

ANT BEHAVIOR AND MICROBIAL PATHOGENS
(HYMENOPTERA: FORMICIDAE)

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ABSTRACT

The effectiveness of microbial controls for pest ants can be reduced by ant behaviors. Introductions of pathogens, including nematodes, into ant nests result in behavioral responses by ants that affect infection rates to ants exposed to inocula, affect the dissemination of inocula among nestmates, and affect the dispersal of inocula outside the nest. These behaviors include grooming, secretion of antibiotics, nest hygiene, avoidance, and dispersal. Ant behaviors must be considered in developing microbial control agents. Approaches to overcoming the behavioral responses of the red imported fire ant to the entomopathogen *Beauveria bassiana* (Balsamo) Vuillemin are discussed.

RESUMEN

La eficiencia del control microbiano contra hormigas plaga puede ser reducida debido al comportamiento de las hormigas. La introducción de patógenos, incluyendo neámatodos, en el nido de las hormigas lleva a cambios comportamentales que afectan la porcentaje de infección de las hormigas expuestas al inóculo, la dispersión del inóculo entre las hormigas de un mismo nido, y la dispersión del inóculo fuera del nido. Estos comportamientos incluyen limpieza del cuerpo de las hormigas, secreción de antibióticos, higiene del nido, el evitar al patógeno, y dispersión de las hormigas. El comportamiento de las hormigas debe ser considerado durante el desarrollo de agentes microbianos para control biológico. Propuestas para superar las respuestas comportamentales de la "hormiga brava" al entomopatógeno *Beauveria bassiana* (Balsamo) Vuillemin.

Ants, as social insects, have many unique behavioral adaptations that facilitate their survival. Many of these adaptations have frustrated man's attempts to control ants by various means. Understanding these adaptations is especially important when the use of biological control agents is desired. The successful control of pest ants through the use of parasitoids, predators, or pathogens has not been documented, although natural enemies do exist (Wojcik 1989, Jouvenaz 1983). Perhaps the lack of success or even attempts at biological control may be partly attributable to the behavior of ants. Their ability to fend off parasitoids to protect scale insects (DeBach 1974), or their ability to defend themselves against phorid flies (Wojcik 1989), are indicative of the inherent difficulty in finding effective biological control agents for ants. Behavioral responses to the presence of natural enemies may be especially important when pathogens are used as microbial insecticides, in contrast to the use of classical biological control methods. Behavioral responses and interactions of ants with their arthropod parasites were reviewed by Wojcik (1989). With respect to microbial pathogens, Wheeler (1910) questioned whether ants could be controlled with pathogens given the environment that they inhabit. He reasoned that ants had evolved mechanisms that prevented their nests and themselves from being overrun by fungi and other microorganisms. However, Evans (1982) disputed reports (Allen & Buren 1974) that fungal epizootics of ants are uncommon, and has reported extensively on *Cordyceps* and other fungi parasitizing ants in the tropics. Thus, the allure of finding a microbial biological control for pest ants is still present as evidenced by recent research in this area by Drees et al. (1992), Jouvenaz & Martin (1992), Pereira & Stimac (1992), Pereira et al. (1993a, 1993b), Sánchez-Peña & Thorvilson (1992), Siebeneicher et al. (1992), and Stimac et al. (1993) who examine the potential of controlling the red imported fire ant, *Solenopsis invicta* Buren, which immigrated into the southeastern U.S. over fifty years ago. Yet, these recent works again confirm the difficulty of obtaining control with this strategy.

In this paper, we review examples of reported ant behaviors that occur in the presence of pathogens, including nematodes (Table 1). While these behaviors may not have evolved specifically in response to microbial antagonists, they have negative and positive effects on the efficiency of infection and spread of disease. We have categorized these behaviors as affecting: 1) infection of ants exposed to inoculum; 2) intracolony dissemination of inoculum among nestmates; and, 3) dispersal of inoculum outside the nest (Table 2). The implications of these behaviors on the development of microbial control agents for imported fire ants will then be discussed, using our research on *Beauveria bassiana* as an example.

TABLE 1. REPORTED ANT BEHAVIORS ASSOCIATED WITH PATHOGENS.

