

UNIVERSITY OF CA RIVERSIDE LIBRARY



3 1210 00789 3132

APPLIED MYRMECOLOGY

A World Perspective

.....



edited by
Robert K. Vander Meer, Klaus Jaffe,
and Aragua Cedeno

.....

Westview Studies in Insect Biology

Behavioral Interactions of Fire Ants and Their Parasites, Predators and Inquilines

D.P. Wojcik

INTRODUCTION

Arthropods that live with, or are associated with, ants are termed myrmecophiles (Wilson 1971, Kistner 1982). This relationship can be permanent or temporary, obligatory or facultative, integrated or nonintegrated. The biology and behavior of these relationships is inadequately known, with much of the information reported in the literature based on cursory observations or invalid interpretations (e.g. miscellaneous soil arthropods floated out of fire ant colonies, Collins and Markin 1971). References to myrmecophiles and their host relationships are numerous, widely scattered and often as difficult to find as the myrmecophiles.

The generally accepted classification of arthropod symbionts is based on a series of works by E. Wasmann, translated into English by Wheeler (1910). Wasmann devised 5 behavioral categories (1) synechthrans (persecuted guests), (2) synoeketes (indifferently tolerated guests), (3) symphiles (true guests), (4) ectoparasites and endoparasites and (5) trophobionts (provide secretions to the ants). While the categories are mutually exclusive, the myrmecophiles can often be placed in different categories at different stages in their life-cycles (Wilson 1971). Several other classification systems have been proposed (Kistner 1979), but none have become as generally accepted as the Wasmannian system. In most cases, the true relationships of the myrmecophiles are unknown, indeed many are still being discovered and their relationships with their hosts defined.

The mechanisms by which myrmecophiles integrate into the host societies have been the subject of many studies with much discussion of body shape, color, special morphological adaptations and appeasement substances (reviewed by Wilson 1971, Kistner 1979). Recently, some inquilines have been shown to use chemical mimicry to integrate themselves into the host colony. These organisms, several termitophilous Staphylinidae (Howard et al. 1980, 1982) and a myrmecophilous Scarabaeidae (Vander Meer and Wojcik 1982), acquire the cuticular hydrocarbons (part of the colony odor) of the host. Other studies by Vander Meer, Wojcik and Jouvenaz (unpublished) indicate this is a wide-spread mechanism in myrmecophiles of *Solenopsis* spp., including some discussed in this paper.

The majority of published papers often document only the occurrence

TABLE 1. Insect groups which have been reported associated with fire ants but their biology and behavior have not been studied.

ORDER	Family	Reference
BLATTARIA		
	Atticolidae	Roth and Willis 1960
COLEOPTERA		
	Anticidae	Bruch 1917, Wasmann 1918b
	Carabidae	Wasmann 1918b, Neece and Bartell 1981, Kistner 1982
	Chrysomelidae	Wojcik et al. 1987a
	Histeridae	Wasmann 1918a, 1918b, Bruch 1929, Helava et al. 1985, Wojcik et al. 1987a
	Melandryidae	Neece and Bartell 1982
	Scydmaenidae	Bruch 1917
	Staphylinidae	Wasmann 1912, 1918a, 1925a, Bruch 1917, 1929, Travis 1941, Silveira Guido et al. 1965, Collins and Markin 1971, Kistner 1982, Neece and Bartell 1982, Banks et al. 1985
	Tenebrionidae	Fall 1928, Silveira Guido et al. 1963 Summerlin 1978, Neece and Bartell 1981, 1982, Steiner 1982
DIPTERA		
	Syrphidae	Borgmeier 1923, 1953
HEMIPTERA		
	Cydnidae	Neece and Bartell 1981 Wasmann 1918a, Silveira Guido et al. 1965
HOMOPTERA		
	Cixiidae	Borgmeier 1923, Travis 1941, Anon 1958, Wilson 1971, Bartoszeck 1976, Wojcik 1986
		Sheppard et al. 1979, Neece and Bartell 1982
HYMENOPTERA		
	Bethylidae	Bruch 1917, Kieffer 1921, Wasmann 1925b, Ogloblin 1963
	Ceraphronidae	Bruch 1929
	Diapriidae	Kieffer 1921
	Ichneumonidae	Wasmann 1912
STREPSIPTERA		
	Myrmecolacidae	Ogloblin 1939, Teson and de Remes Lenicov 1979

of myrmecophiles with their hosts. In preparing this review, I have limited citations to those references which present or review biological or behavioral information on fire ant myrmecophiles. Groups which have been reported as associated with fire ants, but where no biology or behavior have been reported

are listed in Table 1. The fire ant names used in this paper are used in the sense of Trager (in press, A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae, Myrmicinae).

DISCUSSION

Acarina

The mite fauna of fire ant nests has not been well studied. In only one case has a mite, a tarsonemid sp., been observed to feed on liquids from the mouthparts of a fire ant, *Solenopsis geminata* (F.) and occasionally feed on excreta at the ant's anus (Travis 1941). The mites stand erect, bobbing up and down on the ants, while tapping them with the first pair of legs. Some species belonging to known predaceous or parasitic groups were collected from fire ant nests (Hermann et al. 1970, Hunter and Costa 1971, Neece and Bartell 1982), but predation or parasitism was not observed. Most of the mites collected while on the ants bodies are assumed to be phoretic. Some have been collected only on workers (Anon 1958), others on female alates before (Hermann et al. 1970, Hirschmann 1972) or after mating flights (Hermann et al. 1970) and some on both ant castes (Hermann et al. 1970, Collins and Markin 1971, Wojcik unpublished). Occasionally the mites were so numerous that the female alates were unable to fly (Hermann et al. 1970). Some phoretic mite species are not host specific and have been collected on several genera of ants including *Solenopsis* (e.g. *Oplitis exopodi* Hunter and Farrier, *Oplitis virgulinus* Hunter and Farrier, Hunter and Farrier 1975, 1976). As might be expected since phoretic mites only use the ants for transportation, they are not always found in association with ants (e.g. *Oplitis* spp., Hunter and Farrier 1975, 1976).

