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NATURAL ENEMIES OF FIRE ANTS

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The red and black imported fire ants (IFA), *Solenopsis invicta* Buren and *Solenopsis richteri* Forel, are beset by a complex of specific natural enemies in their homelands in South America. Most of these organisms—pathogens and parasitic or socially parasitic arthropods—were left behind when their hosts immigrated to the United States (Jouvenaz et al. 1977). Consequently, we know very little about them.

The United States Department of Agriculture funded the first survey of animals associated with fire ants in South America nearly 20 years ago (Silveira-Guido et al. 1973). However, research directed toward biological control subsequently waned as public demand for immediate relief forced the concentration of resources on the refinement of chemical control technology, the feasibility of an eradication program, and attendant environmental concerns. The natural enemies of fire ants were not totally neglected during this period (ca. 1965-1974), however. Williams et al. (1973) observed the behavior of phorid flies toward fire ants in Brazil,

and several investigators searched for natural enemies in the United States (Broome 1974, Collins and Markin 1971; B. A. Federici, Div. Biol. Control, Department of Entomology, University of California, Riverside, Personal communication, 1971). Only inquilines and non-specific, facultative pathogens were found in association with IFA in this country. Whitcomb et al. (1973) studied predation on *S. invicta* queens in the United States prior to colony establishment by general predators (birds, spiders, etc.). Whitcomb et al. found that large numbers of queens were consumed; however, it is extremely doubtful if fire ant populations are affected by these opportunistic predators (Jouvenaz et al. 1981).

The discovery of a host-specific pathogen of *S. invicta* by Allen and Buren (1974) during a period of intense controversy over the use of Mirex (dodecachlorooctahydro-1,3,4- Metheno-1 H-cyclobuta [cd] pentalene) bait for IFA control greatly stimulated interest in the possibility of biological control of IFA; mirex registrations were cancelled in 1978. Several exploratory trips were subsequently made to South America by USDA and University (University of Florida and Mississippi State University) scientists, and several pathogens and parasites of IFA were detected. Beyond confirmation of the existence of a complex of natural enemies of fire ants in South America (and the lack thereof in the United States), little has been learned. Data on the distribution and abundance of the various species of fire ants in South America are limited, and nothing is known about the role of natural enemies in fire ant population dynamics.

We are endeavoring to establish a research station in the State of Mato Grosso, Brazil (the homeland of *S. invicta*), from which long and short-term studies of ecology and surveys for natural enemies can be conducted by a resident scientist and by visiting investigators. We are also studying the diseases of the tropical fire ant, *Solenopsis geminata* (F.), in Florida. From this model we are gaining information on basic pathobiology, and developing and refining techniques for the detection and study of exotic pathogens of fire ants. The ultimate goal of this project is to establish, in the United States, a complex of natural enemies which may exert continuing stress on imported fire ant populations. To be of value, natural enemies may not have to be rapidly fatal to colonies or large numbers of individual ants. Debilitating diseases may enable native or deliberately introduced exotic ants to compete successfully with fire ants.

The status and prospects of research on biological control of fire ants, including the use of non-specific organisms, recently was reviewed by Jouvenaz et al. (1981). Therefore, the biology of the specific natural enemies of fire ants, rather than the strategy of biological control, will be emphasized in this paper.

PATHOGENS

The numbers of specific pathogens of fire ants are listed by type in Table 1. It is not known whether the virus-like particles of *S. invicta* and *S. geminata* are identical. Similarly, a neogregarine which parasitizes *S. invicta* in Brazil has not been differentiated from *Mattesia geminata* Jouvenaz and Anthony, a parasite of *S. geminata*. It is uncertain whether the bacterium detected in *S. invicta* larvae is indeed pathogenic. Only 2 of the 6 species of microsporidia have been described.

TABLE 1. SPECIFIC PATHOGENS OF FIRE ANTS, *Solenopsis* spp.

Type of Pathogen	<i>S. invicta</i> ¹	<i>S. geminata</i>	Total
Virus	1	1	1 or 2
Bacterium	1?	—	1?
Fungus	1	—	1
Protozoa			
Microsporidia	2	4	6
Neogregarine	1	1	1 or 2

¹*S. invicta* and other members of the *S. saevissima* complex in South America.

