ACROCERID (INSECTA: DIPTERA) LIFE HISTORIES, BEHAVIORS, HOST SPIDERS (ARACHNIDA: ARANEIDA), AND DISTRIBUTION RECORDS

ALAN CADY
Department of Zoology, Miami University-Middletown, Middletown, Ohio, USA 45042

ROBIN LEECH
Department of Entomology, University of Alberta, Edmonton, Alberta, Canada T6G 2E3

LOUIS SORKIN
Department of Entomology, American Museum of Natural History, Central Park West at 79th Street, New York, New York, USA 10024-5192

GAIL STRATTON
Department of Biology, Albion College, Albion, Michigan, USA 49224

and MICHAEL CALDWELL
Redpath Museum, McGill University, Montréal, Québec, Canada H3A 2K6

Abstract

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The family Acroceridae (Insecta: Diptera; ''Small Headed Flies'') are a seldom seen yet cosmopolitan group of endoparasitoids of spiders. Recent host and distribution records are presented here for six species of acrocerids: *Ogcodes borealis* Cole, 1919; *Ogcodes pallidipennis* (Loew, 1866); *Ogcodes* sp.; *Acrocera bimaculata* Loew, 1866; *Turbopsebius sulphuripes* (Loew, 1869); and *Exetasis eickstedtae* Schlinger, 1972. New hosts for each fly species are: *O. borealis—Schizocosa rovneri* Uetz and Dondale, 1979, *Pardosa* spp.; *O. pallidipennis—Schizocosa rovneri, Schizocosa* spp.; *Ogcodes* sp.—*Anyphaena californica* (Banks, 1904); *Acrocera bimaculata—Coras montanus* (Emerton, 1890*b*); *T. sulphuripes—C. montanus.*

Detailed field measurements and behavioral observations of host spiders and fly development are described and compared with known data. Examination of these comparisons suggests that host–parasitoid relationships follow spider guild associations (i.e. ground/surface dwelling hosts or those building webs in close contact with surfaces), especially with the spider family Agelenidae. These affiliations probably result from a combination of the spider's web building, web maintenance, hunting behaviors, and fly oviposition activities, which dispose spiders exhibiting these behaviors to greater chances for parasitoidism. These factors act in concert to increase probabilities for host–parasitoid interactions. Compiled data indicate duration of pupation may be related to ambient temperature. Evidence is presented that acrocerid larvae may alter their hosts' behavior to increase the parasitoids' probability of survival.

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Résumé

La famille des Acroceridae (Insecta: Diptera; ''mouches à petite tête'') constitue un groupe d'insectes rarement vus et pourtant cosmopolites, parasites d'araignées. On trouvera ici une liste de données récentes sur les hôtes et les répartitions de six espèces d'acrocères: *Ogcodes borealis* Cole, 1919, *Ogcodes pallidipennis* (Loew, 1866), *Ogcodes* sp., *Acrocera bimaculata* Loew, 1866, *Turbopsebius sulphuripes* (Loew, 1869) et *Exetasis eickstedtae* Schlinger, 1972. Pour chacune de ces espèces, les nouveaux hôtes rencontrés sont: dans le cas d'*O. borealis, Schizocosa rovneri* Uetz et Dondale, 1979 et *Pardosa* spp., dans le cas d'*O. pallidipennis, Schizocosa rovneri* et *Schizocosa* spp., dans le cas d'*Ogcodes* sp., *Anyphaena californica* (Banks, 1904), dans le cas d'*Acrocera bimaculata, Coras montanus* (Emerton, 1890*b*) et dans le cas de *T. sulphuripes, C. montanus.*

Des mesures détaillées et des observations du comportement des araignées hôtes recueillies sur le terrain sont présentées ici et comparées aux données de la littérature. Les comparaisons indiquent que les relations hôtes–parasitoïdes se font en fonction des guildes d'araignées (i.e. hôtes habitant dans le sol ou en surface ou hôtes construisant des toiles très près de surfaces), et impliquent surtout des araignées de la famille des Agelenidae. Ces affiliations résultent probablement de la combinaison de facteurs associés aux araignées, construction de la toile, entretien de la toile, comportement de chasse, et de l'activité de ponte chez les acrocères, et elles prédisposent les araignées qui manifestent ces comportements à une probabilité plus grande d'être parasitées. Ces facteurs agissent de concert pour augmenter la probabilité des interactions hôtes–parasitoïdes. Les données indiquent que la durée de la nymphose peut être reliée à la température ambiante. Une larve d'acrocère peut parasiter un hôte à n'importe quel stade. Une larve qui parasite une araignée qui n'a pas atteint l'avant-dernier stade reste ordinairement quiescente jusqu'à ce que l'araignée atteigne son stade terminal, alors qu'une larve qui infecte une araignée d'avant-dernier stade ou de stade adulte se met à se nourrir immédiatement.

[Traduit par la rédaction]

Introduction

The family Acroceridae (Diptera: Brachycera) is a small yet diverse group of cosmopolitan flies comprising approximately 500 species in 50 genera. The Nearctic Region has about 59 described species (Schlinger 1981). These flies are encountered rarely, but may be found locally in numbers. The common name of "Small-Headed Flies" describes their disproportionally small heads consisting mostly of compound eyes (Figs. 2, 9). Larvae of all known members but one of the Acroceridae are endoparasitoids of spiders (Schlinger 1987).