Diplopoda

Several species of millipedes are considered fire ant myrmecophiles, although little is known of their biology and behavior (Schubart 1950). *Calytodesmus schubarti* Causey is a facultative fire ant myrmecophile also found with other genera of ants in Florida and Georgia (Wojcik and Naves in press). This species scavenges from the nests of *S. geminata* and *S. invicta* Buren, feeding on organic debris that includes dead or injured fire ant adults and brood in the colonies. The millipedes are generally ignored by the ants, but can be killed and eaten by the ants in stress situations. The millipedes have a defensive secretion which usually stops ant aggressive behavior. Similar unidentified species have been found with several fire ant species in Brazil (Banks et al. 1985, Wojcik 1986, Wojcik et al. 1987a) and recently with *S. richteri* Forel in Argentina (Wojcik unpublished).

Coleoptera: Pselaphidae

A number of pselaphids are known myrmecophiles, ranging from well-integrated symphiles with well-developed trichomes to barely tolerated scavengers (Kistner 1982). Pselaphid beetles from 8 genera (8 species) have been collected from fire ant nests (Wojcik in preparation), but nothing is known of most species biology. *Eurhexius putzeyssi* Schauff., *Ctenisis*

fasciculata Raffray and *Pselaphomorphus bruchi* Raffray (Bruch 1917) have been collected only in abandoned or semi-abandoned fire ant mounds. *Metopioxys gallardoii* Bruch is known from *S. richteri* nests in Argentina and Uruguay (Bruch 1917, San Martin 1968a). This species has been kept in laboratory colonies for up to 3 months, with the beetles often observed riding about the nest on the ants' backs (Silveira Guido et al. 1964, San Martin 1968a). The food habits of this species remain a mystery.

Fustiger elegans Raffray is considered a symphile and has been collected from nests of *S. richteri* and *Solenopsis* spp. in Argentina and Uruguay (Bruch 1930, San Martin 1968b, Wojcik unpublished). It is well integrated into the fire ant society with 572 beetles found in one mound (San Martin 1968b) and it survives during stress situations (Wojcik unpublished). San Martin (1968b) reported a laboratory lifespan for this species of up to 154 days. They have been observed moving about the colony with fire ant eggs in their mandibles (Silveira Guido et al. 1963, San Martin 1968b). These findings, coupled with the observations that the beetles usually stay in close proximity to or in the brood piles, are taken as evidence that this species preys on ant eggs (Silveira Guido et al. 1963, San Martin 1968b). This species was collected from *S. richteri* nests in Argentina and was observed preferentially staying in the brood piles in laboratory colonies (Wojcik unpublished). This species has trichomes which are highly attractive to the ants, even to the point of the ants rescuing live and dead individuals in disturbed laboratory situations (Wojcik unpublished). *F. elegans* can often be seen (in laboratory nests) climbing onto the ants and even riding around the nests on the ants (San Martin 1968b, Wojcik unpublished). Hexane washes of this species have shown the presence of the host ant cuticular hydrocarbons (Vander Meer and Wojcik unpublished) which implies chemical mimicry as one of its integrating mechanisms.

Coleoptera: Scarabaeidae

This large and diverse family has many myrmecophilous genera and species in 6 subfamilies (Kistner 1982). A mere 4 species in 4 genera have been associated with fire ants. Collection records are only available for 2 of the species: *Rhyssemus neglectus* Brown was collected from the nests of *S. invicta* and *S. xyloni* McCook (Summerlin 1978) and *Myrmecaphodius proseni* Martinez was collected from nests of *Solenopsis saevissima* (F. Smith) (Martinez 1952).

Euparia castanea Serville occupies the nests of *S. geminata* and *S. xyloni* from the southern United States to Costa Rica (Chalumeau and Howden 1984). Travis (1941) was the first to observe the ants gnawing on the beetles at the junction of prothorax and elytra. I have also seen this behavior, but have never found trichomes (Wojcik unpublished). I found that this beetle ate ant larvae, and fed by strigilation on ant larvae and dead ants (Wojcik 1975). The beetles also feed on other dead insects, indicating scavenging. The flight periods of this species are not correlated with the mating flights of its hosts (Wojcik et al. 1978); the beetles flew in all stages of ovarian development (Wojcik and Habeck 1977).

Chalumeau (1983) described the scarab beetle *Martinezia dutertrei* Chalumeau (= *Myrmecaphodius excavaticollis* Blanchard) from Cuba, giving its distribution as United States, Cuba, Brazil, Paraguay and Argentina. This

species has been found with *S. geminata*, *S. xyloni*, *S. invicta* and *S. richteri* in the United States (Wojcik et al. 1977). *M. dutertrei* and 4 other *Martinezia* spp. were collected in Brazil, Bolivia, Paraguay, Argentina and Uruguay, but identifications of the host ants were not given (Chalumeau 1983). Beetles of this genus have been collected from *S. invicta*, *S. richteri* and *Solenopsis* spp. nests in South America (Banks et al. 1985, Wojcik 1986, Wojcik et al. 1987a, Wojcik unpublished). Wojcik (1975) demonstrated that this beetle is a predator feeding on ant larvae. It also fed as a scavenger on ants and other insects and by strigilation on dead ants. The ants usually treat this species as a symphile, even ignoring the beetles as they consumed living host larvae, but the ants will eat the beetles in stress situations (Wojcik 1975, unpublished). Ants are often observed to gnaw on the beetles at the junction of the prothorax and the elytra as observed on *E. castanea*, though no trichomes have been found (Wojcik unpublished). The beetles have the ability to acquire the host cuticular hydrocarbons even when switching hosts (Vander Meer and Wojcik 1982), allowing them to live with more than one ant host (Wojcik et al. 1977, Summerlin 1978). The flight periods of the beetle are not correlated with the mating flights of the host ants (Wojcik et al. 1978) and the beetles flew in all stages of ovarian development (Wojcik and Habeck 1977). This species was probably introduced into North America with one or more of its imported ant hosts (Lofgren et al. 1975). As its imported hosts, *S. invicta* and *S. richteri*, spread in the United States and displace the native fire ants, *S. geminata* and *S. xyloni*, *M. dutertrei* will probably become more common, while the native *E. castanea* will become rarer (Wojcik et al. 1977).