Behavior	Ant	Pathogen ¹	Reference
Grooming	<i>Acromyrmex octospinosus</i> Reich	Nematodes	Kernarrec 1975
	<i>Cephalotes atratus</i> L.	<i>Cordyceps</i> sp. (f)	Evans & Samson 1982
	<i>Solenopsis invicta</i> Buren	<i>Beauveria bassiana</i> (Bals.) Vuill. (f)	Siebeneicher et al. 1992; unpublished lab. data ²
	<i>S. invicta</i>	<i>Conidiobolus</i> sp. (f)	Sánchez-Peña & Thorvilson 1992
	<i>S. invicta</i>	<i>Heterorhabditis</i> spp. (n) <i>Steinernema</i> spp. (n)	Drees et al. 1992
Secretions	<i>Atta sexdens</i> L. <i>Myrmica</i> sp.	<i>Escherichia coli</i> (Migula) Castellani & Chalmers (b) <i>Staphylococcus aureus</i> Rosenbach (b) <i>Penicillium glaucum</i> Link (f) <i>B. bassiana</i>	Maschwitz et al. 1970
	<i>Myrmecia nigricapa</i> Roger	<i>Pacilomyces tilacinus</i> (Thom.) (f)	Beattie et al. 1985
	<i>S. invicta</i>	----	Beattie et al. 1986
	<i>S. invicta</i>	<i>B. bassiana</i>	Obin & Vander Meer 1985
			Storey 1990

TABLE 1. (Continued)

Behavior	Ant	Pathogen ¹	Reference
Hygiene of Nest	<i>A. octospinosus</i>	Nematodes	Kernarrec 1975
	<i>C. atratus</i>	<i>Cordyceps</i> sp.	Evans 1982
	<i>S. invicta</i>	<i>B. bassiana</i>	Evans & Samson 1982 Storey 1990
	<i>Solenopsis geminata</i> F. <i>Formica rufa</i> L.	<i>Barenella dimorpha</i> Jouvenaz & Hazard (p) <i>Alternaria tenuis</i> Nees (?) ² (f)	Siebeneicher et al. 1992 Pereira & Stimac 1992 Jouvenaz 1983 Marikovsky 1962
Avoidance of Pathogen	<i>A. octospinosus</i>	Nematodes	Kernarrec 1975 ¹
	<i>S. invicta</i>	<i>B. bassiana</i>	Zoebisch & Stimac 1990
	<i>S. invicta</i>	<i>Heterorhabditis</i> spp. <i>Steinernema</i> spp.	Drees et al. 1992
	<i>F. rufa</i>	<i>A. tenuis</i> (?)	Marikovsky 1962
Ant Dispersal	<i>Camponotus castaneus</i> (Latreille)	<i>Rabbium paradoxus</i> Poinar, Chabaud & Bain (n)	Poinar et al. 1989
	<i>C. atratus</i>	<i>Cordyceps</i> sp.	Evans 1982
	<i>Dolichoderis</i> sp.		

TABLE 1. (Continued)

Behavior	Ant	Pathogen ¹	Reference
	<i>Pachycondyla</i> sp.	<i>Erynia</i> (= <i>Entomophthora</i>) <i>myrmecophaga</i>	Balazy & Sokolowski 1977
	<i>Polyrhachis</i> sp.	Turian & Wuest (f)	Loos-Frank & Zimmermann 1976
	<i>Formica</i> spp.	<i>Pandora</i> (= <i>Erynia</i> = <i>Entomophthora</i>) <i>formicae</i> Humber (f)	
	<i>Formica pratensis</i> Emery	<i>Decrocoelium dendriticum</i> (Rudolphi, 1819)	
		Looss, 1899 (t) ⁴	
	<i>F. rufa</i>	<i>A. tenuis</i> (?)	Marikovsky 1962
	Myrmicine ants	Several fungi	Evans 1974
	<i>Pallothyreus tarsatus</i> F.	<i>Cordyceps</i> sp.	Bequaert 1922
			Evans 1982
	<i>Polyrhachis illaudata</i>	<i>Cordyceps</i> sp.	Evans & Samson 1984
	<i>Seriiformica</i> (= <i>Formica</i>)	<i>E. myrmecophaga</i>	Turian & Wuest 1969
	<i>fusca</i> L.		
	<i>S. invicta</i>	<i>B. bassiana</i>	Pereira & Stimac 1992 unpublished field data ²
Colony Movement			
	<i>S. invicta</i>	<i>B. bassiana</i>	unpublished field data ²
	<i>S. invicta</i>	<i>Heterorhabditis</i> spp.	Drees et al. 1992
		<i>Steinernema</i> spp.	
	<i>Tetramorium caespitum</i> L.	Fungus (?)	Marikovsky 1962