Strict host specificity between particular fly and spider species appears to be rare. Schlinger (1987) identified a general relationship among certain fly genera and spider families (or guilds). Evolutionary liaisons are apparent between the more primitive panopine acrocerids and mygalomorph spiders, and between the more derived acrocerine flies and araneomorph spiders. Furthermore, some consistent relationships are evident between the fly genus *Turbopsebius* and the spider family Agelenidae. Habitat, also, may influence host choice (Schlinger 1987).

The purpose of this presentation is to report unpublished locality and host records for six species of acrocerids: *Ogcodes borealis* Cole, 1919; *Ogcodes pallidipennis* (Loew, 1866); *Ogcodes* sp.; *Acrocera bimaculata* Loew, 1866; *Turbopsebius sulphuripes* (Loew, 1869); and *Exetasis eickstedtae* Schlinger, 1972. Field observations are described concerning pupation, adult fly behaviors, and general appearances for *A. bimaculata* and *T. sulphuripes*. In addition, the behaviors of infected host spiders, and alterations of their web structure, are included. Laboratory behavioral observations of *O. pallidipennis* and *E. eickstedtae* and their hosts are provided. Higher rates of parasitoidism suffered by certain groups of spiders are discussed, as are possible reasons for such disparity among available hosts. Furthermore, we present more evidence that parasitoids may alter their hosts' behaviors to enhance the chances of parasitoid survival. It is hoped that these descriptions will alert dipterists and arachnologists to the habits and occurrences of acrocerids. Any additional data added to these records would further our understanding of distribution and life histories concerning these interesting flies.

Materials

All U.S. and South American fly specimens and their spider hosts, when available, are deposited in the American Museum of Natural History, New York, NY, USA; all Canadian fly specimens and their spider hosts are deposited in the Provincial Museum of Alberta, Edmonton, Alberta, Canada.

TABLE 1. Summary of information on acrocerid parasitoids, host spiders, location, date, collector data, notes on range extensions, and laboratory or field rearings

Acrocerid	Host spider(s)	Location/date/collector	Notes
Ogcodes borealis Cole, 1919	*Pardosa* sp. (Lycosidae)	North Cooking Lake, Alberta, Canada; May 1986 (by MC); 2 specimens	**Figures 1–3** –Raised in laboratory
	Schizocosa rovneri Uetz & Dondale, 1979 (Lycosidae)	NW Kentucky (Boone Co.), USA; October 1981 (by GS); 4 specimens	–Range extension in eastern N. Am. –Kentucky State record –Raised in laboratory
Ogcodes pallidipennis (Loew, 1866)	*Schizocosa rovneri* Uetz & Dondale, 1979 (Lycosidae)	Central Illinois (Mason Co.), USA; 1985 (by GS); 2 *S. rovneri*, 1 "*Lycosa*" sp.	–Kentucky State record –All raised in laboratory
	"*Lycosa*" sp. (Lycosidae)	NW Kentucky (Boone Co.), USA; 1980, 1982 (by GS); 2 "*Lycosa*" sp.	–"*Lycosa*" notation because Dondale and Redner (1990) consider *Lycosa* not to occur in North America
Ogcodes sp.	*Anyphaena californica* (Banks, 1904) (Anyphaenidae)	Moraga (Contra Costa Co.), CA, USA; 13 July 1979 (by D.G. Denning); 1 specimen	–Raised in laboratory
Acrocera bimaculata Loew, 1866	*Coras montanus* (Emerton, 1890*a*) (Agelenidae)	East Tennessee (Morgan Co.), USA; (by AC) May 1982; 5 specimens, May 1983; 1 specimen	**Figure 4** –Raised in laboratory
Turbopsebius sulphuripes Loew, 1869	*Coras montanus* (Emerton, 1890*a*) (Agelenidae)	East Tennessee (Morgan Co.), USA; May 1981 (by AC); 1 specimen	–Tennessee State record –Raised in field; taken to lab before pupal eclosion –Few published host records
Exetasis eickstedtae Schlinger, 1972	*Lasiodora klugi* (C.L. Koch, 1842) (Theraphosidae)	Governador Valadares (Minas Gerais), Brazil; 12 March 1983 (by LS); 3 specimens	**Figures 5–9** –New location record –Superparasitoidism: 14 larvae emerged from one spider –Larvae died post-emergence, but before pupation

Localities and Hosts

The distributions and hosts for the six acrocerid fly species and their spider hosts are summarized and annotated in Table 1.

Observations of Fly and Host Spider Behaviors

Behavior and Appearance of Parasitized Hosts. Although endoparasitoids have been shown to alter their hosts' behavior (Brodeur and McNeil 1989), some workers report observing no peculiar behaviors or activities by parasitized spiders (Lamore 1960; Schlinger 1960). This is in strong contrast to mermithid worms, which produce obvious physical and behavioral changes in the host spiders (Leech 1966; Poinar 1985). Lamore (1960) reported a lycosid that produced a mat of silk prior to an acrocerid emergence. However, this was probably the premolting web (a characteristic of wolf spiders), as the spider had not produced any web previously.