Coleoptera: Staphylinidae

Hundreds of staphylinid species from this widespread and diverse beetle family are known myrmecophiles (Kistner 1982). No information is available on 41 species in 23 genera in 4 subfamilies known from fire ant nests (Table 1). Only 4 genera, *Myrmecosaurus*, *Dinardopsis*, *Euthorax* and *Dinusella*, appear to have special morphological adaptations for living in fire ant nests (Kistner 1982). Out of the 22+ species in these genera, behavioral information is available only for *Myrmecosaurus ferrugineus* Bruch. Wojcik (1980) observed this non-predaceous symphile soliciting food and being fed by the host *S. invicta*. It is well integrated into the fire ant society and was probably introduced into North America with one of its imported hosts (Lofgren et al. 1975). Hexane washes of *Myrmecosaurus* spp. (collected from *S. richteri* and *Solenopsis* spp. nests in Argentina) reveal that they acquire the hosts' cuticular hydrocarbons (Vander Meer and Wojcik unpublished).

The genus *Oxypoda* does not have special morphological adaptations for the myrmecophilous existence. Six *Oxypoda* sp. specimens (identified by J.H. Frank, Univ. Florida), collected from a *S. geminata* nest in Gainesville, FL, were observed in laboratory nests for up to 8 days (Wojcik unpublished). The beetles were treated as synechthrans (persecuted guests) with the host ants pursuing and attacking the beetles continuously. The beetles constantly presented their abdominal tips to the ants' heads, an act which neutralized the ants aggressive behavior. Similar behavior has been reported in other staphylinid genera (e.g. 2 *Pella* spp., Kistner and Blum 1971), and there are many reports of defensive secretions in staphylinids (Kistner 1982). The *Oxypoda* sp., often hiding in the brood pile, licked (strigilated) the ant pupae

and appeared in several instances, to grab the pupae with their mouthparts, trying to tear the pupal cuticle without success.

Diptera: Phoridae

Most Phoridae are of an unknown status, including most of the genera associated with fire ants (Kistner 1982, Wojcik in preparation). Biological information exists only for some *Pseudacteon* species from North and South America. The ant head is commonly the oviposition site (*P. obtusus* Borgmeier, Williams and Banks 1987; *P. crawfordii* Coquillett, Coquillett 1907, Wheeler 1910 and Smith 1928), although Feener (1987) provided detailed observations of *P. crawfordii* ovipositing on the host's prothorax at the junction of the dorsal and ventral sclerites. In only a few instances have eggs (*P. obtusus*; Williams and Banks 1987), or pupae (unknown genus, species; Wojcik et al. 1987b), been observed on or in the host. Generally when the flies attack the ants, they hover over foraging trails (*P. obtusus*, William and Banks 1987; *Pseudacteon* spp., Wojcik unpublished), over nests during mating flights (*P. spatulatus* (Malloch), *P. crawfordii*, Smith 1928), or over disturbed nests (*Pseudacteon* spp., Williams 1980; Wojcik unpublished). These situations are probably similar as far as the flies are concerned. The flies dart onto the ants, and quickly attempt to deposit an egg (*P. obtusus*, Williams and Banks 1987) or insert the ovipositor in the appropriate place (*P. crawfordii*, Feener 1987). The ants sometimes appear stunned after oviposition (*P. spatulatus* and *P. crawfordii*, Smith 1928; *Pseudacteon* spp., Williams 1980). The ants vigorously defend themselves against the flies (*P. spatulatus*, *P. crawfordii*, Smith 1928; *P. crawfordii*, Feener 1987; *P. obtusus*, Williams and Banks 1987; *Pseudacteon* spp., Williams et al. 1973; Wojcik unpublished), often chasing the flies away before oviposition (*Pseudacteon* spp., Williams 1980).

In fire ants, the major workers are preferentially attacked while the minors are usually ignored (*P. crawfordii*, Feener 1987; *P. obtusus*, Williams and Banks 1987). The flies probably oviposit selectively on major workers because they represent a larger, more stable and longer-lived food source (Feener 1981, 1987, Williams and Banks 1987). Alate ants, while representing a larger food source, are much less common in colonies and are rarely exposed to parasitism. Only one instance of phorid parasitism of alate ants is known (Wojcik et al. 1987b).

A different scenario of parasitism has been reported for *Apodicrania termilophila* (Borgmeier), a fly found parasitizing several *Solenopsis* spp. in South America (Williams 1980). The adult flies walked around on the disturbed nest and the ants ignored them. Immature fly larvae are endoparasitic in the ant larvae while mature fly larvae and pupae are found in the nest being tended by the ants (Williams 1980).

Commoptera solenopsidis Brues, a wingless species, was discovered running around inside nests of *S. geminata* (Brues 1901). Unidentified wingless phorids have been found in *S. richteri* nests in Argentina (Wojcik unpublished). These phorids, like the ones described by Brues (1901), run jerkily among the ants, never contacting the ants.

Hemiptera

Many free-living Hemiptera prey on ants (Kistner 1982), with *Acanthaspis concinnula* Stal reported as a specific predator of *S. geminata* in Ceylon (Mühlenberg and Maschwitz 1976). The bugs lie in wait for an ant to pass by, then pierce the ants with their mouthparts and inject poison. Once subdued, the ant is sucked dry. The carcass, added to the debris on the bugs back, acts as camouflage and an attractant for more ants. This relationship needs more study because *S. geminata* is not native to Ceylon, but was probably introduced in colonial times.

Two species of true myrmecophiles are known from fire ant nests in South America. *Anommatorcoris coleopteratus* (Kormilev), family Tingidae, is known from *S. richteri* and *S. saevissima* nests in Argentina and Uruguay, but nothing is known of its biology (San Martin 1966b). *Neoblissus parasitaster* Bergroth, family Lygaeidae, is a well-known associate found in *S. richteri* and *S. saevissima* nests in Argentina and Uruguay (San Martin 1966a). These bugs can be extremely numerous in fire ant mounds. Bruch (in San Martin 1966a) reported thousands in one nest and San Martin (1966a) commonly captured several hundred from one nest. I have collected over 100 from a single nest sample several times (Wojcik unpublished). The bugs are treated as symphiles by the ants and only killed in laboratory-created stress situations (San Martin 1966a, Wojcik unpublished). The bugs are aided in ecdysis by the ants (San Martin 1966a). The feeding relationship of bug to ant is unclear at this time. Although they commonly accumulate in brood piles, the ants sometimes chase them away (San Martin 1966a, Wojcik unpublished). This species has a distinctive strong defensive odor which it uses on the ants when they become too aggressive (Wojcik unpublished). San Martin (1966a) thinks the bugs feed on the abundant plant roots, particularly grasses, found in the ant mounds.