¹ Types of pathogen: f = fungus; b = bacterium; p = protozoan; n = nematode; t = trematode

² Unpublished observations or data by authors.

³ Pathogen species is uncertain.

⁴ Ant serves as a second intermediate host for this trematode, which cycles from sheep to snails to ants.

TABLE 2. SOME EXAMPLES OF ANT BEHAVIORS AND THEIR EFFECT IN INCREASING (+) OR DECREASING (-) INFECTION RATE, DISSEMINATION OF THE PATHOGENS WITHIN THE ANT NESTS OR DISPERSAL OF PATHOGEN OUTSIDE OF THE NESTS.

Behavior	Infection	Intra-Colony Dissemination	Out of Nest Dispersal
Grooming	-	+ ¹	ne ²
Use of Secretions	-	-	ne
Avoidance of Pathogens	-	-	ne
Nest Hygiene/ Necrophoresis	ne	-/+	-/+
Summit Disease Syndrome	ne	-	+
Altered Activity Time or Place	ne	-	-/+
Colony Movement	ne	-	+

¹This effect reported for termites (Kramm et al. 1982), but not for ants.

²ne = no effect

GROOMING

Self-grooming and mutual grooming by any nestmates can either impede or facilitate the infection and spread of disease. Wilson (1971) described the grooming process as involving the use of tibial combs, the rubbing of legs, and licking to keep body surfaces clean. Inocula are not ingested because they are collected in an infrabuccal pocket, a cavity on the ventral surface of the buccal chamber (Eisner & Happ 1962), and expelled as a pellet with other debris (Siebeneicher et al. 1992). In the fungivorous leaf cutting ant *Acromyrmex octospinosus*, labial gland extracts containing chitinases were hypothesized to have a fungistatic function against microflora in the infrabuccal pocket (Febvay et al. 1984).

When grooming removes inoculum from the cuticle before infection occurs, it obviously reduces infection rates. Observations at 2 h intervals with scanning electron microscopy of *S. invicta* inoculated with *B. bassiana* conidia has demonstrated the removal of conidia from the integument of adults and larvae (unpublished data) (Fig. 1). Siebeneicher et al. (1992) reported similar observations, and Sánchez-Peña & Thorvilson (1992) inferred that grooming prevented infection from *Conidiobolus* conidia. Likewise another myrmicine ant, *Cephalotes atratus* removed spores of a *Cordyceps* sp. by grooming (Evans & Samson 1982). Drees et al. (1992) reported the incessant preening by red imported fire ant workers of brood, alates, and themselves after exposure to *Steinernema* and *Heterorhabditis* nematodes, in an apparent attempt to remove them.

While grooming may reduce infection by the removal of inocula, grooming might assist in the dissemination of inocula among nestmates. The transfer of inocula to workers may occur by incidental contact during the grooming of contaminated nestmates. While this has not been reported for ants, dissemination of inocula during grooming has been seen in termites (Kramm et al. 1982).