MICROSPORIDIA

Thelohania solenopsae. The first specific pathogen known from fire ants was discovered by W. F. Buren during a taxonomic study of *S. invicta* from Mato Grosso, Brazil (Allen and Buren 1974). While examining alcohol-preserved specimens, Buren observed subspherical, cyst-like bodies in the partially cleared gasters of adult worker ants. These cysts contained spores of a microsporidium which was subsequently described from fresh material by Knell et al. (1977), who named it *Thelohania solenopsae*. Allen and Silveira-Guido (1974) immediately reported similar or identical microsporidia infecting *S. richteri* in Uruguay and Argentina, and an unidentified *Solenopsis* sp. in Uruguay. *T. solenopsae* has since been detected in a dozen or more described or undescribed *Solenopsis* spp. (Jouvenaz et al. 1977). Of the 865 colonies of fire ants (primarily *S. invicta*) from Mato Grosso that I have examined, 67 (7.8%) were infected with this microsporidium.

According to Knell et al. (1977), *T. solenopsae* infects adipose tissue of workers and sexuals, and the ovaries of queens. Infected cells hypertrophy, forming the cysts observed by Buren. These typically number 4 to 6 per gaster, but as many as 22 cysts of different sizes have been observed in a single specimen. The fat body is reduced or destroyed, but the disease is not rapidly fatal and produces no gross pathological signs or changes in behavior. The life expectancy of infected adults may be reduced. Knell et al. reported that infected colonies cannot be maintained in the laboratory as long as healthy colonies. Thus, the effect of *T. solenopsae* infection appears to be debilitation due to destruction of the fat body.

T. solenopsae produces 2 morphologically distinct types of spores which develop simultaneously in the same tissues. It is the only species of *Thelohania* which is known to exhibit spore dimorphism, although 2 other genera (*Amblyospora* and *Parathelohania*) of the family Thelohaniidae contain dimorphic species (Hazard and Oldacre 1975). The predominant spore type of *T. solenopsae* is uninucleate, and occurs in octets bound by a membrane (a pansporoblast). The pansporoblast membrane-bounded (PMB) spores arise from octonucleate plasmodia by endogenous budding (cytoplasmic constriction around each nucleus). Spores of the second type are binucleate and are not bound by a pansporoblast membrane (NPMB spores). NPMB spores arise from diplocaryotic sporonts.

Thelohania solenopsae infections cannot be transmitted *per os* or by placing brood from heavily infected colonies in healthy colonies (immatures are adopted) (unpublished data). Thus, the mode of transmission of this parasite remains an enigma.

Burenella dimorpha. My primary model for studies of pathobiology and for the development of techniques has been the microsporidium *Burenella dimorpha* Jouvenaz and Hazard (1978), a parasite of *S. geminata* in Florida. In addition to being locally available, this pathogen can be transmitted *per os* and infected pupae exhibit pathognomonic signs. As the specific name indicates, *B. dimorpha* produces 2 morphologically distinct types of spores: binucleate, NPMB spores develop from disporous sporonts in the hypodermis; uninucleate, PMB spores develop in octets (pansporoblasts) from plasmodia in the fat body. The NPMB spores are infective *per os* for larvae; pure suspensions produce the pathological manifestations characteristic of this infection and both spore types in normal ratios. The PMB spores are not infective; they are expelled unextruded in the meconium upon pupation.

The function of the PMB spores remains unknown (Jouvenaz et al. 1981a); however, we hypothesize that they may provide a mechanism for the intercolonial transmission of the parasite (fire ants are territorial and aggressive toward conspecific ants). Inquilines are known to eat fire ant pupae and to travel between colonies (Wojcik 1975). One of these could serve as an alternate host, or as a mechanical vector in which the PMB spores are primed for extrusion by passage through the gut. Even if PMB spores do not function in intercolonial disease transmission, some sort of vector seems necessary because of the behavior of the ants. We are searching for such a vector, but the task is made difficult by the variety of arthropods associated with fire ants and the sporadic occurrence of disease.

