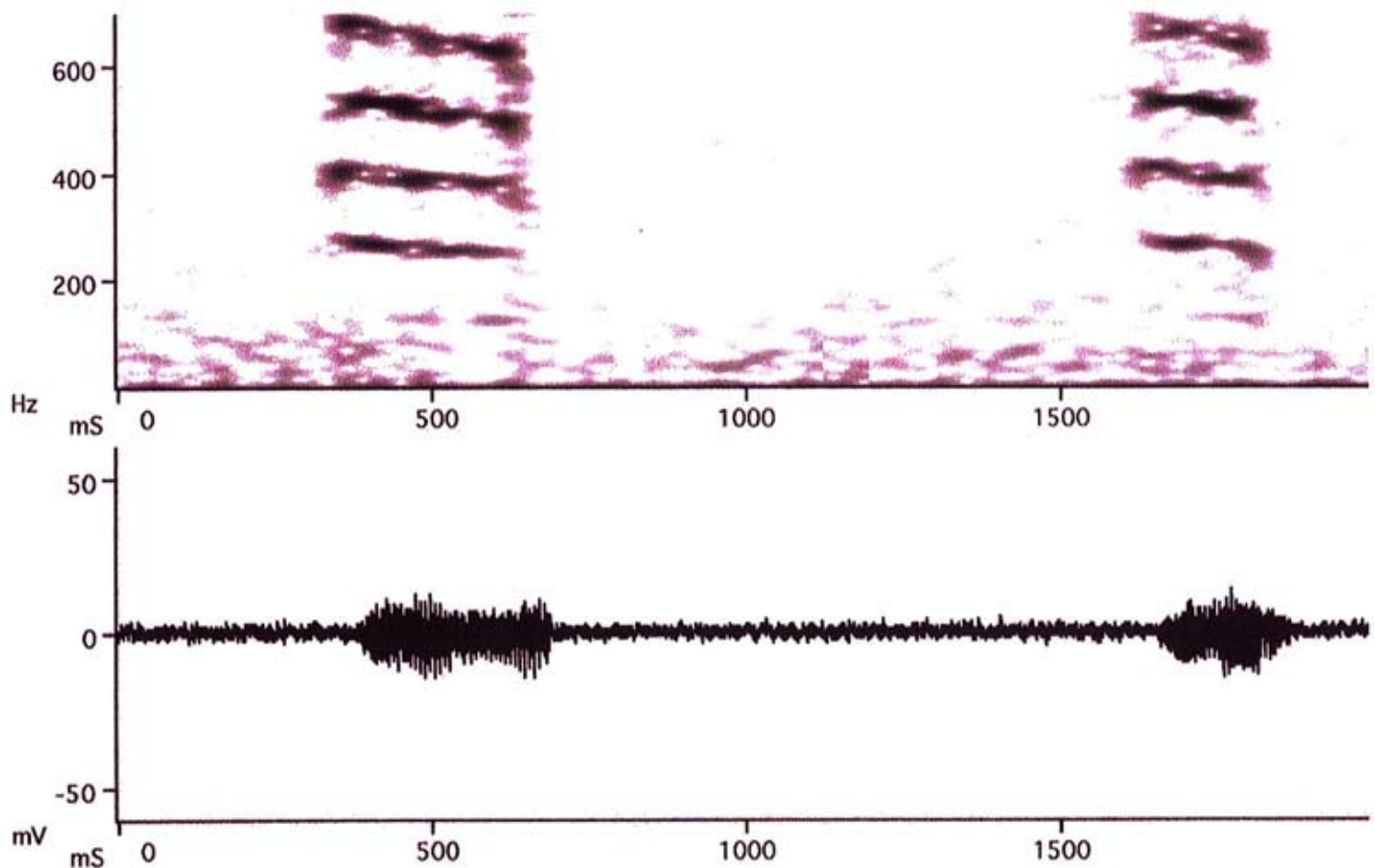


Figure 2. Spectrogram (top) and waveform (bottom) of a *F. tarquinius* larval call.