Hymenoptera: Eucharitidae

All eucharitid wasps are considered parasites of ants (Kistner 1982). Fire ant parasites are known only from the genus *Orasema* which also includes species parasitic to other ant genera. The following synthesis includes the known information about the fire ant parasites *Orasema crassa* De Santis, *Orasema aenea* Gahan, *Orasema rapo* Walker (Williams 1980) and *Orasema* spp. (Silveira Guido et al. 1964, Williams 1980, Wojcik unpublished). The females lay their eggs in plant tissue away from the hosts; apparently the wasps are not restricted to specific plants or plant parts (Parker 1942, Tochetto 1942). *Orasema* spp. have a highly sclerotized scimitar-shaped ovipositor (Heraty 1985) and insert their eggs singly into incisions in the leaf surfaces (Clausen 1940).

After hatching, planidia (first instar larvae) wait for an appropriate ant host on the plant surface. The legless planidia (Heraty and Darling 1984) climb on to the ant, and ride phoretically back to the ant nest, attached by means of an anal sucker. In the ant nest, the planidia leave the adult ant and transfer to the ant brood (larvae and pupae), probably via the nurse ants during feeding. Upon locating an ant larva, the planidia burrow beneath the larvae's cuticle (Wheeler and Wheeler 1937, Heraty and Wojcik unpublished). The parasite only develops after the ant larva reaches the late prepupal stage

(Wheeler 1907, Clausen 1941). Then the parasite emerges from the host and feeds as an ectoparasite on the host (at least in some cases, Wojcik unpublished) after the host pupates. In other cases (Wheeler and Wheeler 1937), the parasite feeds at least partially as an endoparasite. This feeding results in a characteristically deformed pupae called a phthisergate (Wheeler 1907). Indirect evidence (Wojcik unpublished) indicates that the *Orasema* spp. which parasitize *Solenopsis* spp. in Mato Grosso, Brazil may require more than one host pupae. This is suggested by the mature parasite larvae's size and the variable sizes of the phthisergates. In those instances where the phthisergates survive the feeding by the wasp larvae, they are unable to complete development and eventually die (Wheeler 1910, Wojcik unpublished).

After the mature wasp larva terminates feeding, it leaves the host and is kept with the ant brood, where it is cared for by the worker ants (Wojcik unpublished). The parasite pupates with the assistance of the worker ants (just as they assist the ant larvae) (Silveira Guido et al. 1964, Wojcik unpublished). During the pupal period, the parasite pupae are mixed in with the host pupae, and are cared for like ant pupae (Silveira Guido et al. 1964, Williams 1980, Wojcik unpublished). Worker ants assist eclosion by the parasites in the same manner as the ants assist their own pupae (Silveira Guido et al. 1964, Wojcik unpublished). Fed and groomed by the worker ants, the adult parasites are integrated completely into the ant society (Silveira Guido et al. 1964, Williams 1980, Wojcik unpublished). When a nest is disturbed, the pupal and adult parasites are rescued by the ants in preference to their own brood (Wojcik unpublished). The manner in which the *Orasema* spp. adults leave the nest has not been observed, but in other eucharitid genera the ants either ignore the parasites when they are leaving the nest (Clausen 1923, 1941) or they actively remove them from the nest (Ayre 1962). The males hover over the ant nest, or rest on surrounding vegetation (Williams 1980, Wojcik and Jouvenaz unpublished). The adult parasites must be sexually mature when they leave the nest because mating takes place immediately (Williams 1980). Studies of cuticular hydrocarbons have shown that *Orasema* sp. larvae, pupae and adults possess only *Solenopsis* sp. host cuticular hydrocarbons while in the ant nest; upon leaving the host nest, the adult *Orasema* sp. acquire species-specific cuticular hydrocarbons (Jouvenaz et al. 1988, Vander Meer et al. 1989).

I should note that oviposition by *Orasema* spp. in plant tissue can sometimes cause cosmetic economic damage to bananas and other fruits (Tocchetto 1942, Nicolini 1950, Roberts 1958). In one case, damage to bananas by *Orasema* sp. populations required insecticidal bait treatment of the host ants to alleviate the problem (Ostmark and Evers 1976).

Hymenoptera: Formicidae

Social parasitism of ants by other ants runs the gamut from temporary parasitism by a newly-mated queen to slave-making to obligatory parasitism (Buschinger 1986). Temporary parasitism has been suggested for several *Solenopsis* spp. which produce a worker caste (Williams 1980), but nothing is really known of their biology. The true parasitic ants do not produce a worker caste (Wilson 1971). The workerless *Solenopsis* (*Labauchena*) *daguerrei* Santschi does not execute the host *S. richteri* (Silveira Guido, et al. 1973) as

has been erroneously reported (Bruch 1930, Askew 1971). Instead, it attaches itself to the host queen's neck and steals the food the workers offer their mother queen (Silveira Guido et al. 1968, 1973). Some evidence suggests the parasite queen is preferentially fed before the host queen, and even the parasite immatures are more attractive to the workers than their own brood (Silveira-Guido et al. 1965, 1973). Eventually the host queen is deprived of so much food that her egg production declines and the colony's vigor and size decreases, particularly when more than one parasite queen is present (up to 10 have been found on one host queen, Silveira-Guido et al. 1965, 1973). The host queen eventually dies resulting in the demise of the colony. *S. richteri* colonies have been found with over 3,300 parasite adults (males and females) and immatures (70% of the collected colony) (Silveira-Guido et al. 1965, 1973). The incidence of parasites in active fire ant mounds was as high as 31% in some of the areas sampled (Silveira-Guido et al. 1965, 1973). The method of invasion and integration into the host colony is not understood. This species of parasite is a prime candidate for biological control of fire ants in the United States.