The pathognomonic signs of *B. dimorpha* infection are due to infection of the hypodermis. The first signs are malformation (irregularity of outline and a blistered appearance) of the eyes and slight clearing in the occiput of the pupa. Later, clear blisterlike areas also appear in the petiole and gaster. As the disease progresses, these areas become more extensive and pronounced, and the cuticle becomes very fragile and eventually ruptures. The adult ants cannibalize ruptured pupae but do not ingest the spores. Instead, the spores, together with other particulate matter, are retained in the infrabuccal cavity and formed into an infrabuccal pellet (see Glancey et al., 1981 for a discussion of the mechanism of filtration of such small particles). These pellets are placed on the praesaepia ("bread-baskets") of 4th-instar larvae. The praesaepium, which bears spines specialized for holding solid food while the larva feeds, is absent from earlier instars, which are fed liquid only. Because of this method of feeding, the 4th-instar larva is the only stage that is vulnerable to infection. Infection with *B. dimorpha* appears to be invariably fatal in the pupal stage of development. Intracolony infection rates in field colonies are usually less than 5% but may be 100%. In a sample of 307 colonies of *S. geminata* from 74 collection sites in Florida, only 12 colonies (3.9%) from 7 sites were infected with *B. dimorpha* (32 or 10.4% of these colonies were infected with other species of microsporidia). In this survey, I avoided the type locality, where the infection rate exceeded 40%.

B. dimorpha is readily transmitted *per os* to *S. invicta*, *S. richteri*, and the southern fire ant, *Solenopsis xyloni* McCook (Jouvenaz and Hazard

1978); however, the infection does not persist in laboratory colonies of these species, (unpublished data) and I have not detected it in *S. invicta* colonies collected in areas where this species coexists in close physical proximity with *S. geminata*.

OTHER MICROSPORIDIA

At least one additional microsporidium infects *S. invicta* in Brazil. This parasite (soon to be described) is dimorphic, producing PMB and NPMB spores that develop in the same oenocytes or fat cells, but sequentially. The binucleate NPMB spores appear in late larvae and early pupae, whereas the development of the uninucleate PMB spores is delayed until extremely late in the pupal stage and in young adults. Infected cells hypertrophy, forming thin-walled cysts. As in the case of *T. solenopsae*, attempts to transmit this microsporidium to healthy colonies have failed.

Three distinct, undescribed species of microsporidia infect *S. geminata* in Florida. These have not been studied, but at least one species is dimorphic. Jouvenaz et al. (1977) found these microsporidia in 22 (7.2%), 6 (2.0%), and 4 (1.3%) of 307 colonies of *S. geminata* from Florida. Attempts to transmit these parasites *per os* failed.

NEOGREGARINES

Mattesia geminata Jouvenaz and Anthony (1979) [Apicomplexa: Neogregarinida] and a neogregarine having morphologically similar spores infect, respectively, *S. geminata* in Florida and *Solenopsis* spp. in Brazil. The latter parasite has not been studied.

The members of the genus *Mattesia* have a complex life cycle that includes cycles of merogony in which gamonts bud from micronuclear and macronuclear plasmodia. The interactions of these gamonts are complex, but ultimately an association of 8 cells occurs. These 8 cells fuse in pairs to form 4 binucleate cells, of which 2 degenerate and 2 mature into spores which contain 8 nuclei each. Thus, the sporonts appear to undergo meiosis. The 2 mature spores and 2 "residual bodies" (degenerated cells) are bound by a membrane, forming a gametocyst. The gametocyst membrane is transient in *M. geminata*, but may be seen during early development. The spores of *M. geminata* are obese and oval, and have a protuberance at each pole which gives them a shape reminiscent of a lemon. They are found only in the hypodermis.

The earliest sign of *M. geminata* infection is irregularity of the developing eyes of the pupa. This is followed by melanization of the cuticle, which begins in the legs and posterior margins of the sclerites of the gaster. As the disease progresses, the pupa becomes more and more "sooty" in appearance. Pupae with these manifestations do not mature, and we have not detected the parasite in adults from infected colonies. Thus, the disease appears to be invariably fatal.

