

## Biological Control of Imported Fire Ants: A Review of Current Knowledge<sup>1</sup>

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The black and red imported fire ants (IFA), *Solenopsis richteri* Forel and *Solenopsis invicta* Buren, are medical and agricultural pests that infest ca.  $8 \times 10^7$  ha ( $2 \times 10^8$  acres) in the southeastern United States. *S. richteri* and *S. invicta* apparently were introduced into the United States with products shipped by boat from South America to Mobile, Ala., about 1918 and 1940, respectively. *S. richteri* is now restricted to a relatively small area in northeastern Mississippi and northwestern Alabama, whereas *S. invicta* infests Florida, Louisiana, and parts of North Carolina, South Carolina, Georgia, Alabama, Mississippi, Texas, and Arkansas (Lofgren et al. 1975). Should *S. invicta* be transported by humans across the barrier of the arid southwest to more humid or irrigated areas, its range could greatly increase.

The tropical fire ant, *Solenopsis germinata* (Fabricius), may also be an introduced species; however, it has been a resident of this country long enough to be generally regarded as native. The southern and desert fire ants, *Solenopsis xyloni* McCook and *Solenopsis aurea* Wheeler, are truly native to the United States. These three species are not very important as pests.

Efforts to control IFA by chemical means have been the subject of serious controversy for more than 20 years (Lofgren et al. 1975). Mirex (dodecachlorooctahydro-1,3,4-metheno-1 *H*-cyclobuta [cd]pentalene) incorporated in a soybean oil-corn-cob grit bait (Lofgren et al. 1964) had been the most widely used chemical; however, its registrations were cancelled in 1978 after residues were found in non-target organisms and evidence suggesting that it might be a carcinogen appeared (Ulland et al. 1977). This cancellation has accentuated the need for extensive studies in South America to find and evaluate potential IFA biocontrol agents for introduction into the United States. Our laboratory has conducted and supported research (University of Florida and Mississippi State University) that has led to the identification of several diseases and predators of IFA. In addition, we are seeking approval for establishment of a research station in Brazil, and we have been studying diseases of native fire ants. The ultimate goal would be to establish in the United States a complex of natural enemies which would exert continuing stress on IFA 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 ants that compete with fire ants to do so more successfully. This paper reviews research on biocontrol of IFA.

### Surveys for Biocontrol Agents in the United States

Surveys for pathogens of *S. richteri* were conducted in Mississippi (Broome 1974) and in Florida for *S. invicta* in 1971 (personal communication, B. A. Federici, Division of Biological Control, Department of Entomology, University of California, Riverside), but they failed to identify pathogens other than ubiquitous, nonspecific facultative organisms as the bacterium *Serratia marcescens* Bizio. More recently, Jouvenaz et al. (1977) conducted an extensive survey, the results of which confirmed the paucity of diseases in IFA in the United States. In a sample of 1,007 *S. invicta* colonies from 285 collection sites in six states, only one microorganism, an endozoic mold, was specifically associated with *S. invicta*. It was found in 93 (9.24%) of these colonies and was erroneously reported as a yeast, since only a budding, unicellular form had been seen. Subsequent study has revealed a mycelial stage. The mold can be cultured in insect tissue culture media but grows poorly or not at all in the standard mycological media. It can be transmitted per os. The budding cells are numerous in the hemolymph of immatures and adults but appear to be benign or only mildly pathogenic. Laboratory colonies harboring this organism appear to be abnormally sensitive to stress; however, field populations are not obviously reduced in areas where it is common.

One colony of *S. invicta* was infected with a bona fide pathogen, a microsporidium. However, this parasite infected four colonies of *S. geminata* (in a sample of 307) from collection sites in three Florida counties, and *S. geminata* is probably the normal host. Since the conclusion of the survey, several hundred additional colonies of *S. invicta* (primarily from central Florida) have been examined; all were negative for pathogens.

No potential pathogens were found in 83 colonies of *S. richteri*. Although the sample was small, it actually represented a more intensive sampling of this species than was done with *S. invicta*, since *S. richteri* is restricted to a very small area in northeastern Mississippi and northwestern Alabama. These results substantiate the negative results of Broome (1974), who surveyed *S. richteri* intensively, using different methods.