In the laboratory. The *Pardosa* hosts for *O. borealis* detailed above did not display physical or behavioral reaction to the parasites within them. However, there are reports where the comportment and physical appearance of the spider betray the presence of the larval fly. Montgomery (1903) described *Schizocosa crassipes* (Walckenaer, 1837) [=*Schizocosa ocreata* (Hentz, 1844)] as moving spasmodically and spinning silk often. He could identify an infected spider by its ''poor health'' and condition of the web, and reported that a wolf spider spun a ''sack'' in a corner of its container and remained inside the silken tube while the fly larva emerged. Schlinger (1952) characterized one parasitized spider [*Hololena curta* (McCook, 1894); Agelenidae] as ''nervous'' and making jerking movements followed by silk deposition.

We report here laboratory observations where the host showed unusual behavior. A theraphosid, *Lasiodora klugi* (C.L. Koch, 1842), from Brazil appeared dazed as it moved about its container, because it ran into the walls and could not walk a straight line. Also, it scratched the sides of its abdomen with its hind legs, but not the urticating patch of hairs typically found on the central dorsal abdomen of theraphosids. Later it was discovered that the fly larva's spiracular plates had protruded through the integument where the spider had been scratching. Furthermore, another specimen of *L. klugi* produced a drab grey "dirty-looking" silk mat prior to emergence of an acrocerid larva, not the large white mat normally constructed by captive theraphosids. A third specimen of *L. klugi*, from which 14 larvae of *E. eickstedtae* emerged, appeared to be dead 3 days before the larvae emerged. Another laboratory observation was made of a *Schizocosa* sp. (which produced a specimen of *O. pallidipennis*) hanging inverted on a silk mat inside a water tube prior to larval emergence. This is a very atypical resting position for lycosids.

In the field. Extensive field research of a spider community living on sandstone cliffs on the Cumberland Plateau in eastern Tennessee, USA, permitted close and nearly continuous observations of acrocerids and their hosts in field situations (Cady 1984). Although approximately 15 spider species live on the cliffs, only *Coras montanus* (Emerton, 1890*a*), a funnel web-weaving agelenid, was found to harbor acrocerids. Similarly, Emerton (1890*b*) found numbers of acrocerids as parasitoids of an amaurobiid, *Callobius bennetti* (Blackwell, 1846), living on rocky cliffs. The field observations reported here are compilations of data primarily from nine specimens of *C. montanus* containing acrocerid parasitoids at their websites during 1981–1983.

In the field, those *Coras montanus* containing an acrocerid parasitoid larva exhibited changes of both behavioral and physical characteristics. First, they made themselves obvious by building a poorly structured web and then not maintaining it well. Furthermore, the spiders were slower when responding to vibrations applied to the web, hesitant during prey capture, and appeared generally weaker and less aggressive than their conspecifics. Infected *C. montanus* tended to be smaller, weighed less than others of similar length, and were generally paler in color. Another physical manifestation of parasitoid presence was a small black circular lesion (approx. 1 mm diameter by 0.5 mm high) shaped like a truncate tubercle on the anterior-lateral dorsum of the abdomen (usually right side); this is probably the site of larval fly spiracular attachment. Each spider showing such a scar ultimately had an acrocerid larva emerge from it ($n = 3$). In addition, some acrocerid larvae enter the spider via the abdomen just posterior to the cephalothorax (Schlinger 1981, 1987).

The observed behavior of infected spiders prior to acrocerid emergence was atypical (compared with an uninfected spider), and our observations are similar to those given in other reports (Johnson 1904; Schlinger 1952). *Coras montanus* moved about the main sheet and outer funnel of their web while laying silk, and produced what at first appeared to be a premolting web. The normal premolting web of *C. montanus* covers the web's funnel loosely, but those *C. montanus* specimens containing parasitoids produced webs that were much denser, and nearly occluded the funnel. This web laying activity created a sturdy silk mat, which ultimately provided an anchor where the fly larva would attach upon emergence. Furthermore, millipedes were observed to enter *C. montanus* webs containing fly pupae and eat the host carcass, but not touch the fly pupae. Thus, this thick silk may serve also to protect the vulnerable fly during its pupation.

The Parasite's Behavior and Appearance. In the laboratory. Actual emergence and final feeding on the host by the fly larvae were not observed in the field, but they have been described elsewhere (Millot 1938; Kaston 1937; Lamore 1960; Schlinger 1952, 1981). We present here observations made in the laboratory of larval emergence from an immature *Schizocosa* (collected from Mason County, Illinois, USA, 20 April 1983; observed 6 May 1983).

The spider hung inverted from silk in its water vial with the abdomen hanging perpendicular to the cephalothorax (a very unusual position for lycosids), and the parasitoid emerged from the anterior venter of the abdomen. The spider was not moving at this time, and the larval volume appeared to match that of the host's abdomen. The larva began to pulsate as it emerged and, over time (approx. 10–15 min), the spider's spinnerets and legs twitched intermittently, leg spines were erected, and the legs eventually flexed. After 19 min, the larva had nearly completed emergence, leaving the host's abdomen collapsed and shrivelled; the prosoma and legs were empty. The total emergence period from the *Schizocosa* host in the lab was 1 h 39 min.