The intracolony infection rates are usually less than 2%; however, in 3 colonies the infection rates exceeded 90%. All but one of the infected colonies were found along a roadside ca. 2 km in length. Over a period of 2 years, more than 25 colonies (ca. 20% of the total colonies) collected at this site were infected. Only one colony in a sample of 307 colonies from

74 other sites in Florida and Georgia was infected (Jouvenaz et al. 1977). On several occasions, individual pupae having dual infections with *M. geminata* and microsporidia have been seen. All attempts to transmit the infection to healthy colonies of *S. geminata*, including placing diseased pupae in these colonies, have failed.

FUNGUS

The only microorganism that appears to be specifically associated with *S. invicta* in the United States is an unidentified, endozoic fungus. Jouvenaz et al. (1977) found this parasite in 93 (9.24%) of 1,007 colonies of *S. invicta* from 285 collection sites in 6 states. It has not been reported from *S. richteri* or *S. geminata*; Jouvenaz et al. examined only 83 colonies of the former species during their survey, and only a few colonies have been examined since. Broome (1974) also studied *S. richteri*, but his methods may not have detected this relatively fastidious fungus. It is present but rare in Brazil (unpublished data).

The fungus occurs as club-shaped, budding cells in the haemolymph of immature and adult ants. A mycelial form develops *in vitro* which I have not yet seen *in vivo*. It can be transmitted *per os* to healthy individuals. Although the cells may become very numerous in the haemolymph, the only observable effect of infection on the individual is increased sensitivity to stress. Field populations are not obviously reduced in areas where it is common.

BACTERIUM

A possible bacterial infection in one colony of *S. invicta* was noted by Jouvenaz et al. (1980) in Brazil. A sporeforming bacterium was numerous in a few larvae but was absent in most. The total collection of immatures in this colony was very small, possibly because of the rocky soil. There was no means of cleaning crude larval extracts containing the bacterium, and putrefaction was advanced when *per os* transmission was finally attempted in the United States. At that time only spores remained in the suspension, the sporangia having disintegrated. The infection was not transmitted, and attempts to isolate and culture the bacterium also failed. The bacterium was motile and contained a subterminal spore with a parasporal body that remained attached to the spore after disintegration of the sporangium.

VIRUS

Virus-like particles (VLP) were found by Avery et al. (1977) in an unidentified species of fire ant close to *S. invicta* and *Solenopsis saevissima* (F. Smith) from Brazil. The host colony was infected with an undescribed microsporidium, and some (but not all) individuals had dual infections. The colony was, in fact, collected because of the protozoan infection, and the VLP were discovered in the course of electronmicroscope studies of the protozoan. Similar VLP were subsequently detected in *S. geminata*. The VLP were rod-shaped and slightly tapered at both ends, and enclosed by double membranes. The electron dense core measured $193 \pm 25 \times 50 \pm 2.5$ nm, and the membrane was 15 nm thick. Whole particles measured 252 ± 12

x 89 ± 7 nm, and were frequently curved. Although the particles were seen occasionally in tightly packed spheres, and some of these spheres were bound by a membrane, there was no evidence of occlusion of the particles in a protein matrix.

The VLP occurred in both nuclei and cytoplasm of cells in the adipose tissue. The nuclei of infected cells greatly hypertrophied, and contained considerably less condensed nucleoprotein than normal cells. In a specimen in which ca. 75% of the fat body cells were infected, both cytoplasm and nuclei were completely disrupted. The mortality rate in this colony was elevated; however, because of the dual infection, the cytopathology and mortality could not be attributed exclusively to either infection. There are no signs of infection in living ants, and the infection rate could not be estimated.

The only other indication of a possible virus infection in Formicidae is a report of VLP in nerve and adipose tissue of the wood ant, *Formica lugubris* Zett. (Steiger et al. 1969). These VLP are of 2 types, hexagonal and spherical, and thus are quite unlike the VLP from fire ants.