Lepidoptera

The many species of Lycaenidae and Riodinidae, associated with ants, are considered trophobionts (Wilson 1971, Kistner 1982), although the late-larval instars of some species prey on ant brood (Kistner 1982). To date, only 2 riodinid species are known to associate with fire ants. *S. geminata* (among other species of ants) tended *Eurybia elvina* Stichel in Mexico (Horvitz et al. 1987). This ant frequently constructed soil shelters over late instar larvae on the host plant. *Hameris epulus signatus* Stichel is known from nests of *S. richteri* from Argentina and Uruguay (Bruch 1926, Silveira Guido et al. 1964). The larvae possess excretory organs that secrete fluids upon which the ants feed (Bruch 1926). According to Bruch (1926), the larvae left the ant nests at night to feed on their preferred host plant, *Vicia graminea* Sm. (Leguminosae). The larvae could be predaceous since cuticular fragments of ant larvae have been found in the caterpillar digestive tracts (A. Oglobin in Silveira Guido et al. 1964). The caterpillars, which pupate in the ant nests, and the pupae are not molested by the ants in laboratory nests (Bruch 1926, Silveira Guido et al. 1964, Wojcik unpublished).

Orthoptera

Only crickets from the genus *Myrmecophilia* (monogeneric family Myrmecophilidae) are known myrmecophiles (Kistner 1982). The species of this genus have multiple ant hosts including *Solenopsis* (Kistner 1982). *Myrmecophilia nebrascensis* Lugger has been collected from *S. invicta* and *S. xyloni* nests in Texas (Neece and Bartell 1981, 1982); the biology and behavior of this species was summarized by Wheeler (1910). The cricket is a synoekete which apparently feeds by strigilation on the surface secretions of its ant hosts and may steal food from them. Another species, probably *M. pergandei* Bruner, has been collected from *S. geminata* nests (Travis 1941, Wojcik unpublished) and *S. invicta* nests (Wojcik unpublished) in the southeastern United States. The behavior of these crickets in *S. invicta* laboratory nests was similar to that reported for other species. The crickets

fed on or licked the surfaces of the ants and fled whenever approached by them. The crickets did not follow artificial or natural *S. invicta* trails and were eventually killed by the ants (Wojcik unpublished).

Thysanura

Thysanurans were among the first myrmecophiles studied and are found with many genera of ants (Kistner 1982). They steal food during trophallaxis, feed on body fluids of booty, or are strigilators. Many are found with more than one host, e.g. *Grassiella praestans* Silvestri has been collected from *Atta* spp. and *Solenopsis* spp. nests in Brazil (Eidmann 1937) and *S. geminata* nests in Mexico (Wasmann 1912). *Grassiella* sp., *Mirolepisma* sp. and *Prolepismina* sp. have been collected from several *Solenopsis* spp. nests in the United States (Collins and Markin 1971, Neece and Bartell 1981, 1982), but the only reported behavior is that they flee from the ants (Collins and Markin 1971). I have observed a species of thysanuran collected from Florida and Georgia *S. invicta* nests (Wojcik unpublished), which is probably the same species collected by Collins and Markin (1971) and Neece and Bartell (1981, 1982). The thysanurans displayed rapid movement in the laboratory colony, avoiding the ants. When the opportunity arose the thysanurans appeared to strigilate the cuticle of the ant workers and brood without attempting to pierce the cuticle. In other cases the thysanurans seized the brood and carried them away from the brood pile. The ant pupae were eaten by the thysanurans. The ants acted aggressively towards the thysanurans, killing them when possible. Thysanurans can be abundant in fire ant nests in the United States and Brazil, but are difficult to capture alive and uninjured particularly when the fire ant colonies are floated out in the laboratory (Wojcik unpublished).

CONCLUSION

The true relationship of most myrmecophiles with their ant hosts remains unknown. Much of the older literature on myrmecophiles needs to be critically reevaluated in light of recent knowledge and updated taxonomy. There appears to be more variation in biology and behavior among related genera and species than has been assumed in the past. Therefore, many previous generalizations are invalid. The Wasmannian classification system for myrmecophiles (and other social insect symbionts) is imperfect, as shown in past discussions. However, it is convenient to use and when combined with categories such as predator or parasite, the combined classification system can be very informative. Additional studies on the biology and behavior of myrmecophiles will supply new information on the complex relationships between ants and their inquilines and provide the basis for a better understanding of these relationships.

Although we have little data on the effects of fire ant myrmecophiles on colony longevity, it is reasonable to assume that these organisms reduce colony fitness by usurping resources. Myrmecophiles such as *Solenopsis* (*Labauchena*) spp. can cause colony mortality, albeit slowly. Myrmecophiles, that eat or parasitize fire ant immatures (e.g. some scarab beetles, phorids and Thysanura), cause the malformation and death of immatures (e.g. *Orasema* spp.), or utilize their food resources (e.g. some mites and staphylinid beetles), produce additional stress on fire ant colonies. This combination of additive

mortalities and draining of resources must effect fire ant colony vigor and perhaps survival. The abundance and effects of a biological control agent in its homeland are not necessarily indicative of its utility when introduced into a new environment (Doutt and Debach 1964). Therefore, each myrmecophile must be evaluated for effectiveness in the new environment before it can be discarded from an IPM program for fire ant control.