One of us (LS) found that since their capture, *Exetasis eickstedtae* larvae remained in spiders from 10 days to a few months, and von Eickstedt (1971, 1974) reported larvae within captive spiders from 139 to 577 days. Schlinger (1987) suggested that the fly larvae remain in their theraphosid hosts for many years before emergence.

In the field. Emergence and external feeding times reported elsewhere for araneomorph hosts vary from between 5.0 and 7.5 h (Millot 1938; Schlinger 1952; Lamore 1960). Because spiders on the cliffs were surveyed at least twice a day and larval emergence was not seen, emergence durations were probably less than 5–6 h. Once emerged, each larva secured its posterior end to the silk and began a stereotypical behavior. The entire translucent, shining anterior half of the larva expanded and contracted rhythmically in and out (spanning 4–6 mm) of its opaque, encapsulated posterior half. Its head swung in an arc across and around the anchored posterior during these movements, reminiscent of a lepidopteran larva spinning a cocoon. Indeed, it was thought initially that the larva was actually spinning silk because of its body motions and mouthpart movements. Subsequent inspection suggested that the larva was simply gathering spider silk strands from around itself. Jenks (1940) thought that the larva "... apparently mixes the host spider silk thread with 'saliva' to form gooey strings and guy ropes...."

Occasionally, the larva pulled its head entirely into the posterior section for 2 s at irregular intervals (approx. 10–15 min apart). Head movements of the larva eventually became shorter, slower, and less vigorous. The larva seemed to condense into its posterior end, twisting around many times in place and assuming a more vertical orientation. This is the position in which most pupae were found. The pupation process required 20–30 h, which agrees with published references (Schlinger 1960).

The newly formed pupae were bottle shaped, with the posterior end darker and nearly cylindrical and the anterior neck region lighter and narrower. This same bottle shape was reported by Emerton (1890*a*). Many had a dark midline, and their sizes ranged from 6–7 mm long by 2–4 mm wide. Six to 10 days later, a dark tarry substance (either the cast larval skin, or the meconium of Schlinger 1952) appeared caudad. The pupae gradually became darker (chocolate brown) and shapes of the incipient adult abdomen, thorax, and finally head became visible over a period of 8–17 days (Figs. 1, 4).

Pupation Duration. Pupation duration observed in the field tended to be longer than those reported by other workers (Table 2). Pupae were taken from the field into the lab 10–15

TABLE 2. Mean pupation duration for various acrocerids. (SEM = standard error of the mean)

Acrocerid	Source	Pupation duration (mean days ± SEM)	*n*	Lab or field; mean temp. °C (if available)
Ogcodes pallidipennis (Loew, 1866)	Present study	7.67 ± 5.4	3	Lab 20
Ogcodes pallidipennis (Loew, 1866)	Schlinger 1960	6.56 ± 1.2	9	Lab —
Ogcodes eugonatus (Loew, 1872)	Kaston 1937	5.5 ± 0.7	2	Lab —
Ogcodes adaptatus (Schlinger, 1960)	Schlinger 1960	3.83 ± 0.9	6	Lab —
Ogcodes dispar (Macquart, 1855)	Lamore 1960	3.4 ± 0.6	5	Lab 22
Ogcodes borealis Cole, 1919	Present study	4.0 ± 0	2	Lab 20
Turbopsebius diligens (Osten Sacken, 1877)	Schlinger 1952	9.5 ± 1.3	6	Lab 20.9
Acrocera bimaculata (Loew, 1866)	Present study	16.87 ± 1.4	8	Field 16

days after pupation to determine eclosion dates accurately. Thus, they spent most of their developmental time in the field. Most eclosion occurred during May (earliest = 10 May, latest = 13 June) when temperatures on the Cumberland Plateau dropped to a low of 6–12°C at night. Reported *Exetasis eickstedtae* pupation times varied from 27 to 60 days (von Eickstedt 1971), and 41 days was observed in this study. Vellard (1934) reported that 26 days was required for the pupation of a species of *Exetasis* from *Grammostola actaeon* (Pocock, 1903). Thus, there seems to be a relationship between the mean duration of mean temperature (Fig. 10). The longer pupation duration for the flies observed in the field was probably caused by the cooler temperatures.

General adult fly behavior seems to vary by genus from quick flying and nectar sucking to sluggish hovering without feeding (Schlinger 1981). Imagoes of *A. bimaculata* and *T. sulphuripes* observed on the cliffs were slow, clumsy fliers. They seemed to prefer walking, and flew only when attempting to escape capture or while in short transit between perches. Adult *T. sulphuripes* were seen on two occasions to hover over *C. montanus* webs, dipping and touching the tips of their abdomens to the silk. Although no eggs were seen (they are minute), it was assumed the flies were ovipositing. Cole (1919) observed *Turbopsebius* (*Opsebius*) *diligens* (Osten Sacken, 1877) ovipositing while in flight. The web owners did not seem aware of the flies' activities. The adult *Exetasis eickstedtae* observed in the lab was quite clumsy, did not attempt to fly, and preferred to hang from spider silk. Because this species has especially well-developed tarsal claws, perhaps it normally hangs on silk lines and walks instead of flying.