ARTHROPODS

The specific arthropod enemies of fire ants include endoparasites, socially parasitic ants, and live-in predators (Table 2). Scores of species of arthropods have been collected from fire ant nests (Collins and Markin 1971, Silveira-Guido et al. 1973, Neece and Bartell 1981, Summerlin 1978) but most of these are transient and have no specific association with fire ants. Some of those that are symbiotically associated with fire ants, such as the mite *Gymolaedaps shealsi* Hunter and Costa (1971) and the staphylinid beetle, *Myrmecosaurus ferrugineus* (Frank 1977), are commensals.

SOCIAL PARASITES

Solenopsis (formerly *Labauchena*) *daguerri* (Santschii), a workerless

TABLE 2. ARTHROPODS ASSOCIATED SYMBIOTICALLY WITH FIRE ANTS, *Solenopsis* spp: KNOWN OR SUSPECTED PARASITES AND PREDATORS.

STREPSIPTERA		
Myrmecolachidae:	<i>Stichotrema wigodzinsky</i>	Endoparasitic
DIPTERA		
Phoridae:	<i>Apodicrania</i> sp.	Endoparasitic
	<i>Pseudacteon</i> spp. (14)	Endoparasitic?
HYMENOPTERA		
Eucharitidae:	<i>Orasema crassa</i> DeSantis	Endoparasitic
	<i>Orasema</i> spp.	Endoparasitic
Formicidae:	<i>Solenopsis daggueri</i> (Santschi)	Social Parasite
COLEOPTERA		
Scarabaeidae:	<i>Myrmecophodius excavaticollis</i> (Blanchard)	Predaceous
	<i>Myrmecophodius</i> spp.	Predaceous
	<i>Euparia castanea</i> Serville	Predaceous

social parasite of *S. richteri* in Uruguay and Argentina, has been studied by Silveira-Guido et al. (1973), and the following synopsis is primarily from their report.

The newly mated queens of *S. daguerri* gain entrance to the nests of *S. richteri* and permanently attach themselves to the host queen by grasping her cephalothoracic membrane with their mandibles and embracing her thorax with their legs. Typically, 2 or 3 parasitic queens "yoke" themselves in this manner to the host queen; additional queens (up to a total of 10) may attach themselves to other parts of the body of their host, who becomes immobile. The host workers care for these parasitic queens and their off-spring, apparently preferentially. Under the burden of a growing population of unproductive individuals, the vigor of the colony declines. Probably as a result of nutritional deprivation, the oviposition rate of the *S. richteri* queen declines, the proportion of major workers is diminished, and sexual forms disappear. The workers become less aggressive and allow the nest to fall into disrepair. Heavily infested colonies (*S. daguerri* may constitute 70% or more of the population) can be readily identified by their eroded and unrepaired nest tumuli. This process of progressive debilitation typically lasts for about 2 years and ends with the collapse of the colony.

Despite the fact that *S. daguerri* does eliminate colonies of *S. richteri*, the socially parasitic ants are not promising candidates for use in a biological control program in the United States. Even in the areas of Argentina where *S. daguerri* is most common, *S. richteri* populations appear to be quite high (Silveira-Guido et al. 1973). In Brazil, we found only 2 parasitized colonies in a sample of 1,126 colonies of several species of fire ants. In addition, many problems of logistics, culture, behavior, and ecology will hamper any attempt to introduce these social parasites into the United States (see Jouvenaz et al. 1981b for further discussion).

ENDOPARASITES

Three groups of insects are known or strongly suspected to be endoparasites of fire ants. These are a genus of chalcid wasps, 2 genera of phorid flies, and a species of Strepsiptera.

Oraesema crassa DeSantis and *Oraesema* spp. (Chalcidoidea : Eucharitidae) parasitize, respectively, *S. richteri* in Uruguay and *Solenopsis* spp. in Brazil. The female wasp oviposits in plants (leaves, buds, fruit) that are visited by ants. The newly hatched larvae attach themselves to these foraging ants and are carried to the nest. There they transfer to mature larvae or pupae and complete their development, apparently as endoparasites (Williams and Whitcomb 1974).