LITERATURE CITED

- ANON. 1958. Observations on the biology of the imported fire ant. USDA, ARS 33-49, 21 p.
- ASKEW, R.R. 1971. Parasitic insects. American Elsevier Publ. Co., Inc., New York. 316 p.
- AYRE, G.L. 1962. *Pseudometagea schwarzii* (Asm.) (Eucharitidae: Hymenoptera), a parasite of *Lasius neoniger* Emery (Formicidae: Hymenoptera). Can. J. Zool. 40: 157-64.
- BANKS, W.A., D.P. JOUVENAZ, D.P. WOJCIK and C.S. LOFGREN. 1985. Observations on fire ants, *Solenopsis* spp., in Mato Grosso, Brazil. Sociobiology 11: 143-52.
- BARTOSZEK, A.B. 1976. Afideos de laranjeira (*Citrus sinensis* Osb.) e minoseira (*Citrus reticulata* B.), seus predadores e parasitas. Acta Biol. Parana, Curitiba 5: 15-48.
- BORGMEIER, T. 1923. Novos phorideos brasileiros. Bol. Mus. Nac. (São Paulo) 1: 51-59.
- BORGMEIER, T. 1953. Syrphidenlarven in Ameisennestern. Naturwissenschaften 40: 36.
- BRUCH, C. 1917. Nuevas capturas de insectos mirmecófilos. Physis 3: 458-65.
- BRUCH, C. 1926. Orugas mirmecofilas de *Hameris epulus signatus* - Stich. Rev. Soc. Entomol. Argent. 1(1): 1-9.
- BRUCH, C. 1929. Neue myrmecophile Histeriden und Verzeichnis der aus Argentinien bekannten Ameisengäste. Zool. Anz., Wasmann-Festband 82: 421-37.
- BRUCH, C. 1930. Notas preliminares acerca de *Labauchena daguerrei* Santschi. Rev. Soc. Entomol. Argent. 3: 73-80, plates I, II.
- BRUES, C.T. 1901. Two new myrmecophilous genera of aberrant Phoridae from Texas. Amer. Natur. 35: 337-56.
- BUSCHINGER, A. 1986. Evolution of social parasitism in ants. Trends Ecol. Evolut. 1: 155-60.
- CHALUMEAU, F. 1983. *Batesiana* et *Martinezia*, nouveaux genres d'Eupariini (Coleoptera: Scarabaeidae: Aphodiinae) du nouveau monde. Bull. Mensuel Soc. Linn. Lyon 52: 142-53.
- CHALUMEAU, F. and H.F. HOWDEN. 1984. Le genre *Euparia* (Coleoptera: Scarabaeoidea: Aphodiinae) Saint-Fargeau and Serville, 1828. Mitt. Schweiz. Entomol. Ges. 57: 85-94.
- CLAUSEN, C.P. 1923. The biology of *Schizaspidia tenuicornis* Ashm., a eucharid parasite of *Camponotus*. Ann. Entomol. Soc. Am. 16: 195-217, plates XIV-XV.
- CLAUSEN, C.P. 1940. The oviposition habits of the Eucharitidae (Hymenoptera). J. Washington Acad. Sci. 30: 504-16.
- CLAUSEN, C.P. 1941. The habits of the Eucharitidae. Psyche 48: 57-69.

- COLLINS, H.L. and G.P. MARKIN. 1971. Inquilines and other arthropods collected from nests of the imported fire ant, *Solenopsis saevissima richteri*. Ann. Entomol. Soc. Am. 64: 1376-80.
- COQUILLET, D.W. 1907. A new phorid genus with horny ovipositor. Can. Entomol. 39: 207-8.
- DOUTT, R.L. and P. DEBACH. 1964. Some biological control concepts and questions, p. 118-42. In P. Debauch (ed.), Biological control of insect pests and weeds. Reinhold Publ. Co., NY. 844 P.
- EIDMANN, H. 1937. Die gäste und Gastverhältnisse der Blattschneiderameise, *Atta sexdens* L. Z. Morphol. Oekol. Tiere 32: 391-462.
- FALL, H.C. 1928. *Alaudes*. Pan-Pac. Entomol. 4: 145-150.
- FEENER, D.H., Jr. 1981. Competition between ant species: outcome controlled by parasitic flies. Science 214: 815-7.
- FEENER, D.H., Jr. 1987. Size-selective oviposition in *Pseudacteon crawfordi* (Diptera: Phoridae), a parasite of fire ants. Ann. Entomol. Soc. Am. 80: 148-51.
- HELAVA, J.V.T., H.F. HOWDEN and A.J. RITCHIE. 1985. A review of the new world genera of the myrmecophilous and termitophilous subfamily Hetaeriinae (Coleoptera: Histeridae). Sociobiology 10: 127-382.
- HERATY, J.M. 1985. A revision of the nearctic Eucharitinae (Hymenoptera: Chalcidoidea: Eucharitidae). Proc. Entomol. Soc. Ontario 116: 61-103.
- HERATY, J.M. and D.C. DARLING. 1984. Comparative morphology of the planidial larvae of the Eucharitidae and Perilampidae (Hymenoptera: Chalcidoidea). System. Entomol. 9: 309-28.
- HERMANN, H.R., M.S. BLUM and A.N. HUNT. 1970 (1971). Myrmecophilous arthropods associated with the imported fire ant, *Solenopsis saevissima* (Hymenoptera: Formicidae). Proc. La. Acad. Sci. 33: 13-8.
- HIRSCHMANN, W. 1972. Gangsystematik der Parasitiformes. Teil 103. Von J.C. Moser gesammelte Uropodiden aus Nordamerika und 2 neue *Oplitis*-arten. Acarologie 17: 28-9. Abbildung 36-7.
- HORVITZ, C.C., C. TURNBULL and D.J. HARVEY. 1987. Biology of immature *Eurybia elvina* (Lepidoptera: Riodinidae), a myrmecophilous metalmark butterfly. Ann. Entomol. Soc. Am. 80: 513-9.
- HOWARD, R.W., C.A. MCDANIEL and G.J. BLOMQUIST. 1980. Chemical mimicry as an integrating mechanism: cuticular hydrocarbons of a termitophile and its host. Science 210: 431-3.
- HOWARD, R.W., C.A. MCDANIEL and G.J. BLOMQUIST. 1982. Chemical mimicry as an integrating mechanism for three termitophiles associated with *Reticulitermes virginicus* (Banks). Psyche 89: 157-67.
- HUNTER, J.E., III. and M.H. FARRIER. 1975. Mites of the genus *Oplitis* Berlese (Acarina: Uropodidae) associated with ants (Hymenoptera: Formicidae) in the southeastern United States. Part I. Acarologia 17: 595-623.
- HUNTER, J.E., III. and M.H. FARRIER. 1976. Mites of the genus *Oplitis* Berlese (Acarina: Uropodidae) associated with ants (Hymenoptera: Formicidae) in the southeastern United States. Part II. Acarologia 18: 20-50.