Discussion

Host Selection by Acroceridae. Certain spider families (or guilds) tend to be attacked most often by acrocerids, the frequency of which may be dependent upon where these spiders wander, live, or build their snares. Published records indicate a preference by acrocerids for the cursorial or fossorial spiders (mygalomorph spiders — Antrodiaetidae, Ctenizidae, Migidae, Theraphosidae; araneomorph spiders — Anyphaenidae, Clubionidae, Lycosidae, Salticidae, Thomisidae), or those that construct webs close to the ground, have webs with many connections to vegetation, or visit surrounding vegetation or substratum frequently during their activities (Dipluridae; Agelenidae, Amaurobiidae, some Araneidae, Segestriidae).

Two of the most numerous spiders on the sandstone cliffs of the Cumberland Plateau, Tennessee, were *Achaearanea tepidariorum* (C.L. Koch, 1841) (Theridiidae) and *Araneus cavaticus* (Keyserling, 1882) (Araneidae). Despite very extensive, close, and detailed observations of *A. tepidariorum*, and to a lesser extent of *A. cavaticus*, neither of these spiders was seen to be parasitized. Only *Coras montanus* was found to harbor acrocerids, although these three spider species were close cohabitants. Cole (1919) established that *Turbopsebius diligens* has the ability to attach onto *A. tepidariorum*, but these larvae had been purposely placed onto the spiders by hand. The spiders tried to remove the larvae by scratching frantically at them (Cole 1919), and did manage to kill some of the larvae. Cole (1919) did not verify penetration of the spiders' cuticle by the fly larvae.

The disparity of parasitoidism among the spiders on the cliffs and other spider species may be explained by examining the oviposition habits of acrocerids relative to spider behavior, web types, and resting positions. *Achaearanea tepidariorum* and *Araneus cavaticus* usually rest at the center of their webs (tangle web, orb web, respectively), and do not roam regularly over adjacent vegetation or substratum for protracted periods of time. Thus, their exposure to areas where acrocerids may oviposit, and their larvae lurk, is reduced. Furthermore, the architecture of their webs offers few places suitable for successful fly oviposition or larval movement. On the other hand, *Coras montanus* constructs a non-adhesive sheet web attached to a funnel, typical of agelenids, which extends into cracks and crevices on the cliffs. These webs are in close contact with the substratum and the surrounding vegetation. Thus, *C. montanus* constructs a web that functionally acts as a landing platform, where acrocerids may oviposit directly, and where the spider frequently roams. Also, the snare and the spider are in close and frequent contact with surfaces where the flies commonly oviposit and their larvae move.

In sum, members of the host spider families of acrocerids either live on (or in) the ground or vegetation, build webs, silken mats, sheets, linings in burrows, or other silk structures that are conducive to fly oviposition and larval movement. They also have webs with many connections to the substratum, or the spiders frequently visit vegetation adjacent to or touching their webs.

Alteration of Spider Host Behavior by Acrocerid Parasitoids. The observed changes of spider host behaviors preceding emergence of the fly larva (or larvae) may have an evolutionary basis. It has been reported that site selection behaviors of some aphids are altered by an endoparasitic wasp, resulting in the aphid dying in more favorable sites for wasp pupation, depending upon the season (Brodeur and McNeil 1989). Wolf spiders spun atypical silk structures before fly larva emergence (Montgomery 1903), and production of thick silk mats by *C. montanus* hosts infected by acrocerids in the field resulted in preparation of protected attachment and pupation sites for the flies. Thus, here are more examples of adaptive modifications of a parasitoid's host behavior leading to increased chances for parasitoid survival. The mechanisms affecting these behavioral changes are unknown.

Acrocerid Larval Residence Times. Long periods of quiescent residence times (sometimes lasting years) by a parasitoid acrocerid larva inside its host is a common and consistent observation. This behavior would allow a larva entering a small and immature spider to remain within its host until the spider grew larger, ultimately supplying more food to the parasitoid prior to its exit. Feeding and emergence activities may then be triggered by as yet unknown changes in the host that are possibly associated with its penultimate and ultimate molts. By waiting, the larva garners maximal benefits from its host (protection, energy reserves). Furthermore, a large spider (e.g. mygalomorphs) may support many larvae if the first ones entering the spider do not kill their host immediately. Of course, one problem with delayed consumption is the possible death of the host in the interim. The larval inactive period would necessarily vary among all larvae because of varying maturities of the chosen host spiders. Those larvae encountering a more mature host would have a shorter quiescent period. Thus, acrocerids (and indeed other parasitoids) may possess a mechanism to help them assess the developmental state of their hosts upon entrance, since the parasitoids must synchronize their development with that of the host. There is evidence that an endoparasitoid may evoke specific behaviors of its host leading to increased chances of parasitoid survival (Brodeur and McNeil 1989).