USE OF SECRETIONS

The use of antimicrobial secretions is another behavior that reduces the chance of infection once inoculum is present on the ant. Venom from *S. invicta* includes antibiotic alkaloids (Blum et al. 1958, Jouvenaz et al. 1972, Storey 1990) that are sprayed during gaster flagging behavior (Obin & Vander Meer 1985). This behavior included the raising

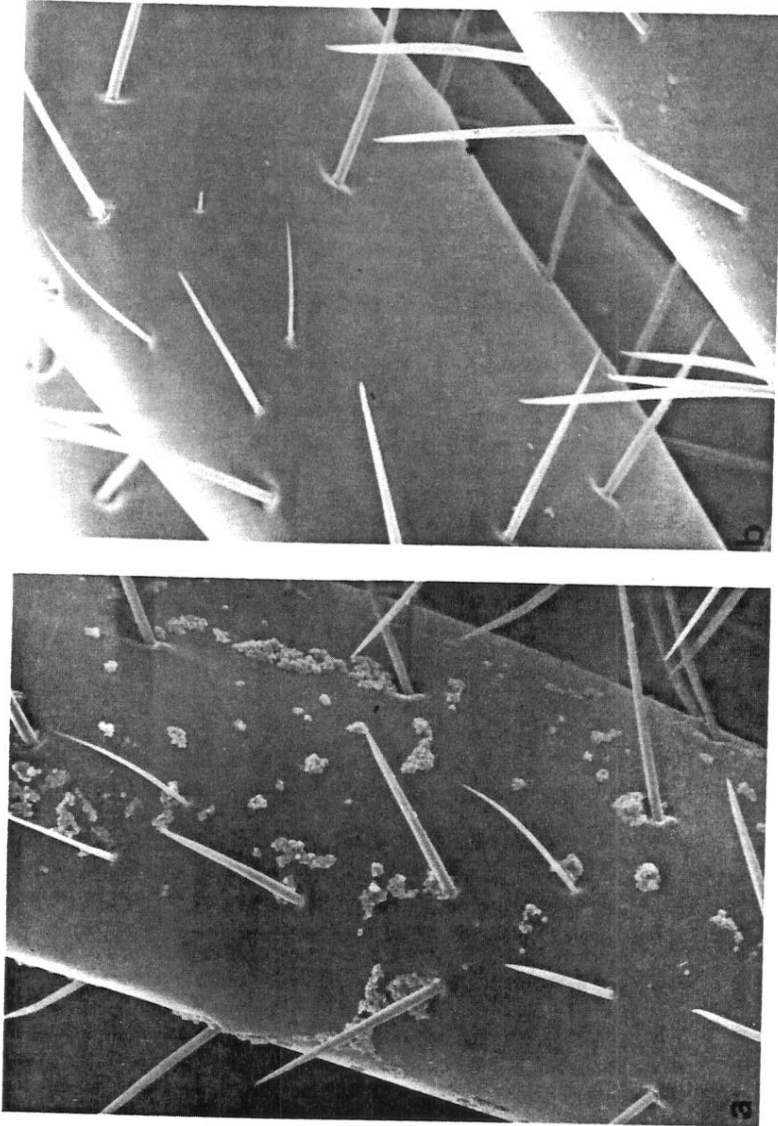


Fig. 1. Scanning electron micrograph of red imported fire ant legs one hour (a, 300X), and six hours (b, 290X) after application of *B. bassiana* conidia.

and wagging of the gaster to provide a directed spray onto brood, and also directed against other ants during heterospecific confrontations. Storey (1990) demonstrated the fungistatic activity of venom alkaloids and recorded increased levels of these products in nest soil containing *B. bassiana* conidia. This suggested that venom release could be induced by the presence of this entomopathogen.

Besides the venom alkaloids, secretions from the metapleural glands of *Myrmica laevinodis* Nyl., *Myrmica rubida* (Latreille), *Atta sexdens*, *Acromyrmex* sp., *Messor barbarus* L., and *Myrmecia nigriscapa* were shown to have antibiotic effects against bacteria and fungi (Maschwitz et al. 1970, Schildknecht & Koob 1971, Beattie et al. 1985, 1986). In the case of the *Myrmica* species, these secretions, which contain phenyl acetic acid and/or myrmicacin (1- β -hydroxydecanoic acid) (Schildknecht & Koob 1971), are spread over the cuticle by self grooming and nestmate grooming. Secretions also were spread over larvae (Maschwitz et al. 1970) presumably to protect these individuals from diseases. However, Beattie et al. (1986) observed the flowing of secretions along the grooves of an ant's integument, perhaps indicating that grooming was not always necessary to distribute the secretions.