### Surveys for Biocontrol Agents in South America

#### Protozoa

The first observation of a protozoan infection in ants was made 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, cystlike bodies in the partially cleared gasters of worker ants. These bodies were found to contain spores of a microsporidium that was subsequently named *Thelohania solenopsae* by Knell et al. (1977),

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who described the parasite from fresh material. Soon after Buren's observation, Allen and Silveira-Guido (1974) reported similar microsporidia infecting *S. richteri* in Uruguay and Argentina and an unidentified *Solenopsis* sp. in Uruguay. Since then, *T. solenopsae* has been detected in ca. 22 described and undescribed *Solenopsis* spp. in South America (Jouvenaz et al. 1977).

*T. solenopsae* infects fat body cells of workers and sexuals, and the ovaries of queens. Infected cells hypertrophy, forming the cysts observed by Buren. The disease is not rapidly fatal, but the fat body is destroyed, resulting in premature death of adult ants and debilitation of the colony. It is uncertain whether *T. solenopsae* represents a single species or a complex of sibling species that we cannot differentiate. Attempts to transmit this microsporidium per os have failed (unpublished data).

At least one additional microsporidium infects fire ants in Brazil. This undescribed parasite produces two morphologically distinct types of spores that develop in oenocytes. Both spore types develop sequentially in the same cells, which hypertrophy. The binucleate, non-pansporoblast membrane-bounded (NMB) spores develop in late larvae and early pupae, whereas development of the uninucleate, pansporoblast membrane-bounded (MB) spores is delayed until extremely late in the pupal stage and in adults.

A neogregarine similar to *Mattesia geminata* Jouvenaz and Anthony also infects *S. invicta* in Brazil but has not been studied (Jouvenaz et al. 1980).

Little is known about the epizootiology of protozoan pathogens of fire ants in South America. In many areas, *T. solenopsae* infects 25% or more of the colonies at the end of the rainy season (Jouvenaz et al. 1977). After a rather dry "rainy" season (January and February 1976), we found *T. solenopsae* infections in 21 (11.4%) of 184 colonies examined. At the end of the dry season (October and November 1979), we found *T. solenopsae* infections in only 31 (6.8%) of 456 colonies (Jouvenaz et al. 1980). The undescribed, dimorphic microsporidium infected 10 (5.4%) and 13 (2.85%) of these colonies in 1976 and 1979, respectively. Additional surveys are needed to determine whether these data represent actual seasonal fluctuations in disease rates.

#### Other Pathogens

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-like particles have been detected in an undescribed *Solenopsis* sp. from Brazil (Avery et al. 1977). Their pathogenicity is yet undetermined, but similar or identical particles in *S. geminata* appear benign or only mildly pathogenic (unpublished data).

#### Arthropods

The most studied arthropod enemy of fire ants is *Solenopsis* (formerly *Labauchena*) *daguerrri* (Santschi), a workerless social parasite of *S. richteri* in Uruguay and Argentina. Unfortunately, *S. daguerri* and related parasitic ants are uncommon and do not appear to significantly affect the populations of their hosts.

According to Silveira-Guido et al. (1972), two or three *S. daguerri* queens permanently "yoke" themselves to the host queen by grasping her cephalothoracic membrane with their mandibles and embracing her thorax with their legs. Occasionally, additional parasitic queens (up to a total of 10) yoke to other parts of the host queen, who becomes immobile. The host workers care for these parasitic queens and their offspring preferentially, reducing attention to their own queen and immatures as the parasite population increases. Probably as a result of reduced nutrition, the oviposition rate of the host queen is reduced, the proportion of major workers declines, and sexual forms disappear. Burdened with large numbers of unproductive individuals (parasites may constitute 70% or more of the total population of a nest), the economy and vigor of the colony are strained, and the colony deteriorates. The host workers appear to become less aggressive. Heavily infested colonies may be identified by simple inspection of their mound tumuli, which appear eroded, unrepaired, and reduced in size. About 2 years is required for *S. daguerri* to eliminate a mature fire ant colony (personal communication, June 1969, M. S. Blum, Dept. of Entomology, University of Georgia, Athens).