One species of *Apodicerania* and 14 species of *Pseudacteon* (Diptera : Phoridae) have been collected in association with fire ants in South America, but only the *Apodicerania* sp. is a proven endoparasite. Larvae of this fly (one per host) have been dissected from worker ant larvae. Mature larvae which have emerged from their hosts and pupae are tended by fire ant workers as if they were ant brood. Williams and Whitcomb (1974) reported that worker ants in parasitized laboratory colonies were observed to carry *Apodicerania* pupae to the surface, place them in a group, and then carry them below when the nest was disturbed. Adult flies are able to walk about on the soil surface of disturbed mounds without aggressive reaction by the ants.

In contrast to the *Apodicrania* sp. which masquerades as an ant quite effectively, the females of *Pseudacteon* appear to attack individual ants. Williams et al. (1973) describe the behavior of *Pseudacteon* sp. as follows: "a few minutes after the surface of a fire ant nest was disturbed, the phorids usually began to appear. They flew in low over the numerous ant workers moving about on the soil surface and began immediately to seek out hosts. The phorid would hover over the host at an elevation of from ca. 0.5 to 1.5 cm for an instant before it would strike. In most cases the ant perceived its aggressor and attempted to escape or defend itself. In the attack, the phorid quickly swooped down, hit the worker, and darted away at great speed. This process was repeated as the phorid located its next host. The foray of a single phorid lasted for several minutes during which many *Solenopsis* workers were attacked. Then the phorid landed on nearby foliage for a few minutes before renewing her attack.

Occasionally, the defensive display of the *Solenopsis* worker was sufficient to cause the *Pseudacteon* to select a new host. The ant was observed to defend itself by elevating and flexing the gaster.

After a successful attack by the phorid, the fire ant worker was often visibly stunned and occasionally remained motionless for a second or 2. At times the ant fell over on its side during the attack. However, in other cases, the ant moved away rapidly flexing its gaster."

This behavior strongly suggests that the flies oviposit in or on the ants; however, attempts to rear the parasites or dissect out parasitic larvae have failed.

Stichotrema wigodzinsky (Oliverira and Kogan) [Strepsiptera : Myrmecolacidae] is listed as an endoparasite of *S. richteri* and species of *Camponotus* and *Pseudomyrmex* in Argentina by Teson and De Remes Lenicov (1979). No further information is given on parasitism in this paper, which treats the taxonomy of several species of Strepsiptera.

PREDATORS

Wojcik (1975) observed that *S. invicta* pupae are occasionally consumed by the myrmecophilous beetle *Myrmecophodius excavaticollis* (Blanchard) (Scarabaeidae) in the United States. Although this beetle and another Scarabaeid, *Euparia castanea* Serville, are specifically associated with *Solenopsis* spp., they infest fewer than 5% of colonies and are sparse in infested colonies (usually fewer than 10, rarely up to 200 individuals). Because their populations are small relative to those of their hosts, and because their diet is varied, the number of ants they destroy is insignificant.

I have attempted to summarize our meager knowledge of the specific natural enemies of fire ants. Obviously, much remains to be learned about the biology of these organisms; nothing is known about their role in the population dynamics of fire ants. The IFA are imported pests that have, in the classic manner, left their natural enemies behind. Whether there exists natural enemies that can significantly reduce the numbers of IFA in the United States, and how these can be employed, remains to be determined.

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MEDICAL AND AGRICULTURAL IMPORTANCE OF RED IMPORTED FIRE ANT

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The red imported fire ant (RIFA), *Solenopsis invicta* Buren, currently inhabits over 90 million hectares in 9 southern states from Texas to North Carolina. In all of these states, the RIFA has been the target of chemical eradication or wide-area control programs. Attempts to eliminate the RIFA have been controversial because of the nontarget impacts of the pesticides used but also because control programs were initiated before the economic importance of the RIFA was thoroughly evaluated. The economic estimates of losses or damage are often based on surveys or extrapolated from the limited published information that is available. Therefore, we will only review investigations published in scientific journals. The mass of unpublished information that has accumulated has been reviewed by Lofgren et al. (1975) and more recently by Canter (1981).