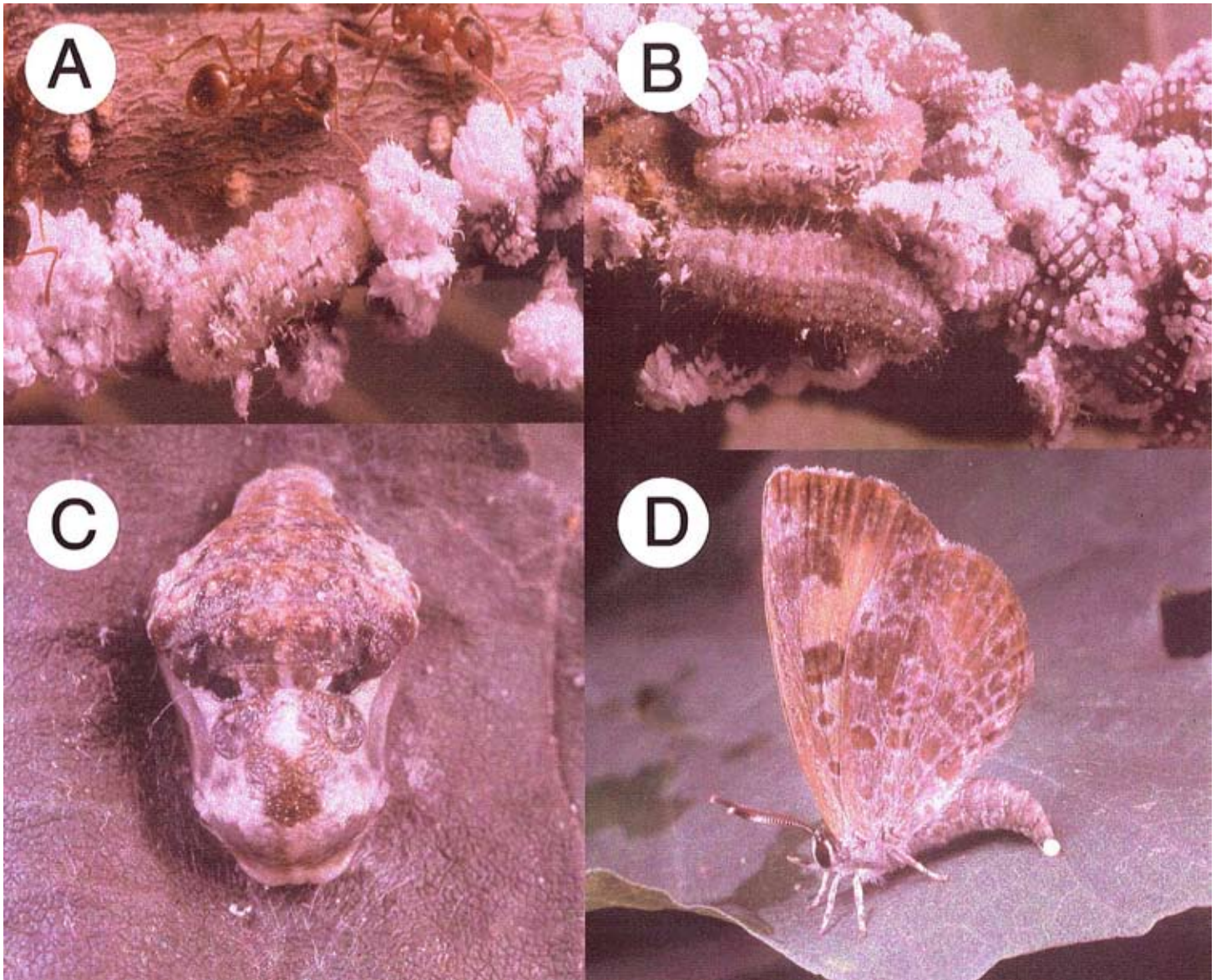


Figure 3. Ecology and habit of *F. tarquinius*: A. Predatory syrphid larva among woolly aphids tended by *Myrmica rubra* ants; B. *Feniseca* larva and syrphid larva among woolly aphids; C. *Feniseca* pupa; D. *Feniseca* adult extruding.

keeping populations of several species of the Pseudococcidae in check, particularly those belonging to the genera *Phenacoccus*, *Planococcoides* and *Pseudococcus* (Ackery, 1990).