Addressing hypotheses concerning acrocerid natural history and behavior will be difficult, given the secretive nature of these flies and the difficulty in determining which spiders are harboring larvae. Perhaps other workers will report their observations or experiences with acrocerids and their hosts in order to establish clearer connections between the behavioral ecologies of these arthropods.

We pose the following questions:

1. Does the acrocerid larva require a long period of quiescence as first-instar and third-instar endoparasitoid larvae? That is, if it entered the host spider during the ante-penultimate instar, would there be sufficient time for the larva to develop normally?
2. Are the larvae able to assess and enter a particular developmental stage of host spider?
3. Does the larva produce ecdysis-like chemicals that regulate the spider's molting, or does it somehow manipulate the spider physically to induce ecdysis?
4. How does an acrocerid larva deal with an adult female mygalomorph spider that undergoes post-adult molts, and could her eggs develop if she possesses one or more acrocerid larvae?
5. What are the proximal and ultimate mechanisms inducing behavioral modifications of the spider by the parasitoid that lead to enhanced survival of the acrocerid?

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FIG. 1. Puparium of *Ogcodes borealis* reposing atop the dried remains of flies (*Drosophila melanogaster* Meigen, 1830) used as spider food, and a small patch of webbing spun by the spider, *Pardosa* sp., shortly before the acrocerid larva emerged (RL photo).

FIG. 2. Adult acrocerid fly, *Ogcodes borealis*, about a day after eclosing from its puparium. Note the small head, typical of all members of this family. The fly is about 5 mm long (RL photo).

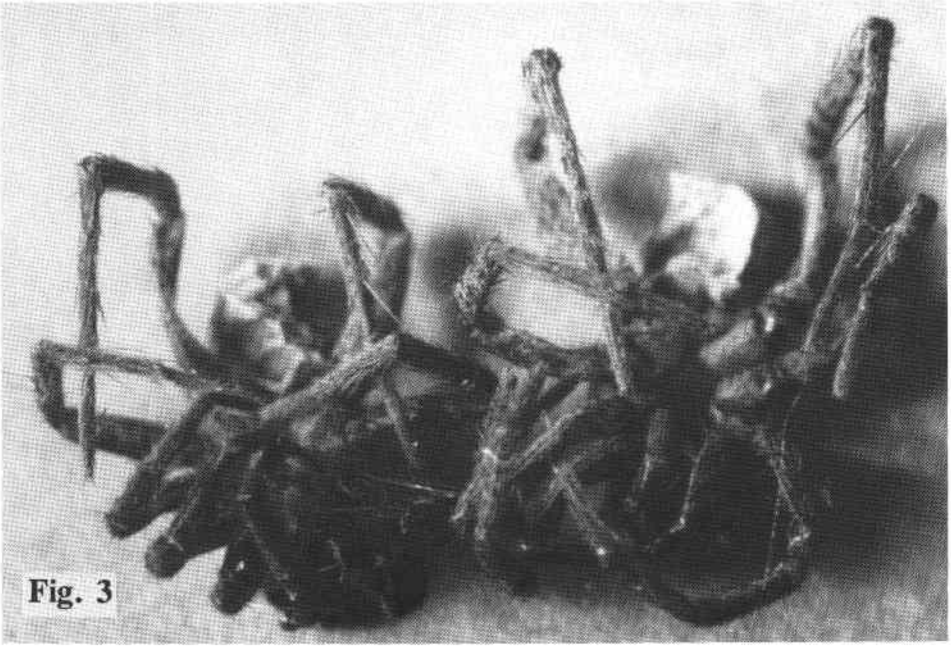

Fig. 3

FIG. 3. The dried, shrivelled exoskeletons of the spider, *Pardosa* sp., from which the fly larvae of *Ogcodes borealis* emerged. The larvae emerged from the venter of the abdomen anterior to the epigastric furrow (RL photo).