The greatest densities of *S. daguerri* have been reported from Las Flores, Argentina, in 1964. Silveira-Guido et al. (1973) found 284 active nests of *S. richteri* in 1 ha, of which 109 (38.4%) were infested by *S. daguerri*. There were also 67 abandoned nests in this hectare. In 1965, the same workers found 152 active nests, of which 48 (31.6%) were infested, and 39 nests that were abandoned. In most areas containing dense populations of *S. richteri*, however, the rate of parasitism was ca. 4% (personal communication, M. S. Blum).

Parasitic ants have not been reported from nests of *S. invicta* and are not common in nests of other *Solenopsis* spp. In Brazil, we have found only two parasitized colonies in a sample of 1,126 nests of several species of fire ants (unpublished data).

Because of the low densities of parasitic ants in their native lands, and the lack of evidence that they suppress their hosts, investigators familiar with these

ants discount their potential for use in a biological control program in the United States (personal communication, M. S. Blum; W. F. Buren, Dept. of Entomology, University of Florida). Obviously, either poor searching ability or ecological factors other than host density regulate the density of parasitic ants in South America. If ecological factors are limiting, and if these are inoperative in this country, a parasite (assuming one is eventually found for *S. invicta*) could conceivably become abundant enough to affect the populations of their hosts; however, the probability of this seems remote. Many problems of logistics, culture, behavior, and ecology will hamper any attempt to introduce these parasites into the United States. Uruguayan entomologists have repeatedly attempted to introduce *S. daguerri* from Argentina without success. These efforts involved only moving material by air in 1 day from Buenos Aires to Montevideo and then to areas of eastern Uruguay heavily infested with *S. richteri* (personal communication, M. S. Blum).

Species of two other groups of parasitic insects, chalcid wasps, and phorid flies, are associated with fire ants in South America. However, these parasites attack relatively small numbers of workers only and are thus of dubious value as biological control agents. The little information that is available about them has been reviewed by Williams and Whitcomb (1974).

*Orasema crassa* De Santis and *Orasema* sp. (Chalcidoidea: Eucharitidae) have been found parasitizing fire ants in Uruguay and the State of Mato Grosso, Brazil, respectively. The female wasp inserts her eggs into leaves, flower buds, or fruits, and thus is a potential plant pest. The planidia (newly emerged larvae) attach themselves to ant workers that frequent the "host" plant and are carried into the nest. The planidia subsequently transfer to mature larvae or pupae and complete their development, apparently as endoparasites.

Fourteen species of *Pseudacteon* and one species of *Apodicrania* (Phoridae) have been collected in association with fire ants in South America. The females of *Pseudacteon* spp. hover for an instant 0.5 to 1.5 cm above a worker, then swoop down, strike the worker, and dart away. This process is then repeated with a succession of worker ants. After an attack, the ant worker is often visibly stunned, remaining immobile for 1 or 2 sec and even falling on its side. 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.

Larvae of the *Apodicrania* sp. (one per host) have been dissected out of worker ant larvae. In laboratory colonies, worker ants have been observed carrying *Apodicrania* pupae about and placing them in groups on the surfaces of the nests. When the nests were disturbed, the ant workers carried all of the fly pupae below the nest surface. Adult flies are known to be attracted to disturbed fire ant mounds and to be able to land and walk about without aggressive reaction by the ants.

### Studies with Diseases of Native Fire Ants

Because we have not yet been to establish a field research station in South America, our opportunities to study the diseases of IFA have been limited. Therefore, we have turned our attention to the pathogens of our native tropical fire ant, *S. geminata*, as models for basic biological studies and for the development of techniques. Our primary subject has been a microsporidium, *Burenella dimorpha*, which was recently described by Jouvenaz and Hazard (1978) as the type species of a new genus that represents a new family.

*B. dimorpha* produces two morphologically distinct types of spores: a binucleate, NMB spore that develops from disporous sporonts in the hypodermis, and a uninucleate, MB spore that develops in octets from plasmodia in the fat body. The NMB 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 MB spores are not infective; they are expelled unextruded in the meconium upon pupation.