The function of the extrusion by the adult female of *F. tarquinius* on the surface of a leaf remains unclear (Figure 3. D.). One possibility is that she may be extruding a pheromone to attract mates, but in the absence of more conclusive evidence, this must remain speculative. She was observed to extrude the putative organ and retract it several times during 10 minutes of observation. This would indicate that it was, indeed, an extrusible gland and not a meconial defecation.

Morphology

It is unsurprising that the SEM examination of *F. tarquinius* revealed few surface structures, given such a trend overall for the Miletinae (Cottrell, 1984). Compared to *T. hamada*, which was also examined under SEM (Figure 1. B), the dorsum of *F. tarquinius* larvae possesses many dorsal setae, and it may be that these play a defensive role against ant attack. Hinton (1951) suggests that the waxy secretions of the aphid prey become

entangled among the dorsal setae of *F. tarquinius*, and this, along with the web constructed by the larva, protects it against ants. SEM examination of 4th instar *F. tarquinius* larvae by Youngsteadt and DeVries (2005) suggest that despite the fact that chemical camouflage seems to be important to the species, their setae show no evidence of increased surface area or abrasive qualities that could facilitate either uptake or dissemination of aphid chemical signatures. The authors argue that such a situation is akin to the setae of non-myrmecophilous lycaenid caterpillars, which in turn is reflective of chemical camouflage through the passive acquisition of unspecialised lipids.

Sound

This is the first experimental demonstration of acoustical signal in a miletine. Like other lycaenids, *F. tarquinius* larvae produce substrate-borne vibrations. However, their calls are distinctive in two ways. The pulse length is almost five times longer than the grunt of *Jalmenus evagoras*, previously the longest reported call of a lycaenid (Travassos and Pierce, 2000). In addition, the calls possess the narrowest bandwidth reported for lycaenid caterpillars.

Table 1. Locality data for *F. tarquinius* in this study.

No.	Date	Locality	Co-ordinates	Attendant ant species
1	4/9/98	Phillipston, MA	42°31'10"N, 72°08'00"W	<i>Formica rubicunda</i> (Formicinae)
2	7/9/98	Petersham, MA	42°29'15"N, 72°11'15"W	<i>Camponotus noveboracensis</i> , <i>Camponotus pennsylvanicus</i> , (Formicinae)
3	14/9/98	Mt. Washington Regional Airport, NH	44°22'03"N, 71°32'40"W	No ants observed tending
4	15/9/98	Berlin, NH	44°28'07"N, 71°11'08"W	<i>Formica fusca</i> (group) (Formicinae)
5	17/9/98	Mt. Carleton Park, near Nictau, NB.	47°14'00"N, 67°09'00"W	<i>Myrmica incompleta</i> , <i>Formica fusca</i> (group) (Formicinae)
6	17/9/98	Bathurst, NB	47°25'00"N, 65°55'00"W	<i>Formica fusca</i> (group) (Formicinae)
7	18/9/98	St. Louis de Kent (Site 1), Kent, NB	46°35'00"N, 65°15'00"W	<i>Lasius pallitarsus</i> , <i>Formica integra</i> (<i>rufa</i> group) (Formicinae)
8	18/9/98	St. Louis de Kent (Site 2), Kent, NB	46°35'00"N, 65°15'00"W	<i>Camponotus noveboracensis</i> , <i>Formica fusca</i> (group), (Formicinae)
9	19/9/98	Rt. 114, north of Fundy, NB	45°37'00"N, 65°02'00"W	<i>Formica fusca</i> (group) (Formicinae)
10	20/9/98	Searsport, ME	44°27'30"N, 68°55'29"W	<i>Formica integra</i> , <i>Formica fusca</i> (group) (Formicinae)
11	3/7/99	Arnold Arboretum, Boston, MA	42°17'55"N, 71°07'42"W	<i>Camponotus noveboracensis</i> , (Formicinae) <i>Myrmica rubra</i> (Myrmicinae)
12	19/7/99	Bar Harbor, ME	42°17'55"N, 71°07'42"W	No ants observed tending
13	28/7/99	Petersham, MA	42°29'15"N, 72°11'15"W	<i>Camponotus noveboracensis</i> , <i>Camponotus pennsylvanicus</i> , (Formicinae)
14	4/9/99	Gorham (Site 1), NH	44°30'89"N, 71°09'91"W	<i>Formica glacialis</i> , <i>Camponotus herculeanus</i> (Formicinae)
15	4/9/99	Gorham (Site 2), NH	44°31'85"N, 71°09'91"W	<i>Myrmica incompleta</i> (Myrmicinae)