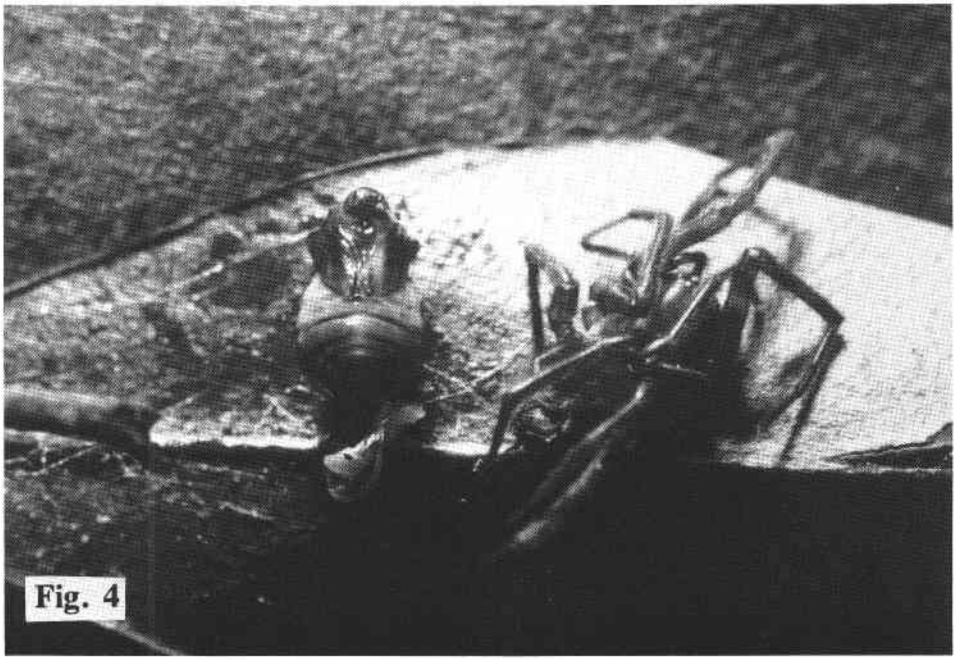

Fig. 4

FIG. 4. The shrivelled carcass of the spider, *Coras montanus*, and the puparium of the acrocerid, *Acrocera bimaculata*. The larva of *A. bimaculata* molted to the puparium shortly after emerging from the spider. A few, widespread strands of webbing are visible around the puparium (Mark H. Evans photo).

Fig. 5

FIG. 5. The dead host theraphosid spider, *Lasiodora klugi*, with emerged and emerging larvae of the acrocerid, *Exetasis eickstedtae* (LS photo).

Fig. 6

FIG. 6. Close-up view of three acrocerid larve of *Exetasis eickstedtae*, which had emerged recently from the theraphosid, *Lasiodora klugi* (LS photo).

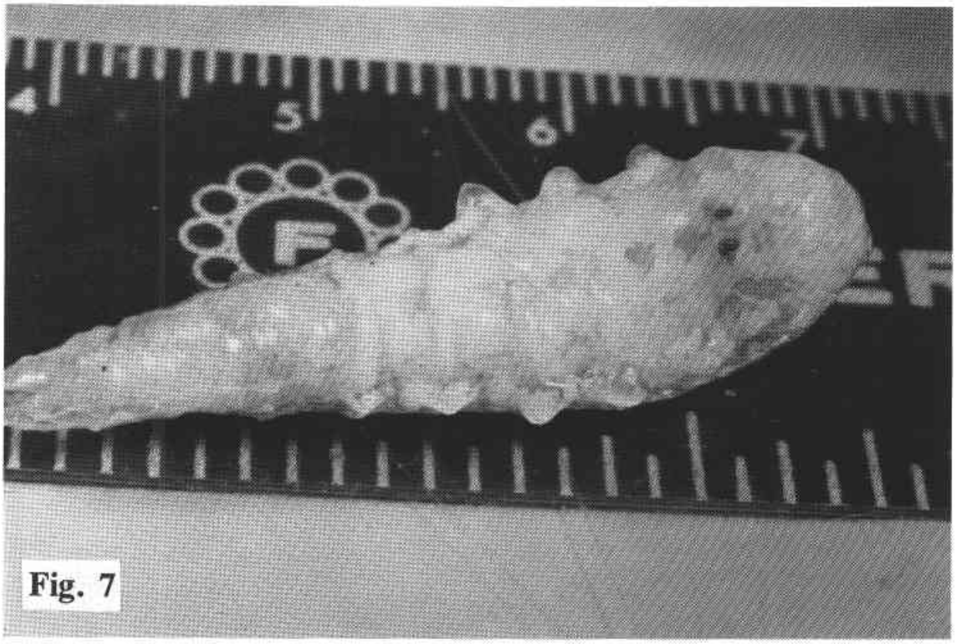

Fig. 7

Fig. 7. Larva of the acrocerid, *Exetasis eickstedtae*. Note that it is over 30 mm long (LS photo).

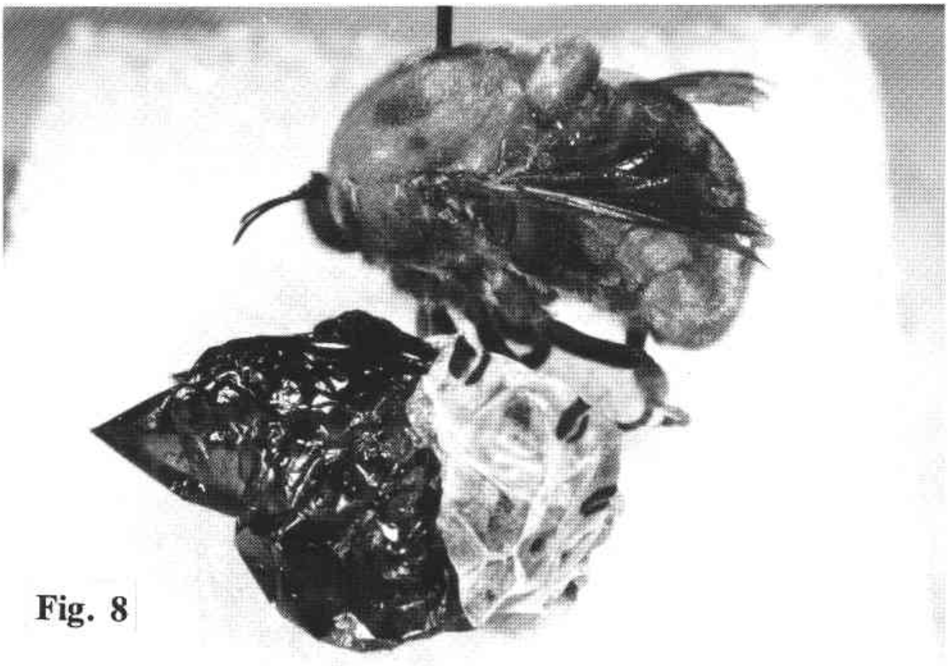

Fig. 8

Fig. 8. Pinned adult acrocerid, *Exetasis eickstedtae*, with puparial skin and shed larval exuvium below. The fly is about 16 mm long (LS photo).