The function of the MB spores remains unknown (Jouvenaz et al. 1981); 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 MB spores are primed for extrusion by passage through the gut. Even if MB spores do not function in intercolonial disease transmission, some sort of vector seems necessary. 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. Collins and Markin (1971) listed 52 species of insects that have been collected from fire ant nests (not all of these are inquilines); other invertebrates also occur there.

The pathological manifestations of *B. dimorpha* infection are distinctive and 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. These pellets are placed on the praesaepia ("breadbaskets") 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%.

*B. dimorpha* has been transmitted per os to *S. xyloni*, *S. invicta*, and *S. richteri*, as well as to its normal host, *S. geminata*. All four species are readily infected by feeding them boiled egg yolk wetted with a suspension of spores; however, the infection does not persist as well in colonies of *S. xyloni*, *S. invicta*, or *S. richteri* as in those of *S. geminata*. In other respects, the course of infection appears similar in all four species of ants. Ants of eight other genera tested thus far were not susceptible to infection by *B. dimorpha*.

Three undescribed species of microsporidia infect *S. geminata*. These develop in oenocytes, fat cells, or both, causing hypertrophy but not formation of cysts, as occurs in *T. solenopsae* infection. At least one of the three undescribed species of microsporidia of *S. geminata* is dimorphic, the spore types developing in different fat body cells. Ants infected by these microsporidia survive to the adult stage.

A neogregarine, *M. geminata* Jovenaz and Anthony, also infects *S. geminata* in the United States. This protozoan develops in the oenocytes of the hypodermis, causing destruction of the hypodermis, melanization, and eye malformation of pupae (Jovenaz and Anthony 1979). The disease appears to be invariably fatal in the pupal stage of development. Attempts to transmit the infection per os (with fresh, aged, and variously treated spores) and by placing infected pupae in healthy colonies (conspecific pupae are adopted) have failed thus far. Intracolony infection rates in field colonies are usually less than 2% but may exceed 90%. A similar or identical neogregarine occurs in *S. invicta* in Brazil.

Virus-like particles have been detected in *S. geminata* (Avery et al. 1977) but appear to be benign or very mildly pathogenic (unpublished data).

#### Predators of IFA in the United States

Wojcik (1975) observed that *S. invicta* pupae are occasionally consumed by the myrmecophilous beetles *Myrmecophodius excavaticollis* (Blanchard) and *Euparia castanea* Serville (Scarabaeidae) in the United States. Although these beetles have symbiotic relationships 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.

Buren (personal communication) suspects that small, subterranean ants of the genus and subgenus *Solenopsis* (*Diplorhoptrum*) may be important predators of fire ant queens during the claustral period (after construction of a subterranean chamber by a newly mated queen but before eclosion of her first offspring). Unfortunately, these ants appear to be readily destroyed by soil disturbances, and reductions in their populations may be a reason that fire ants invade environmentally disturbed areas so suc-

cessfully. Research is needed to determine whether these tiny ants play a role in IFA population dynamics, and whether their populations can be manipulated.

During the mating and nest-founding period, IFA queens are subject to predation by numerous general predators of insects, such as birds, dragonflies, and spiders (Whitcomb et al. 1973). However, IFA perpetuate themselves by inundating the environment with many more queens than can possibly survive. Morrill (1974) estimated mean annual production of alate *S. invicta* females in four habitats in north Florida at ca. 240,000/ha (97,000/acre). The carrying capacity of prime north Florida habitat is ca. 45 colonies/ha (personal communication, October 1980, R. Brown, Division of Plant Industry, Florida Department of Agriculture Consumer Services, Gainesville). Assuming a life expectancy of 4 years for a mature colony and a stable population at carrying capacity, only 11 to 12 (0.005%) of the 240,000 alates can establish colonies that survive to maturity. (The life expectancy of field colonies which have survived the vulnerable early period is unknown, but our experience with laboratory colonies maintained in soil indicates that 4 years is reasonable.) We seriously doubt that opportunistic general predators affect IFA populations, or that biological control can be achieved by manipulating the populations of these predators. The tremendous reproductive potential of fire ants will doubtless prove to be a serious obstacle to biological control.