All on *Alnus rugosa*, except 11 on *Alnus glutinosa*; All use aphid *Paraprociophilus tessallatus*.

Unlike most lycaenid calls, which typically are short, broad bandwidth pulses (DeVries 1991), *F. tarquinius* larvae produce calls that have a high level of structure, suggesting that they may have a well-defined function. Qualitatively, these larval calls resemble the sounds produced by certain ant-tended membracids (Cocroft, 1996, M. Travassos, personal observation). It is possible that *F. tarquinius* larvae may mimic the acoustical signals produced by the woolly aphids upon which they feed. It is not known, however, whether such aphids, like other ant-tended homopterans, produce substrate-borne vibrations. Non-ant-tended woolly aphids were silent when monitored.

Although most lycaenids that produce vibrational signals (customarily as later instars) associate with ants as larvae, Downey and Allyn (1978) did not find a strict correlation between ant association and sound production in lycaenid pupae. Downey (1966) reported hearing sound produced by pupae of *F. tarquinius*, which are far less tended than larvae in the species. The demonstration of sound production in *F. tarquinius* larvae was conducted in the laboratory without the presence of attendant ants. Our attempts to induce sound production in *F. tarquinius* pupae were unsuccessful. Further observations monitoring call production in a natural setting may shed light on the role of sound in the larval and pupal stages of *F. tarquinius*, particularly its potential role in mimicry and ant association. The chemical signatures of later instar *F. tarquinius* larvae have been shown to be remarkably similar to the *Paraprociophilus* aphid prey (Youngsteadt and DeVries, 2005; Lohman et al. 2006). This phenomenon has been called 'chemical camouflage', as opposed to chemical mimicry, because the source of the hydrocarbon is external to the lycaenid larvae themselves (Youngsteadt and DeVries, 2005). However, the structure of the larval calls of *F. tarquinius* suggests active mimicry, indicating that acoustic and chemical signaling in this system warrant further investigation.

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Table 2. Aphid prey of *F. tarquinius* and their reported hostplants (after Scott, 1986).

No	Host plant species	Family	Associated Aphids
1	<i>Acer saccharinum</i>	Aceraceae	<i>Neoprociophilus aceris</i>
2	<i>Alnus glutinosa</i>	Betulaceae	<i>Paraprociophilus tessallatus</i>
3	<i>Alnus rugosa</i>	Betulaceae	<i>Paraprociophilus tessallatus</i>
4	<i>Alnus serrulata</i>	Betulaceae	Undescribed
5	<i>Echinocystis lobata</i>	Cucurbitaceae	Undescribed
6	<i>Fagus grandiflora</i>	Fagaceae	<i>Grylloprociophilus</i> ; <i>Imbricator</i>
7	<i>Fraxinus americana</i>	Oleaceae	<i>Meliorhizophagus</i> ; <i>Fraxinifolii</i>
8	<i>Hamamelis virginiana</i>	Hamamelidaceae	Undescribed
9	<i>Ilex verticillata</i>	Aquifoliaceae	<i>Paraprociophilus tessallatus</i>
10	<i>Smilax herbacea</i>	Smilacaceae	<i>Neoprociophilus aceris</i>
11	<i>Smilax hispida</i>	Smilacaceae	Undescribed
12	<i>Malus pumila</i>	Rosaceae	Undescribed

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