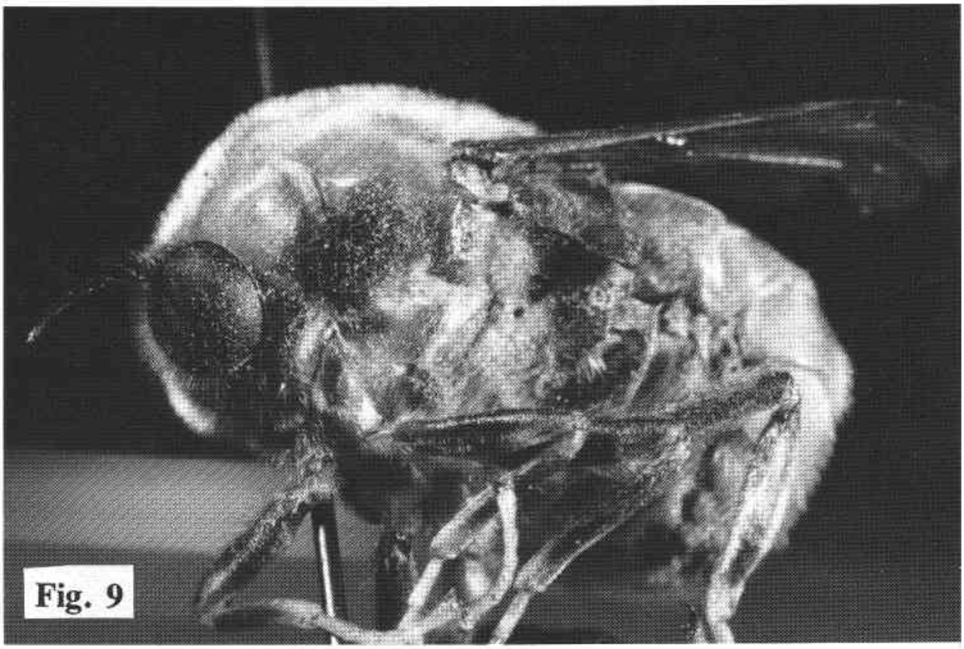

FIG. 9. Prolateral view of adult acrocerid, *Exetasis eickstedtae* (LS photo).

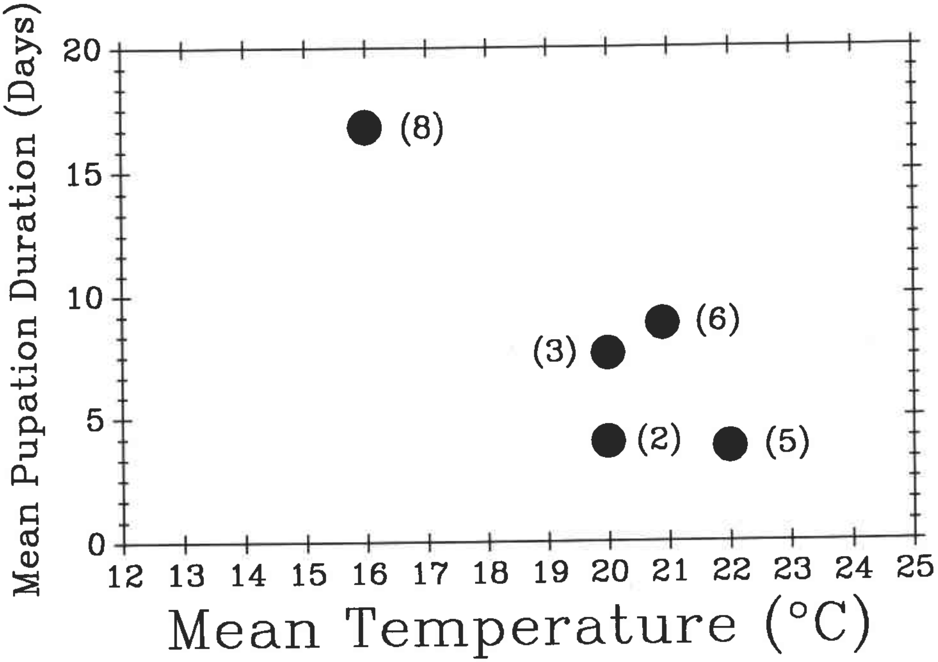

Fig. 10

FIG. 10. Mean duration of acrocerid pupation (days) versus mean ambient temperature (°C). Numbers next to plotted points indicate sample sizes. Generally, higher ambient temperatures result in shorter pupation times.