#### Studies with Nonspecific Biotic Agents

In addition to natural enemies of IFA, a number of nonspecific or "unnatural" enemies have been evaluated as biocontrol agents. These include a nematode, *Neoaplectana carpocapsae* Weiser (= *N. dutkyi* Welch or "DD-136"); bacteria, including *Bacillus thuringiensis* Berliner, *B. sphaericus* Meyer and Neide, *B. larvae* White, *B. pulvificiens* Katznelson, *Serratia marcescens*, *Pseudomonas aeruginosa*, (Schroeter) Migula, and *P. chloroaphis* (Guignard and Savageau) Bergy et al.; fungi, including *Beauveria bassiana* (Balsamo) Vuillemin and *Metarhizium anisopliae* (Metschnikoff) Sorokin; a microsporidium, *Vairimorpha necatrix* (Kramer); various viruses including baculoviruses and iridescent viruses; and a mite, *Pyemotes tritici*. The most effective of these is *N. carpocapsae*, one application (10<sup>6</sup> 2nd-stage daurlarvae) of which can inactivate ca. 80% of treated mounds in 90 days (personal communication, B. R. Norment and P. P. Sikorowski, Dept. of Entomology, Mississippi State University, Mississippi State). This nematode can be reared cheaply in artificial media and stored for months (Lindegrin et al. 1979); however, its use is limited to single mound treatments, and for this purpose degradable chemical toxicants are more efficacious.

The straw itch mite, *P. tritici*, can also inactivate fire ant mounds. Bruce and LeCato (1980) reared mites in synchronous culture on insect pupae (cigarette beetle, *Lasioderma serricorne*) and applied ca.

100 ml of pupae to single mounds as the first progeny emerged from the gravid female mites. Three to 10 applications at ca. 2-week intervals gave 70% control. Practical use of *P. tritici* for IFA control must await the development of more efficient methods of mass production and increased effectiveness. Also, *P. tritici* is frequently regarded as a pest (Weiser and Slama 1966). Thus, proof must be obtained that this mite can be used without risk to those handling it or to persons exposed to it after its dispersal.

At this time it appears that infestations of either *N. carpocapsae* or *P. tritici* do not spread to nearby mounds; thus, their use would require treatment of each individual IFA mound. For individual mound treatments, we believe that biodegradable chemical toxicants would be more efficacious.

The remaining organisms mentioned had little or no effect on fire ants.

### Discussion

The role of natural enemies in population dynamics of fire ants in South America is unknown. Indeed, little is known even about fire ant population densities in various habitats. The intercolonial incidence of disease in fire ants is assumed to be density dependent and may be limited, at least in part, by the dry season. Presumably, this season is a period of stress. It seems reasonable, therefore, to expect higher mortality among diseased colonies than among healthy colonies at this time. If this expectation is true, the overall incidence of disease would be lowest at the end of the dry season. During the wet season, the environment is much more favorable to the ants. The numbers of colonies and, after a lag period, the incidence of disease may increase at this time. Recurrence of the dry season would prevent disease from reaching epizootic proportions.

In the United States, extended dry seasons comparable to those of Mato Grosso do not occur, although our more severe winters may exert a similar control of epizootics. Other (unknown) abiotic or biotic factors that limit the incidence of disease in South America also may not operate in this country.

The protozoan pathogens of *S. geminata* do not appear to offer promise as biological control agents for the IFA. *S. invicta* and *S. richteri* have been residents of the United States for ca. 40 and 60 years, respectively, yet evidently have not permanently acquired any of the diseases of *S. geminata*. Experimental laboratory and field transmissions, where successful, have not produced infections that persist and spread in the *S. invicta* population. Adaptation of a parasite of *S. geminata* to *S. invicta* through strain selection may, of course, be possible. Our primary purposes in studying the diseases of *S. geminata* are to gain basic knowledge of the taxonomy and biology of fire ant pathogens and to develop techniques for the propagation, study, and possible eventual introduction of exotic pathogens, especially those of *S. invicta* and the *S. invicta* complex.

In summary, IFA in the United States present a classic imported pest problem in which the pest has

been freed of natural enemies. The importation and establishment of a complex of natural enemies needs to be explored as a means of ameliorating the problem.

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