NEST HYGIENE

Nest conditions, such as high humidity and relatively stable temperatures, favor growth of microbial pathogens. Thus, behaviors that limit the occurrence of epizootics within a colony are vital for survival. The elimination of potential sources of inocula is an obvious benefit of nest hygiene. This occurs regardless of the presence of pathogens and is evidenced by kitchen middens in the vicinity of nests. Necrophoresis, or cadaver removal, has been seen in *S. invicta* infected with *B. bassiana* (Storey 1990, Siebeneicher et al. 1992, Pereira & Stimac 1992), and in *C. atratus*, infected with *Cordyceps* sp. (Evans & Samson 1982, Evans 1982). We have observed piles of sporulating *B. bassiana* - infected cadavers of *S. invicta* outside of nests. These sporulating piles promoted dispersal of the pathogen. However, this external nest dispersal apparently does not occur in the case of *Formica rufa* adults infected with an unknown pathogen, where their removal and supposed consumption by healthy nestmates was reported (Marikovskiy 1962). Consumption of infected individuals, however does not always preclude the dispersal of pathogens. In *Solenopsis geminata*, spores of the protozoan *Burenella dimorpha* are transferred to fourth instar larvae when they are fed infected pupae cannibalized by workers (Jouvenaz 1983).

Another aspect of nest hygiene would include the isolation of infected cadavers within the nest. *S. invicta* workers pack soil around dead individuals infected with *B. bassiana* (Storey 1990), and this behavior contributed to the lack of transmission of fungal disease within artificial fire ant nests in the presence of soil (Pereira & Stimac 1992). From these results, one may infer that the isolation of infected cadavers with nest soil may provide an effective barrier to the spread of *B. bassiana*.

AVOIDANCE OF PATHOGENS

In addition to the removal or isolation of inoculum sources, the simple avoidance of inocula is another behavior that limits the spread of infections. Marikovskiy (1962) reported the avoidance by *F. rufa* of infected nestmates covered with conidia. These cadavers were contagious, and were not removed or consumed, in contrast to nonsporulating, infected individuals. Similarly, during bait testing, Zoebisch & Stimac (1990) reported that *S. invicta* avoids baits containing *B. bassiana* conidia.

COLONY MOVEMENT

Field applications of nematodes to *S. invicta* nests resulted in the movement of at least a third of the treated colonies to new nest sites (Drees et al. 1992). We observed a similar tendency of nest relocation for fire ant colonies injected with conidia of *B. bassiana* (unpublished data). These colony movements probably reflect an avoidance by the ants from further contact with the nematodes or *Beauveria* conidia.

DISPERSAL

The most frequently recorded behavioral response to microbial pathogens is the dispersal of ants infected with fungal pathogens (Table 1). Whether the prevalence of this behavior in the literature is a reflection of its actual frequency of occurrence in ant populations, or whether it is just a function of its conspicuousness, is not clear. In general, infected ants were reported to disperse to the tops of grass blades or other vegetation, and then die clinging to the vegetation with their legs and mandibles. Some fungi, fasten the ants firmly to the substrate by fungal outgrowths, or rhizoids (Evans 1974, Balazy & Sokolowski 1977, Humber 1981). Subsequently fruiting bodies will emerge from the cadaver, whose elevated location would facilitate dispersal of inoculum. Loos-Frank & Zimmerman (1976) attributed the propensity to climb in ants infected with *Pandora* (*Erynia* = *Entomophthora*) *formicae*, to the growth of hyphae within the nervous system.

In addition to dispersal to elevated locations, ants with fungal infections have been observed to leave their nest while displaying erratic, spasmodic movements (Marikovsky 1962, Evans 1982). In arboreal ant species, dispersal was toward the ground, where individuals were found under leaf litter (Evans 1982). Uncharacteristic behavior also has been reported in *Camponotus castaneus* infected with the nematode *Rabbiium paradoxus*; infected individuals of this nocturnal ant became diurnal (Poinar et al. 1989). In laboratory experiments with small *S. invicta* colonies, 3 to 5 days after application of *B. bassiana*, infected ants were observed wandering outside of the nest cells. Likewise, in field injections of *B. bassiana* into fire ant nests, we observed erratic movements of masses of ants around the nests also within 3 to 5 days of exposure (unpublished data). Contrary to their typical behavior of walking on the surface of the ground, these undisturbed fire ants moved to the tops of the blades of grass and apparently were not foraging or alarmed. Such behavior may be related to the fever responses or "summit disease syndrome", reported for fungus-infected grasshoppers and caterpillars which climb up vegetation to sun themselves to increase body temperatures and eliminate the fungal infection (Marikovsky 1962). However, despite the many examples of upward dispersal of infected ants, the elimination of infection has not been reported.