- HUNTER, P.E. and M. COSTA. 1971. Description of *Gymnolaelaps shealsi* n. sp. (Acarina: Mesostigmata) associated with the imported fire ant. J. Ga. Entomol. Soc. 6: 51-3.
- JOUVENAZ, D.P., R.K. VANDER MEER and D.P. WOJCIK. 1988. Chemical mimicry in a parasitoid, *Orasema* sp., (Hymenoptera: Eucharitidae) of fire ants. Proc. 18th Intern. Congr. Entomol., Abstr. p. 243.
- KIEFFER, J.J. 1921. Proctotrypides hôtes des fourmis en Argentine. An. Soc. Cientif. Argent. 91: 36-41.
- KISTNER, D.H. 1979. Social and evolutionary significance of social insect symbionts, p. 339-413. In H.R. Hermann (ed.), Social insects. Academic Press, New York. Vol. 1. 437 p.
- KISTNER, D.H. 1982. The social insects' bestiary, p. 1-244. In H.R. Hermann (ed.), Social insects. Academic Press, N.Y. Vol. 3. 459 p.
- KISTNER, D.H. and M.S. BLUM. 1971. Alarm pheromone of *Lasius (Dendrolasius) spathepus* (Hymenoptera: Formicidae) and its possible mimicry by two species of *Pella* (Coleoptera: Staphylinidae). Ann. Entomol. Soc. Am. 64: 589-94.
- LOFGREN, C.S., W.A. BANKS and B.M. GLANCEY. 1975. Biology and control of imported fire ants. Annu. Rev. Entomol. 20: 1-30.
- MARTINEZ, A. 1952. Scarabaeidae nuevos o poco conocidos, III (Coleoptera). Publ. Misión Estud. Patol. Region. Argentina 23: 53-118.
- MULENBERG, M. and U. MASCHWITZ. 1976. E1937/1975 *Acanthaspis bistillata* und *Acanthaspis concinnula* (Reduviidae) Maskierung (Freilandaufnahmen). Encycl. Cinematogr. 1975: 3-12.
- NEECE, K.C. and D.P. BARTELL. 1981. Insects associated with *Solenopsis* spp. in southeastern Texas. Southwest. Entomol. 6: 307-11.
- NEECE, K.C. and D.P. BARTELL. 1982. A faunistic survey of the organisms associated with ants of Western Texas. Grad. Stud. Texas Tech. Univ., Lubbock, TX. 25, 36 p.
- NICOLINI, J.C. 1950. La avispa costurera y la tuberculosis del olivo. Rev. Agron., Porto Alegre (35-36): 20.
- OGLOBLIN, A.A. 1939. The Strepsiptera parasites of ants. Verh. 7th Intern. Kongr. Entomol. 2: 1277-84.
- OGLOBLIN, A.A. 1963. Especies nuevas del genero *Pseudoisobrachium* Kieff. (Fam. Bethyidae, Hymenoptera). Rev. Soc. Entomol. Argentina 26: 133-8.
- OSTMARK, H.E. and C. EVERS. 1976. Manipulation of ant populations to control *Orasema costaricensis* in bananas. Paper presented at the XV Intern. Congr. Entomol., Washington, D.C. 23 August 1976.
- PARKER, H.L. 1942. Oviposition habits and early stages of *Orasema* sp. Proc. Entomol. Soc. Washington 44: 142-5.
- ROBERTS, F.S. 1958. Insects affecting banana production in central America. Proc. X Intern. Congr. Entomol. 3: 411-5.
- ROTH, L.M. and E.R. WILLIS. 1960. The biotic associations of cockroaches. Smithson. Misc. Collect. 141, 470 p.
- SAN MARTIN, P.R. 1966a. Nota sobre *Neoblissus parasitaster* Bergroth, 1903 (Blissinae, Lygaeidae, Hemiptera). Rev. Bras. Biol. 26: 247-51.
- SAN MARTIN, P.R. 1966b. Nota sobre *Anommatorcoris coleopteratus* Kormilev, 1955 (Vianaidinae, Tingidae, Hemiptera). Rev. Bras. Biol. 26: 327-8.

- SAN MARTIN, P.R. 1968a. Nuevo hallazgo de *Metopioxys gallardoi* Bruch, 1917 (Coleoptera, Pselaphidae, Metopiinae). Rev. Bras. Biol. 28: 27-8.
- SAN MARTIN, P.R. 1968b. Notas sobre *Fustiger elegans* Raffray (Coleoptera, Pselaphidae) en el Uruguay y la Argentina. Physis 28: 59-64.
- SCHUBART, O. 1950. Ameisen und Diplopoden in ihren gegenseitigen Beziehungen. Rev. Entomol. 21: 615-22.
- SHEPPARD, C., P.B. Martin and F.W. Mead. 1979. A planthopper (Homoptera: Cixiidae) associated with red imported fire ant (Hymenoptera: Formicidae) mounds. J. Ga. Entomol. Soc. 14: 140-4.
- SILVEIRA-GUIDO, A., J. CARBONELL and C. CRISCI. 1973. Animals associated with the *Solenopsis* (fire ants) complex, with special reference to *Labauchena daguerrei*. Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage. 4: 41-52.
- SILVEIRA-GUIDO, A., J. CARBONELL-BRUHN, C. CRISCI-PISANO and J. BRIOZZO-BELTRAME. 1968. Investigations on natural enemies of ants. Second report. Entomol. Sect., Centro de investigación en Fruiticultura, Horticultura y Vitivinicultura, Minist. de Granaderia y Agric. Montevideo, Uruguay. 22 p.
- SILVEIRA-GUIDO, A., C. CRISCI-PISANO, P. SAN MARTIN and J. CARBONELL-BRUHN. 1965. Investigations on the biology and biological control of the fire ant, *Solenopsis saevissima richteri* Forel in Uruguay. Final report. Departamento de Sanidad Vegetal, Facultad de Agronomía, University of the Republic. Montevideo, Uruguay. 70 p., 36 plates.
- SILVEIRA-GUIDO, A., P. SAN MARTIN, C. CRISCI-PISANO and J. CARBONELL-BRUHN. 1963, 1964. Investigations on the biology and biological control of the fire ant, *Solenopsis saevissima richteri* Forel in Uruguay. Second and third reports. Departamento de Sanidad Vegetal, Facultad de Agronomía, University of the Republic. Montevideo, Uruguay. 78 p., 67 p.
- SMITH, M.R. 1928. *Plastophora crawfordi* Coq. and *Plastophora spatulata* Malloch (Diptera: Phoridae), parasitic on *Solenopsis geminata* Fabr. Proc. Entomol. Soc. Washington 30: 105-8.
- STEINER, W.E., Jr. 1982. *Poecilocrypticus formicophilus* Gebien, a south american beetle established in the United States (Coleoptera: Tenebrionidae). Proc. Entomol. Soc. Washington. 84: 232-9.
- SUMMERLIN, J.W. 1978. Beetles of the genera *Myrmecaphodius*, *Rhyssemus* and *Blapstinus* in Texas fire ant nests. Southwest. Entomol. 3: 27-9.
- TESON, A. and A.M.M. de REMES LENICOV. 1979. Estrepsipteros parasitoides de himenopteros (Insecta - Strepsiptera). Rev. Soc. Entomol. Argent. 3: 115-22.
- TOCCHETTO, A. 1942. Bicho costureiro. Rev. Agron., Porto Alegre 6: 587-8.
- TRAVIS, B.V. 1941. Notes on the biology of the fire ant *Solenopsis geminata* (F.) in Florida and Georgia. Fla. Entomol. 24: 15-22.
- VANDER MEER, R.K., D.P. JOUVENAZ and D.P. WOJCIK. 1989. Chemical mimicry in a parasitoid (Hymenoptera: Eucharitidae) of fire ants (Hymenoptera: Formicidae). J. Chem. Ecol. 15:2247-61.