Regarding the dispersal of infected ants away from the nest, some have speculated on the altruistic nature of this behavior, since potential sources of inocula are removed from the nest (Evans 1982, 1989). If infected ants die within their nests, either they would be removed from the nest, or sequestered within the nest before the pathogen reached the infective stage. Thus, dispersal behavior does not seem to be a major factor in mitigating colony exposure to the pathogen, unless infection rates are so rapid and extensive that the hygienic response of the ants is overwhelmed. However, ant dispersal may aid in inoculum dissemination outside a nest, and thus is a benefit to the pathogen, especially if the pathogen is not an obligate parasite of a single host.

Table 2 summarizes the positive or negative effects of the ant behaviors discussed above on infection rate and dissemination of pathogens. Published reports on the effectiveness of different ant behaviors inhibiting the development of diseases tend to be anecdotal. Studies quantifying the effects of ant behavior on rates of infection under

field conditions would be difficult to conduct. Nevertheless, the value of these behaviors in disease prevention is attested to by the fact that (1) a majority of the behavioral responses of ants to pathogens are described as limiting infection or pathogen dissemination, and (2) relatively few examples of disease epizootics are reported for ant populations.

IMPLICATIONS OF ANT BEHAVIORAL RESPONSES TO MICROBIAL PATHOGENS ON THE DEVELOPMENT OF MICROBIAL CONTROL AGENTS FOR ANTS

The responses of ants to microbial pathogens must be considered in developing microbial control agents for ants. Research with *B. bassiana* for imported fire ant control can be used as an example of some of the implications of the behavioral responses of ants toward the development of a microbial control.

Stimac et al. (1989) demonstrated the pathogenicity of an isolate of *B. bassiana* recovered from fire ants in Brazil to *Solenopsis* spp. This isolate was brought to Florida for further study as a potential biological control agent for imported fire ants in the U.S. Initially, the idea was to use the fungus as an inoculative introduction that would initiate naturally occurring epizootics in ant nests. However, after considering the results of initial studies, and the effects of ant behaviors on the performance of the fungus (Pereira & Stimac 1992, Pereira et al. 1993a, 1993b), it became clear that two major problems related to ant behavior needed to be addressed: 1) overcoming the behaviors, such as grooming, that prevent infection when individual ants are exposed to inoculum; and, 2) bypassing the negative effects of behaviors, such as necrophoresis and dispersal of infected ants, that prevent transmission among nestmates.

A potential approach toward overcoming the first problem is to improve contact between the ant cuticle and conidia by finding a formulation that is resistant to grooming. As an added measure, a large developing dose of conidia needs to be delivered to the ants to allow some of the conidia to escape removal by grooming, and inactivation by antibiotic secretions. To overcome the lack of nestmate transmission, a mass inoculation was sought by injecting conidia directly into the nest. Provided that the injection application obtained good dispersion throughout the nest, the need for transmission among nestmates could be eliminated. Given good dispersal throughout a nest, and a formulation that cannot easily be groomed off by the ants, it should be possible to obtain a mass infection that would overwhelm the hygienic response of ants, disrupt social order, and eliminate the colony.

In conclusion, ant behaviors affect both directly and indirectly the performance of pathogens within the nests. These behaviors may or may not have evolved in response to challenges by pathogens or due to interactions of the pathogens with the neurological system of the ants. Although some behaviors favor the dispersal of inocula, most of the reported behaviors are detrimental to the pathogens and may frustrate us in our attempts to develop microbial controls for pest ants. The ants' amazing and fascinating abilities to adapt and survive have to be understood better if we are ever going to control pest ants with microbial pathogens.

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