- VANDER MEER, R.K. and D.P. WOJCIK. 1982. Chemical mimicry in the myrmecophilous beetle *Myrmecaphodius excavaticollis*. Science 218: 806-808.
- WASMANN, E. 1912. Neue Beiträge zur Kenntnis der Termitophilen und Myrmecophilen. Z. Wiss. Zool. 101: 70-115, Taf. 5-7.
- WASMANN, E. 1918a. Ueber *Solenopsis geminata saevissima* Sm. und ihre Gäste. Entomol. Blätter 14: 69-76.
- WASMANN, E. 1918b. Übersicht der myrmecophilen Paederinengattung *Myrmecosaurus* Wasm. (Staphylinidae). Entomol. Blätter 14: 210-4.
- WASMANN, E. 1925a. Drei neue myrmecophile Staphyliniden (Col.). Deuts. Entomol. Zeit. 1: 1-10.
- WASMANN, E. 1925b. Die Ameisenmimikry. Ein exakter Beitrag zum Mimikryproblem und zur Theorie der Anpassung. Abh. Theort. Biol. 19: 1-164.
- WHEELER, G.C. and E.H. WHEELER. 1937. New hymenopterous parasites of ants (Chalcidoidea: Eucharidae). Ann. Entomol. Soc. Am. 30: 163-73, plates I, II.
- WHEELER, W.M. 1907. The polymorphism of ants, with an account of some singular abnormalities due to parasitism. Bull. Amer. Mus. Natur. Hist. 23: 1-93, plates I-VI.
- WHEELER, W.M. 1910. Ants their structure development and behavior. Columbia Univ. Press, New York. 663 p.
- WILLIAMS, D.F. and W.A. BANKS. 1987. *Pseudacteon obtusus* (Diptera: Phoridae) attacking *Solenopsis invicta* (Hymenoptera: Formicidae) in Brazil. Psyche 94: 9-13.
- WILLIAMS, R.N. 1980. Insect natural enemies of fire ants in South America with several new records. Proc. Tall Timbers Conf. Ecol. Anim. Control Habitat Manage. 7: 123-34.
- WILLIAMS, R.N., J.R. PANAI, D. GALLO and W.H. WHITCOMB. 1973. Fire ants attacked by phorid flies. Fla. Entomol. 56: 259-62.
- WILSON, E.O. 1971. The insect societies. Belknap Press, Cambridge, Ma. 548p.
- WOJCIK, D.P. 1975. Biology of *Myrmecaphodius excavaticollis* (Blanchard) and *Euparia castanea* Serville (Coleoptera: Scarabaeidae) and their relationships to *Solenopsis* spp. (Hymenoptera: Formicidae). Ph.D. dissertation, University of Florida, Gainesville, FL. 74 p. [Dissert. Abstr. Int. B 36: 5962]
- WOJCIK, D.P. 1980. Fire ant myrmecophiles: behavior of *Myrmecosaurus ferrugineus* Bruch (Coleoptera: Staphylinidae) with comments on its abundance. Sociobiology 5: 63-8.
- WOJCIK, D.P. 1986. Observations on the biology and ecology of fire ants in Brazil, p. 88-103. In C.S. Lofgren, R.K. Vander Meer (ed.), Fire ants and leaf-cutting ants, Biology and management. Westview Press, Boulder, CO, 435 p.
- WOJCIK, D.P., W.A. BANKS and D.H. HABECK. 1978. Fire ant Myrmecophiles: Flight periods of *Myrmecaphodius excavaticollis* (Blanchard) and *Euparia castanea* Serville (Coleoptera: Scarabaeidae). Coleopt. Bull. 32: 59-64.

- WOJCIK, D.P., W.A. BANKS, D.M. HICKS and J.W. SUMMERLIN. 1977. Fire ant myrmecophiles: new hosts and distribution of *Myrmecaphodius excavaticollis* (Blanchard) and *Euparia castanea* Serville (Coleoptera: Scarabaeidae). *Coleopt. Bull.* 31: 329-34.
- WOJCIK, D.P. and D.H. HABECK. 1977. Fire ant Myrmecophiles: Breeding period and ovariole number in *Myrmecaphodius excavaticollis* (Blanchard) and *Euparia castanea* Serville (Coleoptera: Scarabaeidae). *Coleopt. Bull.* 31: 335-8.
- WOJCIK, D.P., D.P. JOUVENAZ, W.A. BANKS and A.C. PEREIRA. 1987a. Biological control agents of fire ants in Brazil, p. 627-628. In J. Eder, H. Rembold (ed.), *Chemistry and biology of social insects*. Verlag J. Peperny, München. 757 p.
- WOJCIK, D.P., D.P. JOUVENAZ and C.S. LOFGREN. 1987b. First report of a parasitic fly (Diptera: Phoridae) from a red imported fire ant (*Solenopsis invicta*) alate female (Hymenoptera: Formicidae). *Fla. Entomol.* 70: 181-2.
- WOJCIK, D.P. and M.A. NAVES. *Calytodesmus schubarti* (Diplopoda: Stylodesmidae: Polydesmida) as a facultative myrmecophile. *Sociobiology* (in Press)